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## Acclimation of photosynthesis in canopies: models and limitations

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**Abstract** Within a time-scale of several days photosynthesis can acclimate to light by variation in the capacity for photosynthesis with depth in a canopy or by variation in the stoichiometry of photosynthetic components at each position within the canopy. The changes in leaf photosynthetic capacity are usually related to and expressed as changes in leaf nitrogen content. However, photosynthetic capacity and leaf nitrogen never match exactly the photon flux density (PFD) gradient within a canopy. As a result, photosynthetic light use efficiency, i.e. photosynthetic performance per incident PFD, increases considerably from the top of the canopy to the lower shaded part. Many of existing optimisation models fail to express the actual pattern of nitrogen or photosynthetic capacity distribution within a canopy. This failure occurs because these optimisation models do not consider that the quantitative aspect of photosynthesis acclimation is a whole plant phenomenon. Although turnover models, which describe the distribution of the photosynthetic apparatus within a canopy as a dynamic equilibrium between breakdown and regeneration of apparatus with respect to nitrogen availability, photosynthetic rate and export of carbohydrates, produce realistic results, these models require confirmation. The mechanism responsible for changes in the relative share of light-harvesting apparatus as acclimation to irradiance remains unknown. Ability of the photosynthetic apparatus to balance properly the light harvesting capacity with electron transport and biochemical capacities is limited. As a result of this fundamental limitation, photosynthetic light use efficiency always increases with increasing thickness of the photosynthetic apparatus.

**Keywords** Leaf nitrogen · Optimality · Turnover theory · Light response curve · Chlorophyll

### Introduction

Several environmental factors vary with depth in a leaf canopy, but the most important with respect to photosynthesis is light, in both quantity and quality. Although evidence suggests that the photosynthetic apparatus acclimates to temperature gradient in the canopy (e.g. Niinemets et al. 1999b), this and other possible aspects of acclimation are not considered in this study. Physiologists have written several comprehensive and pioneering reviews on leaf photosynthesis and its acclimation to light conditions (Anderson and Osmond 1987; Marder and Barber 1989; Anderson et al. 1995; Pearcy 1998). Ecologists are more concerned with photosynthetic properties of entire plants, canopies, communities or regions – especially when understanding the global carbon cycle is a primary goal. Far more details on the physiology of photosynthesis are available than required to calculate total canopy photosynthesis with suitable accuracy to validate alternative assessments. Successful scaling from leaf to canopy depends on whether the important processes are recognised and understood (Norman 1993). Consequently, the scientific aim of this study is to determine the minimum amount of physiological knowledge and the relevant processes needed for proper scaling from leaf to canopy. It should be emphasised that there is a continuum of time-scales involved in adjustment of photosynthesis to environmental conditions. Mechanisms of photoprotection against excess energy through the xanthophyll cycle or photosynthetic induction work within time scales of seconds or minutes. These fine-tuning mechanisms are not usually considered as acclimation (Pearcy 1994, 1998; Anderson et al. 1995; but see Geiger and Servaites 1994), evidently because of the relatively short time scale involved compared to changes in leaf nitrogen or chlorophyll content. In general, the relevance of these fine-tuning processes in predicting the photosynthetic

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production of the whole canopy is still unclear and they are not considered in this study. However, with improvements in technology for large-scale estimates of photosynthetic production, consideration of short-term fluctuations in environment and plant responses to these fluctuations will evidently become gradually more important.

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### A “big leaf” – an oversimplification?

Estimates of photosynthetic production of a canopy are usually calculated through integration of the single-leaf photosynthetic rate with respect to canopy position and time (Jarvis 1995; Leuning et al. 1995). This was first done by Monsi and Saeki (1953), although their model did not consider diversity of photosynthetic apparatus due to acclimation inside the canopy. Investigators have more recently improved this approach to include profiles of leaf photosynthetic properties. Calculation of total canopy photosynthesis involves two major steps: prediction of the photon flux density (PFD) profile and its application to the distribution of photosynthetic capacity within the canopy. Accurate calculation of the PFD profile is important, because large spatial and temporal variability of radiation leads to uncoupling of profiles of average and instantaneous irradiance. Light flecks and sun angle changes throughout the day in natural canopies cause the proportion of canopy light absorbed by individual leaves to change on a time scale too rapid for the acclimation of leaf photosynthetic capacities (De Pury and Farquhar 1999). However, the methods of describing radiation profiles within a canopy are not a topic of this study.

When the problem of radiation field description is solved, knowledge of the actual distribution of leaf photosynthetic properties allows calculation of total canopy photosynthesis. Many studies have documented that photosynthetic capacity of leaves declines parallel to time-averaged PFD within a canopy. This decline is most easily measured by leaf nitrogen content, because most leaf nitrogen is associated with the photosynthetic apparatus (Evans 1989, 1993a; Hikosaka and Terashima 1996). Since the study by Field (1983), this decline has been explained through optimality (i.e. that a given amount of resources maximises leaf or canopy total production). Farquhar (1989) showed that if costs of construction and maintenance of the photosynthetic apparatus are ignored, the optimal distribution of photosynthetic capacity and nitrogen is proportional to light. The proportionality between nitrogen (or photosynthetic capacity) and light profile within a canopy has been explored in several scaling models (Woodward et al. 1995; Friend et al. 1997). Kull and Jarvis (1995) show that for two frequently explored assumptions: (1) leaf nitrogen is distributed exactly proportionally to light distribution, and (2) only the light saturated rate of photosynthesis depends on leaf nitrogen content (i.e., the shape or curvature of the light response does not change within the canopy);

the entire canopy behaves like a single unshaded leaf in the upper canopy. Although total production of such a canopy is proportional to intercepted light – as described in many studies (e.g. Monteith 1977; Jarvis and Leverenz 1983), – this behaviour violates two known facts. First, such a simplified canopy has a light response curve exactly akin to that of an upper leaf, although many studies conclude that canopy photosynthesis is unsaturated at realistic light intensities. Second, total photosynthesis and nitrogen in such a canopy is less than that of the upper leaf and could achieve equality only if leaf area index (LAI) increased to infinity. Total photosynthesis in real canopies is usually more than twice that of a single leaf and total canopy nitrogen exceeds single leaf nitrogen content even more. Consequently, a canopy cannot be treated in such a simplified manner. Acclimation of the leaf photosynthetic apparatus in real canopies is more complex and includes two principal types of processes: those related to the amount of photosynthetic apparatus in leaves, and those related to changes of apparatus quality (changes in composition of the apparatus, often referred to as chloroplast level acclimation).

