Co-optimal distribution of leaf nitrogen and hydraulic conductance in plant canopies

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Leaf properties vary significantly within plant canopies, due to the strong gradient in light availability through the canopy, and the need for plants to use resources efficiently. At high light, photosynthesis is maximized when leaves have a high nitrogen content and water supply, whereas at low light leaves have a lower requirement for both nitrogen and water. Studies of the distribution of leaf nitrogen (N) within canopies have shown that, if water supply is ignored, the optimal distribution is that where N is proportional to light, but that the gradient of N in real canopies is shallower than the optimal distribution. We extend this work by considering the optimal co-allocation of nitrogen and water supply within plant canopies. We developed a simple ‘toy’ two-leaf canopy model and optimized the distribution of N and hydraulic conductance (K) between the two leaves. We asked whether hydraulic constraints to water supply can explain shallow N gradients in canopies. We found that the optimal N distribution within plant canopies is proportional to the light distribution only if hydraulic conductance, K, is also optimally distributed. The optimal distribution of K is that where K and N are both proportional to incident light, such that optimal K is highest to the upper canopy. If the plant is constrained in its ability to construct higher K to sun-exposed leaves, the optimal N distribution does not follow the gradient in light within canopies, but instead follows a shallower gradient. We therefore hypothesize that measured deviations from the predicted optimal distribution of N could be explained by constraints on the distribution of K within canopies. Further empirical research is required on the extent to which plants can construct optimal K distributions, and whether shallow within-canopy N distributions can be explained by sub-optimal K distributions.

Keywords: allocation, canopy structure, hydraulic conductance, nitrogen, optimization, photosynthesis.

Introduction

Leaf properties vary substantially within plant canopies. Leaves near the canopy top are consistently shown to have high nitrogen and phosphorus content per unit leaf area, high leaf mass per area and high photosynthetic capacity, compared with leaves deeper in the canopy (Hollinger 1989, Bond et al. 1999, Niinemets and Valladares 2004). These observations have been explained theoretically in terms of the optimal distribution of resources, particularly nitrogen, throughout the canopy. This explanation stems from three basic observations. First, light availability declines with canopy depth. Second, leaf photosynthesis has a saturating response to light level. Third, the light-saturated rate of photosynthesis depends on the leaf photosynthetic protein content, which is strongly related to the leaf nitrogen content (Field and Mooney 1986). Under these three assumptions, it can readily be shown that, if total canopy nitrogen content is fixed, total canopy photosynthesis is greatest when leaf nitrogen content at a given height is proportional to the light penetrating to that height (Field 1983, Badeck 1995, Sands 1995). Thus, leaf nitrogen content should be highest in the uppermost part of the canopy.
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This observation has proved very useful. If nitrogen is opti-

mally distributed throughout the canopy, then total canopy pho-
tosynthesis can be calculated analytically, using a ‘big-leaf’

model (Sands 1995). This approximation is employed in most of

the large-scale land-surface models currently being used to

investigate Earth system responses to climate forcing (Sellers et

al. 1997, Friedlingstein et al. 2006). Most measurements,

however, indicate that the gradient of nitrogen through the can-

opy is somewhat less steep than predicted by optimization

theory (Pons et al. 1989, Ellsworth and Reich 1993, Dang et


A number of authors have proposed reasons for this departure

from optimality, including the cost of herbivory (Stockhoff

1994), competition between individuals in a canopy (Anten

2005) and constraints on maximum photosynthetic capacity in

suntlit leaves (Lloyd et al. 2010). One possibility that has not yet

been considered is the need for water transport to leaves.

Leaves with high photosynthetic capacity also tend to have

high stomatal conductance and high transpiration rates (Wong

et al. 1978, Schulze et al. 1994). It can be shown that, in the

absence of other constraints, optimal stomatal conductance

increases in proportion with photosynthetic rate (Hari et al.

1986, Lloyd 1991, Medlyn et al. 2011), suggesting that transpi-

ration rates should also be highest in the upper canopy.

However, water use is constrained by the need to transport

water from the soil to the leaves. The rate of water transport

depends on the hydraulic conductance of the soil–leaf

pathway.