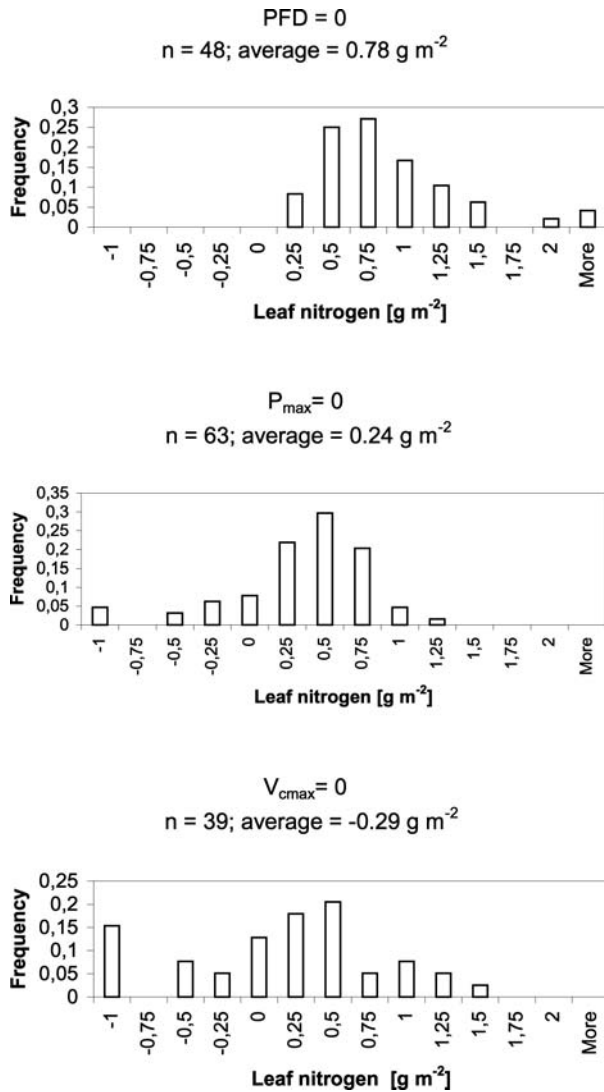
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### Two aspects of acclimation: quantity and quality

Acclimation through changes in quantity of leaf photosynthetic apparatus

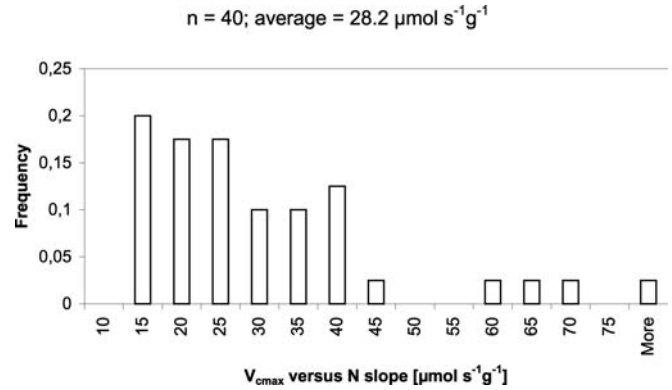
Although the content of leaf area-based nitrogen almost always declines within a canopy, careful examination of available data shows that the nitrogen gradient in a canopy is never proportional to the light gradient. Several authors have noted that leaf nitrogen is often saturated with respect to PFD, though it seems to depend heavily on species (Hollinger 1996; Kull and Niinemets 1998; Bond et al. 1999; Hikosaka et al. 1999). The common relationship is fairly linear in the upper canopy and curves with lower PFD values. In some studies, nitrogen distribution has been approximated exponentially, revealing that the extinction coefficient for PFD is always higher than the extinction coefficient for nitrogen (Hirose and Werger 1987b; Anten et al. 1998b).

The other important feature of the leaf nitrogen versus PFD relationship is a relatively large intercept on the nitrogen axis when the relationship is extrapolated to zero PFD (Fig. 1A). This can be explained by the existence of a relatively constant non-photosynthetic nitrogen pool (Charles-Edwards et al. 1987; Anten et al. 1995b; Kull et al. 1998). However, comparison of this intercept on the nitrogen axis with that of nitrogen versus the photosynthetic parameter  $P_{\max}$  (photosynthesis at saturating PPFD and ambient  $\text{CO}_2$  concentration) or  $V_{\text{cmax}}$  (maximal carboxylation efficiency measured from the photosynthesis  $\text{CO}_2$  response curve) plot (Fig. 1B, C) reveals that a considerable amount of photosynthetic capacity exists even at the most shaded canopy positions. The limited survey of literature reported in this review shows that nitrogen



**Fig. 1** Distribution of intercept values on leaf nitrogen content axis at zero values of PFD (A),  $P_{\max}$  (B) and  $V_{c\max}$  (C). Data from published linear equations or assessed from published graphs if equations were not given. Based on studies: (Field 1983; Chazdon and Field 1987; Hirose and Werger 1987a; Hirose et al. 1988, 1989; Van Keulen et al. 1989; Pons et al. 1990; Lemaire et al. 1991; Leuning et al. 1991a; Harley et al. 1992; Schieving et al. 1992a, b; Ellsworth and Reich 1993; Evans 1993a; Pons et al. 1993; Hikosaka et al. 1994; Reich et al. 1994, 1995; Hirose and Werger 1994; Anten et al. 1995a, b, 1996; Anten and Werger 1996; Brooks et al. 1996; Hikosaka and Terashima 1996; Hollinger 1996; Dang et al. 1997; Kellomäki and Wang 1997; Anten et al. 1998a, b; Hikosaka et al. 1998; Kuers and Steinbeck 1998; Stenberg et al. 1998; Osborne et al. 1998; Wohlfahrt et al. 1998; Schoettle and Smith 1999; Bond et al. 1999; Hikosaka et al. 1999; Le Roux et al. 1999a, b; Medlyn et al. 1999; Rosati et al. 1999; Wohlfahrt et al. 1999; Carswell et al. 2000; Jach and Ceulemans 2000)

versus  $V_{c\max}$  relationships average a small negative intercept on the nitrogen axis, indicating that the concept of constant structural nitrogen may be inappropriate, possibly because the amount of non-photosynthetic nitrogen in a leaf correlates with the amount of photosynthetic nitrogen. Most of the data in Fig. 1 come from studies



**Fig. 2** Distribution of slope values of published leaf nitrogen versus  $V_{c\max}$  relationships. Based on studies: (Field 1983; Leuning et al. 1991a; Harley et al. 1992; Nijs et al. 1995; Anten et al. 1996; Kellomäki and Wang 1997; Osborne et al. 1998; Porté and Loustau 1998; Wohlfahrt et al. 1998, 1999; Le Roux et al. 1999b; Medlyn et al. 1999; Carswell et al. 2000; Jach and Ceulemans 2000)

where the main source of nitrogen variation are differences in growth PFD. If we suppose that with decreasing growth PFD, relatively more nitrogen is associated with light-harvesting functions and less with electron transport and biochemical apparatus of photosynthesis, we would expect a higher positive intercept on the nitrogen axis (Evans 1989). However, the frequency distribution of these intercepts shows that the median remains positive (Fig. 1C) with only a few negative outliers. These outliers may result from studies with methodical problems or with very limited ranges of nitrogen variability, thus providing poor accuracy in predicting the intercept. The frequency distribution of slope values of nitrogen versus  $V_{c\max}$  relationships has a pattern qualitatively different from intercept values (Fig. 2). Carboxylation capacity per nitrogen varies considerably between studies and plant species, requiring an explanation beyond differences in growth light, as proposed by Evans (1989). Because the slope of nitrogen versus  $V_{c\max}$  is one of the most sensitive parameters in predicting leaf or canopy photosynthetic production in models with leaf nitrogen content as a driving variable (e.g. Kull and Kruijt 1999), this variability should be studied carefully.

In addition to the variability in the nitrogen cost of photosynthetic capacity, nitrogen distribution within the leaf canopy depends not only on species, but on plant position in the community. For instance, in a canopy of two co-occurring species, light-demanding *Populus tremula* leaves contain more nitrogen and have a higher photosynthetic capacity than *Corylus avellana* leaves at common PFD (Kull and Niinemets 1998). Differences in canopy nitrogen distribution patterns have been shown to exist between species of the same herbaceous canopy (Hirose and Werger 1994) or even between dominant and subordinate plants of the same species (Anten and Werger 1996).

## Acclimations in composition (quality) of the apparatus

Construction and functioning of the photosynthetic apparatus is known in great detail. However, some reasonable simplifications are required to apply this physiological knowledge to ecological applications. For instance, physiologists often describe changes in stoichiometry of photosystem II (PSII) and photosystem I (PSI) as one aspect of light acclimation (Burkey and Wells 1991; Chow et al. 1991; Maxwell et al. 1999). Although important in maximising quantum yield, the ratio of PSI/PSII influences quantum yield only with rapid changes in spectral quality of light; hence this aspect is irrelevant in most ecological applications.

Traditionally, photosynthesis models in ecological applications use the approach by Farquhar et al. (1980), by which photosynthesis has two limitations: electron transport and biochemistry. This has led to simplified two-component apparatus in many leaf or canopy photosynthesis models. In some circumstances, a feedback limitation involving suppression of the photosynthesis rate by high levels of carbohydrates is considered (Sharkey 1985), although there are also more sophisticated approaches. For instance, to find optimal leaf nitrogen content at a particular PFD, Hikosaka and Terashima (1995) used a five-component model of photosynthesis with nitrogen distributed between RUBISCO, electron transport components, core complex of PSII, PSI, and light harvesting chlorophyll-protein complexes of photosystem II (LHCII).

Electron transport *sensu* Farquhar consists clearly of two distinct limitations: electron transport capacity and light harvesting, and, when acclimation to light is considered, it seems reasonable that these limitations be quantified separately. Under normal conditions, the ratio of  $V_{\text{cmax}}/J_{\text{max}}$  seems to be conserved and is independent of growth PFD (Wullschleger 1993; Tinoco-Ojanguren and Pearcy 1995; Porté and Loustau 1998; Wohlfahrt et al. 1999). Consequently, electron transport capacity and capacity of biochemistry change proportionally, and the number of parameters in the model can be reduced. What really changes in response to light acclimation is the relative share of light harvesting apparatus as expressed by changes in Chl/N ratio or Chl *a/b* ratios. An additional argument for separate quantification of electron transport and light harvesting is the strong light gradient within a leaf. Even with relatively high radiance, some chloroplasts at the most shaded part within the leaf may function below the maximum capacities of electron transport or biochemistry and are limited by light harvesting capacity (Terashima and Saeki 1983).

Changes in the relative share of light-harvesting complex in response to light intensity are well documented (e.g. Anderson and Osmond 1987; Evans 1989; Vapaavuori and Vuorinen 1989; Burkey and Wells 1991). A comparison of data from several studies reveals that leaf chlorophyll content in response to shade acclimation may increase (Lewandowska et al. 1976; Chow et al. 1988; Tinoco-Ojanguren and Pearcy 1995; Poorter

and Evans 1998) or decrease (Vapaavuori and Vuorinen 1989; Evans 1993a; Tinoco-Ojanguren and Pearcy 1995; Hikosaka and Terashima 1996; Kull and Niinemets 1998; Herrick and Thomas 1999). The discrepancy seems to be caused by two opposing changes: nitrogen content declines with decreasing light while the Chl/N ratio increases. On the basis of available data, it seems that the increase in Chl/N ratio is consistent in all experiments; hence the pattern of chlorophyll distribution depends on the steepness of the nitrogen versus PFD relationship.