The conductance of this pathway ( , conductance per unit

leaf area, mol m$^{-2}$ s$^{-1}$ MPa$^{-1}$) depends on sapwood properties,

including sapwood conductivity (a function of vessel diameter)

and the sapwood area : leaf area ratio (Huber value)

(Whitehead 1998). Although plants have some capacity to

modify the conductance in the short term, through potassium

release (Sellin et al. 2010, Nardini et al. 2011) and regulation

of aquaporins (Cochard et al. 2007), to a large extent the con-
ductance represents a long-term investment in building of con-
ductive tissue by the plant.

It has been argued that plants should co-ordinate investment

in hydraulic conductance with investment in photosynthetic

capacity (Katul et al. 2003). Leaves with high photosynthetic

capacity will have high water use requirements, and therefore

need to be serviced by a high-capacity water transport path-

way. According to this argument, hydraulic conductance should

be highest to the upper canopy. In support of a direct response

to light availability, increased in beech seedlings a year after

they were exposed to higher light due to canopy opening

(Caquet et al. 2009).

However, it is generally thought that is inversely related to

path length; the longer the path, the lower the conductance


If this is the case, then is highest to the lower canopy.

Photosynthesis in the upper canopy is then also likely to be

water-stressed while lower canopy leaves are amply supplied

with water (cf. Niinemets et al. 2004), representing an ineffi-

cient distribution of resources. Thus, if hydraulic conductance

decreases with path length, the consequent limited water sup-

ply to the upper canopy may reduce the benefit of nitrogen

allocated to upper foliage.

It is possible, therefore, that the distribution of hydraulic con-
ductance within canopies changes the optimal distribution of

photosynthetic nitrogen. Alternatively, it is also possible that

plants are not constrained to have path length-dependent con-
ductance, but can organize their hydraulic architecture to maxi-

mize nitrogen use efficiency. Recent empirical research tends

to show higher hydraulic conductance to upper leaves com-

pared with lower leaves (Lemoine et al. 2002a, Jerez et al.


2008), which argues that plants may be able to tailor their

hydraulic systems to match water supply with light supply.

Our objective in this paper was to explore the optimal co-
distribution of hydraulic conductance ( ) and nitrogen ( )

within canopies. We use a hydraulically based model of stoma-
tal conductance and photosynthesis (Tuzet et al. 2003), cou-
ped with a simple ‘toy’ canopy model to simplify model

interpretation. We first ask, what is the optimal distribution of

nitrogen when is constant for all leaves in the canopy? We

then allow conductance to vary within the canopy and quantify

the optimal co-distribution of and . Our goal in identifying

these optimal distributions is to provide a point of reference

against which to compare empirical data. By quantifying how

different the measured distributions are from optimal, we can

gain a real insight into the physical limitations that govern plant

growth and canopy architecture.

Methods

General approach

We used a very simple representation of a plant canopy: a plant

with two leaves, one of which partially shades the other. This

simple approach made model analysis and interpretation rela-

tively straightforward, while the results can still be generalized

to real plant canopies, because the two leaves compared could

be located anywhere in the canopy. By considering many pair-

wise comparisons between leaves with different incident

photosynthetic photon flux density (PPFD), we can make infer-

ces about how the whole canopy operates, and how and are

coordinated within the canopy. It should be stressed that

comparison of between different canopy positions is funda-

mentally different from comparison of between plants of dif-

ferent total height and age. We do not discuss the latter (see

Ryan et al. (2006) for a review). We focus on an individual

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plant. We assume that the total plant hydraulic conductance ($K_T$) is fixed. This total hydraulic conductance represents the total carbon investment that the plant has made to construct and maintain conductance. We then ask how this conductance should be distributed among canopy leaves to maximize total photosynthesis.

We studied how our two-leaf plant should allocate nitrogen ($N$, g m$^{-2}$) and leaf-specific hydraulic conductance ($K$, mmol m$^{-2}$ s$^{-1}$ MPa$^{-1}$) between leaves by calculating distributions that maximize the net photosynthesis of the whole plant ($A$, μmol m$^{-2}$ s$^{-1}$). The two leaves of the plant were assumed to be identical, except for (i) incident PPFD, (ii) nitrogen content $N_i$, which determines leaf net photosynthesis rate ($A$) and respiration rate ($R_d$); and (iii) $K$, which affects stomatal conductance ($g_s$) and therefore the leaf transpiration rate ($E$). In the following, we use subscripts for the variables $A$, $N$ and $K$: ‘sun’ indicates the ‘sun leaf’, and ‘shade’ the ‘shade leaf’, which receives lower PPFD than the sun leaf. Except for incident PPFD, leaves are subjected to the same environmental conditions (vapour pressure $D$, atmospheric CO$_2$ concentration $C_a$, and temperature $T$). In all simulations, we use constant environmental drivers, because the aim was to study long-term acclimation patterns in plant canopies, and how they affect total carbon uptake.