Introduction of new micro-methods for measuring light, fluorescence, CO<sub>2</sub> uptake and O<sub>2</sub> evolution within a single leaf has produced much evidence to suggest that acclimation to light also occurs within a leaf. Features of the photosynthetic apparatus that change along a light gradient within a leaf are chloroplast size, thylakoid structure, carboxylation capacity and Chl *a/b* ratio (Terashima 1989; Nishio et al. 1993). These changes are similar to those occurring in whole leaves along a canopy light gradient. However, acclimation within a leaf is incomplete because with increasing incident PPFD light saturation tends to occur earlier in upper, better-illuminated parts of leaves (Nishio et al. 1993; Evans 1995; Han et al. 1999). Possible causes of incomplete acclimation may be related to chloroplast movement, equalisation of the light profile within a leaf due to strong scattering, and a highly variable and unpredictable ambient PFD field (Terashima 1989; Brugnoli and Björkman 1992; Terashima and Hikosaka 1995).

Several leaf-level photosynthesis models have been suggested whereby within-leaf heterogeneity in the light environment and photosynthetic properties are considered (Farquhar 1989; Evans 1995; Kull and Kruijt 1998). As shown by Badeck (1995), intraleaf acclimation greatly affects the estimates of optimal nitrogen allocation and needs to be considered if the assimilation flux is to be modelled on a mechanistic basis.

The environmental factor that drives the changes in the relative size of antennae is still unclear. It seems logical to assume that light quantity is regulating antenna size because adjustment of antenna size, relative to the rest of the photosynthetic apparatus, is one method to equilibrate light harvesting and biochemical capacity. Experiments with green algae *Chlorella vulgaris* have demonstrated that an increased Chl *a/b* ratio can be achieved at low temperatures, when the biochemistry of photosynthesis is slow, revealing that balancing capacities of different parts of the photosynthetic apparatus is more relevant than light *per se* (Maxwell et al. 1994). However, this was the case with neither wheat and rye (Huner et al. 1999) nor barley (Montané et al. 1998). Several experiments have investigated acclimation with respect to the R:FR ratio of radiation. The results of manipulative experiments are diverse, with some studies showing no effect of the R:FR ratio on the relative amount of LHCII or Chl *a/b* ratio (Chow et al. 1990; Smith et al. 1990; Walters and Horton 1994; Tinoco-Ojanguren and Pearcy 1995; Walters and Horton 1995b),



and other studies revealing a strong effect (Bradburne et al. 1989; Buisson and Lee 1993; Cockburn et al. 1996). Serious attention should be paid to studies that show the possible involvement of blue-light receptors in regulating LHCII size (Anderson et al. 1995; Lopez-Juez and Hughes 1995; Walters and Horton 1995a). As shown by Eskins et al. (1989) this mechanism seems to operate more strongly in mature leaves.

## Acclimation in canopy models

### Light response curve

The assumption that the shape of the light response curve does not change along a growth light gradient is clearly inconsistent with many findings (Kwesiga et al. 1986; Hirose and Werger 1987a; Schieving et al. 1992a; Turnbull et al. 1993; Herrick and Thomas 1999; Rosati et al. 1999). A flexible function often used in acclimation studies and models to approximate the photosynthetic light response is a non-rectangular hyperbola relating photosynthesis rate ( $P$ ) with PPFD ( $I$ ):

$$\Theta P^2 - (\Phi I + P_{\max})P + \Phi I P_{\max} = 0 \quad (1)$$

with three parameters:  $P_{\max}$  – maximal photosynthesis,  $\Phi$  – initial slope, and  $\Theta$  – convexity. Although simpler two parameter functions (excluding a respiration parameter) are still sometimes used (e.g. Hanson et al. 1987; Acock 1991; Harley and Tenhunen 1991; Kubiske and Pregitzer 1996; Bond et al. 1999), these functions are too inflexible to fit properly all the measured changes in the shape of the photosynthesis light response curve. Not all investigators have reported changes in the shape parameter,  $\Theta$ , along the light gradient (Pons et al. 1990; Evans and Farquhar 1991; Schieving et al. 1992b; Sands 1995b). This discrepancy may be caused by several factors. Leverenz (1987) showed that convexity was a function of leaf chlorophyll content, but often leaf-area-based chlorophyll content changes much less along the canopy light gradient than leaf morphology or nitrogen content (Evans 1993a; Kull and Niinemets 1998). The other possible reason that some investigators have not found systematic trends in parameter  $\Theta$  stems from the curve-fitting procedure. All three parameters of Eq. 1 appear to be interdependent (Evans and Farquhar 1991) and the results of ordinary least-squares regression depend on the data distribution along the curve. A complication in evaluating parameters of the photosynthesis light response curve also arises because the actual light response, which has a completely linear section below PFD values of  $50 \mu\text{mol m}^{-2}\text{s}^{-1}$  and saturates at finite values of PFD, differs qualitatively from a non-rectangular hyperbola (Leverenz 1987; Terashima 1989). This complication is compounded because stomatal conductance and temperature often vary during measurements; both factors strongly influence the resultant light response curve.

Due to acclimation, leaves in a canopy usually operate under conditions where the bend of the photosynthet-

ic light response curve is greatest (Kull and Kruijt 1998). Therefore, the convexity parameter has a strong influence on the scaling of photosynthesis from leaves to the entire canopy (Sands 1996). If convexity does not change with canopy depth and the maximal photosynthesis is distributed exactly according to the average light environment, the means of photosynthesis and light are proportional (Terashima and Hikosaka 1995; Dewar et al. 1998), but such a homogeneity is lost when  $\Theta$  changes with canopy depth (Farquhar 1989).

Evans and Farquhar (1991) state that the many steps between light absorption and RuBP regeneration, in combination with the complexity of the leaf optics, imply that a precise theoretical explanation of the light response is impossible. However, several attempts to understand and model this complicated feature have been made since. It is now clear that the main factors that influence the shape of the leaf light response are the heterogeneity of the light profile within a leaf and the local acclimation of the photosynthetic apparatus within a leaf (Terashima 1989; Ögren and Evans 1993; Evans 1995; Terashima and Hikosaka 1995). Experiments have shown that the convexity responds to changes in leaf light environment within several days (Laisk and Oja 1976; Ögren and Evans 1993). The photosynthesis light response of a thin leaf layer or single chloroplasts without photoinhibition is quasi-Blackman (i.e. has a convexity close to 1) (Terashima and Saeki 1985; Anderson and Osmond 1987; Leverenz 1987). Factors that can modulate this response are very high light or  $\text{CO}_2$  concentration (Falk et al. 1992; Ögren 1993). The first attempts to model heterogeneous leaf photosynthetic light response accounted only for heterogeneity in the light profile within a leaf, but still produced realistic results (Gutschick 1984; Terashima and Saeki 1985; Badeck 1995). However, in order to explain and model leaf light responses that differ when illuminated from different directions, acclimation must be considered, as was done by Farquhar (1989) and Evans (1995). Additionally, Kull and Kruijt (1998) included hypothetical mechanisms of acclimation. Such models allow calculation of realistic light responses with known quantitative and qualitative properties (e.g. a completely linear section at low light or saturation at finite values of PFD), although some difficulties still remain. The light gradient within a leaf is complex due to scattering and anatomical peculiarities, and cannot be described simply as exponential decline within a homogeneous solution of chlorophyll (Terashima and Saeki 1983; Vogelmann 1993). Additionally, acclimation on the chloroplast level seems to be incomplete because complete acclimation (when light harvesting, electron transport capacity and biochemistry match perfectly) would produce a Blackman-type light response (Farquhar 1989; Kull and Kruijt 1998). Consequently, because the convexity of measured light responses is less than 1, acclimation to local light conditions inside a leaf is not ideal. Additional evidence comes from a study by Han et al. (1999), which showed that  $\text{O}_2$  evolution along leaf thickness is more uniform than  $\text{CO}_2$  uptake as measured by

Nishio et al. (1993; see also Evans 1995). The incomplete acclimation may be also caused by chloroplast movement (Terashima 1989; Brugnoli and Björkman 1992) or by variability of the actual light environment.

## Distribution of photosynthetic apparatus within a canopy

### *Optimality models*

The idea that photosynthetic performance in a canopy is optimally distributed has been explored in many studies since the work by Field (1983). Based on scale, these optimality models can be divided roughly into three groups. The first group includes models that deal with optimality of photosynthetic apparatus within a single leaf (Chen et al. 1993; Hikosaka and Terashima 1995; Hikosaka and Terashima 1996; Medlyn 1996). Because each different part of the photosynthetic apparatus has its own nitrogen cost (Hikosaka and Terashima 1995), under given total leaf nitrogen and light conditions, photosynthesis is maximal at optimal nitrogen distribution between these parts. In some single leaf approaches where only parameters of light response curve related to leaf nitrogen content are considered, the optimal nitrogen content is taken that maximises nitrogen use efficiency (NUE) (e.g. Hirose and Werger 1987a). In other models the photosynthetic apparatus has been described in more detail (Evans 1993a; Hikosaka and Terashima 1995; Medlyn 1996). The single leaf optimality approach is sometimes called the “coordination theory” according to Chen et al. (1993).

The second group of models considers optimality at the leaf canopy level (Hirose and Werger 1987b; Pons et al. 1990; Schieving et al. 1992a; Evans 1993a; Sands 1995a; Hollinger 1996), where the merit function is usually the entire canopy carbon gain. With a given amount of total nitrogen and LAI and with no consideration of any respiratory or other costs, an optimal distribution of photosynthetic capacity appears to be proportional to the PFD profile within the canopy (Sands 1995a). In addition, at a fixed total foliar nitrogen only, LAI appears to have an optimal value at which total canopy photosynthesis is maximal (Schieving et al. 1992b; Anten et al. 1995a; Sands 1995a).

A comparison of measured and theoretical nitrogen distributions from these first two groups of optimisation models shows without exception that the real nitrogen profile is less steep than the calculated optimum and that the total canopy photosynthesis is 1–15% less than the theoretical maximum (Field 1983; Hirose and Werger 1987b; Schieving et al. 1992a; Evans 1993a; Hollinger 1996). Additionally, the actual photosynthetic capacity at the top of the canopy is often considerably less than that predicted by an optimal distribution (Pons et al. 1990; Evans 1993a; Hollinger 1996) and total canopy photosynthesis in a real canopy is usually higher than that of upper unshaded leaves – in contrast to the prediction of simplified canopy models (e.g. Kull and Jarvis 1995).

Real LAI is also greater than optimal LAI (Werger and Hirose 1991; Schieving et al. 1992b; Anten et al. 1998b; Schieving and Poorter 1999). Optimality at the leaf or canopy level fails to explain differences in distribution of photosynthetic performance between species (e.g. Kull and Niinemets 1998) or between dominant and subdominant plants of the same species (e.g. Anten and Werger 1996) within the canopy.

These arguments suggest that an inappropriate merit function leads to discrepancies between the models and reality. Terashima and Hikosaka (1995) have shown that, at the leaf level, actual photosynthesis lies between maximal leaf net carbon exchange and maximal NUE, and that reality can be estimated as a compromise between these two. The other possible explanation for the discrepancy between the models and reality may be due to overly simplified photosynthesis models. For instance, photosynthesis and nitrogen values for upper leaves often lie beyond the range of measured values used in parameterisation of the optimisation model (Pons et al. 1990; Evans 1993a; Hollinger 1996), and extrapolation is likely to be erroneous. As shown by Badeck (1995) these out-of-range photosynthesis values result from an unrealistic homogeneous leaf model.

In reality, leaf or canopy level optimisation fails because the acclimation in quantity of the photosynthetic apparatus, acquisition and redistribution of resources is clearly a whole-plant phenomenon (Mooney and Gulmon 1979). The third group includes optimisation models that incorporate the cost of construction and acquisition of resources in cost-benefit analysis. Unfortunately, these models are not yet elaborate enough (e.g. Givnish 1988) or have very simplified compartmentation with foliage of essentially one leaf (e.g. Hilbert et al. 1991).

An additional reason to explain unrealised optimality comes from the modelling study by Schieving and Poorter (1999), whose simulation study of a community of two hypothetical species suggests that competition for light results in an evolutionarily stable situation with higher LAI and lower canopy photosynthesis than in the optimal stand.

Poor results in optimum modelling are not proof that optimality fails; they merely imply that the function to be maximised in a natural community remains undiscovered. However, even when the proper merit function is found, it will merely describe the observed canopy pattern of photosynthesis, not the underlying mechanism.

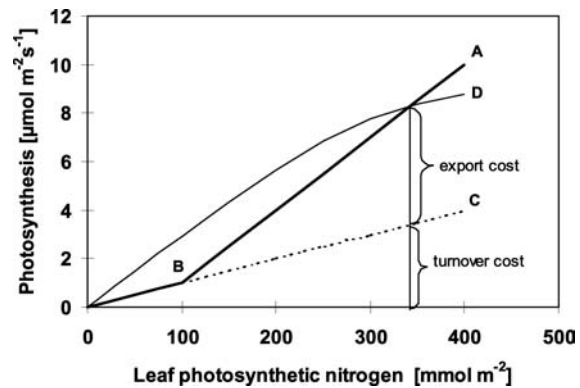
### *Turnover models*

The turnover theory states that acclimation of the amount of photosynthetic apparatus occurs due to permanent turnover of this apparatus, and, because the equilibrium amount of this apparatus depends on resource availability, primarily nitrogen and carbohydrates (Dewar et al. 1998; Thornley 1998; Kull and Kruijt 1999). It is widely accepted that this type of acclimation is related to reallocation of resources and depends on metabolic signals de-

rived from the physiological state of the plant, particularly photosynthesis (Anderson et al. 1995). Depending on the directional change in irradiance, part of the apparatus is broken down or new apparatus is built. These adjustments are relatively slow, usually taking 5–30 days. The relatively slow rate of change and evidence that, in addition to the known permanent turnover of proteins, chlorophyll turnover also occurs throughout the lifespan of a leaf (Matile et al. 1999), ensure that the adjustment in the amount of the photosynthetic apparatus reflects a dynamic equilibrium within regeneration and breakdown rather than switching on and off synthesis and degradation.

The turnover model as presented by Kull and Kruijt (1999) relies on regeneration of the photosynthetic apparatus based on levels of available nitrogen and carbohydrates. Evidence suggests that changes in nitrogen nutrition strongly influence leaf photosynthetic capacity and the distribution of photosynthetic properties within a canopy (Hikosaka et al. 1994; Anten et al. 1998a; Kuers and Steinbeck 1998). Despite the apparently strong correlation between leaf photosynthetic performance or between nitrogen and nonstructural carbohydrates (Jiao and Grodzinski 1996; Kull and Niinemets 1998; Le Roux et al. 1999b), a high carbohydrate level may simply be a result of high photosynthesis rate. Possible positive feedback between carbohydrates and photosynthetic capacity is supported indirectly, because respiration that feeds protein turnover with energy depends on substrate concentration (Cannell and Thornley 2000). In short-term manipulative experiments with altered sink strength, CO<sub>2</sub> concentration or light, a negative feedback between carbohydrate concentration and leaf photosynthesis capacity that operates through limitation of inorganic phosphorus has been found (Sharkey 1985; Layne and Flore 1995). However, this limitation usually ceases once plants have adapted to the new conditions.

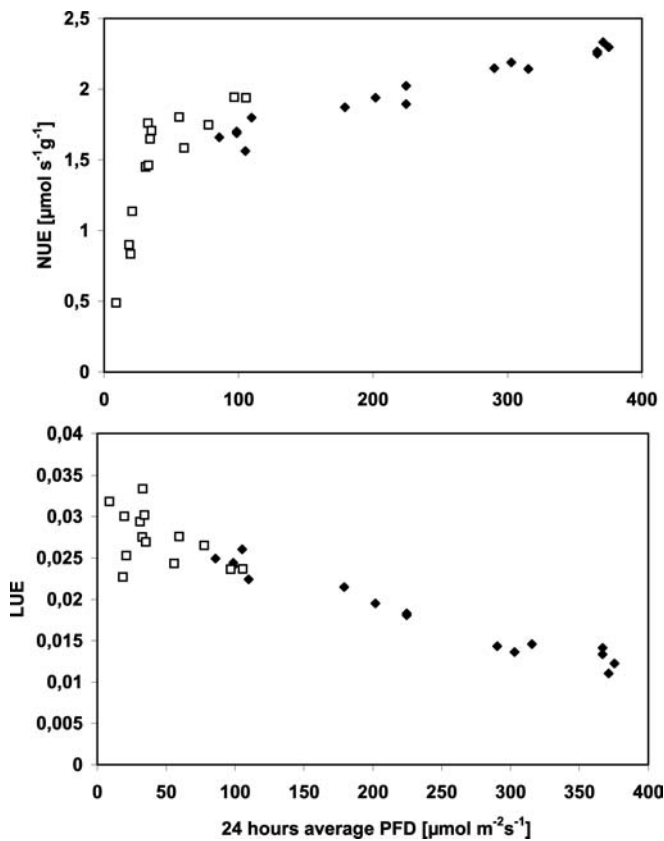
Acclimation through the amount of leaf photosynthetic apparatus is clearly a whole plant phenomenon, as shown by Givnish (1988). This is supported by studies that show that patterns of nitrogen or photosynthetic capacity with respect to irradiance depend on plant size, canopy position or age (Leverenz and Jarvis 1980; Anten and Werger 1996; Tognetti et al. 1997; Anten et al. 1998a). Additional studies indicate that different species sharing the same canopy usually have different nitrogen distributions (Anten et al. 1995b; Kull and Niinemets 1998). Manipulative experiments with green pruning of part of the foliage (e.g. Layne and Flore 1995; Pinkard and Beadle 1998) clearly show that leaves of the same plant share a common source of information. The model by Kull and Kruijt (1999) proposes that this common source of information is plant common pools of nitrogen and carbohydrates. Every leaf has its own local environment to which it acclimates, depending on nitrogen availability from the plant common pool and on the level of carbohydrates, which is in itself dependent on the dynamic equilibrium formed between rates of photosynthesis, respiration and export into the plant common pool.



**Fig. 3** According to the turnover theory, actual leaf nitrogen content in a particular PFD environment is predicted by common solution of two functions. Firstly, photosynthesis versus leaf nitrogen content as predicted by photosynthesis model at given PFD (curve D), which is saturated at high values of leaf nitrogen. Secondly, photosynthesis versus leaf nitrogen content as predicted by the demand model (curve O-B-A), which has shape of a broken line. In circumstances when the leaf is not exporting (e.g. when leaf carbohydrates concentration is too low) photosynthesis has to cover only the turnover cost and then the average photosynthesis rate should be proportional to leaf nitrogen content (O-B). However, if conditions allow photosynthesis rates high enough to build up a carbohydrate pool and to start export then photosynthesis has to cover the export in addition to the turnover cost. In these circumstances the relationship between average photosynthesis rate and leaf nitrogen content has a negative intercept (B-A)

The main implication of the turnover model is a linear relationship between time-averaged leaf photosynthesis and leaf nitrogen content in leaves taken from the same canopy (Fig. 3). The intercept of this relationship depends on carbohydrate export. If a leaf does not export, all photosynthetic production is spent on turnover of the leaf photosynthetic apparatus in steady-state conditions. At constant cost of this turnover (expressed as the amount of photosynthesis products needed to support this turnover with substrate and energy), leaf photosynthetic production and leaf nitrogen content would be proportional. When a leaf with a given leaf nitrogen content exports carbohydrates, photosynthesis must increase to accommodate both the turnover and export. This means that exporting leaves can maintain the same leaf nitrogen content only at higher light conditions than non-exporting leaves. Field measurements confirm that the relationship between leaf photosynthetic production and leaf nitrogen content is linear with a negative intercept on the photosynthesis axis (Kull and Kruijt 1999). Because mature leaves cannot import carbohydrates due to physiological restrictions (Turgeon 1989), these canopies contain no non-exporting leaves; otherwise the data would lie on a curve (Fig. 3). Few measurements of export rates confirm the model prediction that the export rate decreases to zero at positive photosynthesis values (Jiao and Grodzinski 1996; Grodzinski et al. 1998). It seems likely that the lower limit in a leaf canopy is where export is zero (Kurachi et al. 1993; Kull et al. 1999; Kull and Kruijt 1999). If so, the turnover theory can be used





**Fig. 4** Nitrogen use efficiency, calculated as 24-h average photosynthesis per unit of leaf nitrogen, versus PFD within the canopy at Järvelja, Estonia (*upper graph*), and light use efficiency, calculated as 24-h average photosynthesis per incident 24-h average PFD in dependence of leaf position in the same canopy (*lower graph*). *Populus tremula* (filled diamonds) is dominant in the community with foliage in a height range of 19–27 m; *Tilia cordata* (open squares) grows beneath with foliage in a height range of 5–19 m. Total LAI of the canopy is about 6.5. Photosynthesis is calculated by the model of Kull and Kruijt (1998) using measured diurnal courses of PFD, leaf nitrogen and chlorophyll values, and laboratory-measured relationships between leaf nitrogen content and photosynthetic parameters,  $V_{\max}$  and  $J_{\max}$ , in leaves from the same canopy. Data are recalculated from the study of Niinemets et al. (1999a)

to predict not just nitrogen distribution within a canopy, but also its lower limit and, hence, LAI. Investigating this assumption, Kull and Kruijt (1999) found that total canopy nitrogen is a good estimate of canopy total photosynthesis, a conclusion supported by Leuning et al. (1991b) and Matson et al. (1994).

An important message from the turnover model is that the strong relationship between leaf nitrogen and photosynthetic performance appears, not because the nitrogen is mainly in photosynthetic apparatus, but because a certain amount of energy must be captured through photosynthesis to maintain this nitrogen within a leaf. However, the photosynthesis nitrogen relationships revealed by the photosynthesis model for certain PFD values (curve D in Fig. 3) predict the actual nitrogen distribution within the canopy with respect to PFD distribution.

The weakest aspect of the current turnover models is the import-export feature. In the models of Thornley (1998) and Kull and Kruijt (1999), import-export is modelled using a transport-resistance approach (Thornley 1991); the model of Dewar et al. (1998) is even more simplified. In fact, export of assimilates is most likely realised by a mass-flow mechanism, but few attempts with a high degree of simplification have been made to incorporate mass-flow mechanism in plant growth models (Dewar 1993). The mass-flow mechanism has important implications because it links plant water status with carbohydrate transport. This link may have led Pons and Bergotte (1996) to conclude that manipulations with individual leaf vapour pressure differences lead to changes in nitrogen and photosynthetic apparatus distribution between leaves.

In some sense, the turnover theory explores the idea that the photosynthetic apparatus is relatively independent – it grows and operates within the plant body using resources and space provided by the plant, and this environment for photosynthesis is provided by plants only when plants get a return of carbohydrates. Figure 3 shows that if the turnover cost of the photosynthetic apparatus is constant, photosynthetic NUE of non-exporting leaves is independent of leaf nitrogen content. NUE increases with leaf export with the maximum at the top of the canopy (Fig. 4A). Therefore, NUE should reflect the benefits plants receive from photosynthesis as exported carbohydrates.

### Benefits of being in the shade of others – the limits of acclimation

Light saturation at high PFD seems to be a fundamental feature of the photosynthetic apparatus. This can be seen at all levels of organisation: chloroplast, leaf and canopy. The most evident is light saturation at the chloroplast level from analysis of the leaf photosynthesis light response curve. The light response starts to deviate from a completely linear relationship at PFD levels of about 20–50  $\mu\text{mol m}^{-2}\text{s}^{-1}$  (Leverenz 1987; Kursar and Coley 1999). This occurs when some chloroplasts near the upper leaf surface become saturated. Earlier saturation of some of the leaf photosynthetic apparatus with increasing PFD is supported by studies of  $\text{CO}_2$  uptake and  $\text{O}_2$  release across leaf cross-sections, which show that upper, illuminated parts saturate at lower incident PFD levels than the apparatus deeper in the leaf (Nishio et al. 1993; Evans 1995; Han et al. 1999). The reason seems to lie in the principal construction of the photosynthetic apparatus. It is likely that, for this apparatus to remain intact, some of the core antenna is needed and even this minimal antenna is excessive for the co-occurring electron transport chain at ambient PFD levels. A plot of Chl/N ratio versus PFD shows that this ratio achieves a plateau at high PFD values (Kull and Niinemets 1998). Consequently, fundamental construction peculiarities do not allow for an elementary photosynthetic



apparatus to acclimate properly with reasonable matching capacities of light harvesting and electron transport at light levels above ca  $50 \mu\text{mol m}^{-2}\text{s}^{-1}$ . As a result of this limited acclimation, other means of dissipating excitation energy must be involved. For instance, in the long term, xanthophyll cycle like mechanisms are needed when the ability to decrease antenna size has been exhausted. Therefore xanthophyll cycle pigments must be localised at the core antenna and not at LHCII (Gilmore 1997). If assessed through photosynthetic production, it is clearly beneficial for a photosynthetic apparatus to be in the shade of others to avoid over-excitation. At the leaf level, this benefit is seen as increased quantum yield with an increased amount of photosynthetic apparatus in leaves (e.g. measured as leaf nitrogen content) at PFD values beyond the region of linear response. With an increasing amount of photosynthetic apparatus, a relatively smaller portion becomes light saturated. The same effect is seen at the canopy level: light use efficiency (LUE) decreases substantially with height in the canopy (Fig. 4B). Similar results have been found by Hikosaka et al. (1999). The LUE of the entire canopy is also shown to increase with total canopy nitrogen (Sinclair and Shiraiwa 1993).

With complete and full acclimation, LUE should be constant at every canopy position and at every level of organisation. In fact, with increasing thickness of the canopy photosynthesising layer, the photosynthetic light response in realistic PFD conditions deforms from sharply saturating to an almost linear response, i.e. at a given PFD, LUE of a layer increases with increasing amount of the photosynthetic apparatus. The almost linear light response of the entire canopy is mainly caused by mass effect – the relative amount of saturated photosynthetic apparatus decreases with increasing photosynthetic tissue.

Because of the fundamental limit of the photosynthetic apparatus to acclimate to most natural PFD conditions, it is beneficial to be in the shade of others at an elementary photosynthetic machinery level. However, at the plant or canopy level it is still useful, in terms of carbon gain, to build thick layers of this machinery and to position leaves at high PFD as far as NUE is increasing (Fig. 4A). This may have been a selective evolutionary force that led to the development of thick photosynthesising canopies.

The acclimation ability of the photosynthesising apparatus has some additional limitations. Beside the inability to acclimate properly at high PFD with balanced size of the light harvesting antenna, there seems to be a discrepancy at very low light as well. Spinach leaves grown in shade have a Chl/N ratio much lower than needed to maximise photosynthesis (Terashima and Evans 1988). Calculations by Kull and Kruijt (1998) yield similar results. The actual Chl/N ratio in the lower canopy of a *Populus* and *Corylus* stand was clearly lower than needed to maximise photosynthesis, although the theoretical benefit from increased chlorophyll content would be relatively small in terms of photosynthesis. Perhaps, as discussed by Evans (1993b), there are con-

struction limits in the number of LHCII units that can be associated with a core antenna or at what distance excitation can be passed to the reaction centre. However, the ability to acclimate in extreme shade may depend on plant species (Hikosaka and Terashima 1995).

The additional limit of proper acclimation is related to the dynamics of environmental variables and time constants of acclimation processes. Turnover of the photosynthetic apparatus is slow compared to environmental variability, especially PFD; hence acclimation is unending and fine-tuning mechanisms are necessary to cope with the highly variable environment.

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## Conclusions

Two major aspects of photosynthesis acclimation in leaf canopies must be considered in ecological applications. Firstly, acclimation leads to specific distribution patterns of the amount of leaf photosynthetic apparatus within a canopy. The quantitative aspect is expressed as leaf photosynthetic capacity or leaf nitrogen content. Secondly, qualitative changes in photosynthetic apparatus, expressed as alterations in stoichiometry of different functional parts of this apparatus, occur in response to prevailing irradiation. The most important stoichiometric shift related to within-canopy acclimation involves the relative share of light-harvesting apparatus with respect to electron transport and the biochemical apparatus of the photosynthesis. The qualitative changes occur at the chloroplast level, and the stoichiometry of photosynthetic apparatus also changes along the intraleaf irradiance gradient. The qualitative aspect of the acclimation is most important in predicting the shape of the photosynthetic light response curve and should be considered in proper scaling of the photosynthetic production within a canopy.

Photosynthetic capacity and leaf nitrogen never exactly match the PFD gradient within a canopy. The common pattern of nitrogen distribution is slightly saturated at high PFD and has a significant positive intercept on the nitrogen axis, which is unattributable to non-photosynthetic leaf nitrogen. As a result, photosynthetic LUE, i.e. photosynthetic performance per incident PFD, increases considerably from the top of the canopy to the lower shaded part. The distribution pattern of photosynthetic capacity depends on species, site quality and plant position within a canopy. Additional variability is caused by large differences in the relationship between nitrogen versus photosynthetic capacity across species and studies. The reasons for these differences require careful examination.

Distribution of the photosynthetic capacity of leaves within a canopy is a whole plant phenomenon. Optimality models that do not consider plant level interactions and costs fail to predict accurately the measured canopy distributions of nitrogen and photosynthetic capacity. In addition to optimality-based models, a turnover model has been used to describe these distributions. The turn-

over model makes several predictions about canopy level behaviour of photosynthesis; however, these models require experimental confirmation.

Photosynthesis acclimation to light is limited at both ends of the PFD scale. The limited ability to acclimate with a proper balance between light harvesting and biochemical parts of the photosynthetic apparatus, in conjunction with the time constraints of acclimation, are the major reasons why proper scaling of photosynthesis from leaf to canopy is not a trivial task.

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