**Leaf-level model of photosynthesis and transpiration**

The leaf net photosynthesis rate ($A$) is modelled using the standard model of Farquhar et al. (1980).

$$A = \min(A_c, A_j) - R_d$$  

where $A_c$ is the gross photosynthesis rate when Rubisco activity is limiting, $A_j$ when RuBP regeneration is limiting and $R_d$ the rate of dark respiration. In this model, both $A_c$ and $A_j$ are saturating functions of the intercellular CO$_2$ concentration ($C_i$) (see the Appendix for a full set of equations). We assumed that the maximum rate of carboxylation ($V_{cmax}$) and the maximum rate of electron transport ($J_{max}$) were linear functions of the leaf nitrogen content ($N$).

We used the Tuzet model of stomatal conductance ($g_s$) (Tuzet et al. 2003), which accounts for the hydraulic control of $g_s$ through the leaf water potential ($\Psi_L$) (cf. Comstock and Mencuccini 1998, Franks 2004).

$$g_s = g_0 + g_1 \frac{A}{C_a - \Gamma} \Psi_L$$  

where $g_0$ is a ‘residual’ $g_s$ (that includes cuticular conductance and stomatal leakiness), $g_1$ a parameter, $C_a$ the atmospheric CO$_2$ concentration (ppm), $\Gamma$ the CO$_2$ compensation point and $\Psi_L$ a sigmoidal function that describes the effect of $\Psi_L$ on $g_s$. Both vapour pressure deficit (VPD) and soil moisture potential affect $g_s$ through their effects on $\Psi_L$ (see the Appendix).

We assumed that the soil-to-leaf hydraulic pathway was in steady state, so that $\Psi_L$ can be estimated from Darcy’s law:

$$E_L = K (\Psi_S - \Psi_L)$$  

where $E_L$ is the leaf transpiration rate (mmol m$^{-2}$ s$^{-1}$), $K$ the leaf-specific hydraulic conductance (mmol m$^{-2}$ s$^{-1}$ MPa$^{-1}$) and $\Psi_S$ the soil water potential (MPa).

The system of equations (Eqs. (1)–(3)) can be solved using an additional constraint on basic diffusion through the stomata:

$$A = g_s (C_a - C_i)$$  

where $C_i$ is the stomatal conductance to CO$_2$ ($= g_s/1.6$).

**Whole-plant optimization**

We assumed that the plant has a total amount of $N$ and $K$ at its disposal, which can be allocated to the two leaves. This way, both leaves have their own shares of $N$ and $K$ from the total plant pools of $N_T$ and $K_T$, so that $N_T = N_{sun} + N_{shade}$ and $K_T = K_{sun} + K_{shade}$. To find the optimal distribution of $K$ and $N$ among the leaves, $N_T$ and/or $K_T$ were divided between the two leaves in such a way that the total plant photosynthesis $A_T (=A_{sun} + A_{shade})$ was maximized.

To investigate effects of varying light conditions, we varied the total incident PPFD ($I_T$) and the distribution of the PPFD between the plant’s two leaves, which we characterize as the ratio $I_{shade} : I_{sun}$ (shaded to sunlit PPFD). We present distributions of nitrogen and conductance between the two leaves analogously, as $N_{shade} : N_{sun}$ and $K_{shade} : K_{sun}$.

The following optimization cases are presented:

(i) Optimization of $N$

(a) $K$ is assumed infinite. This case represents standard big-leaf scaling, where $N$ is optimized and water transport is not limiting to carbon uptake.

(b) $K_{sun}$ and $K_{shade}$ are assumed equal and equal to $K_T/2$. $N_{sun}$ and $N_{shade}$ are optimized.

(c) $K$ is assumed to be path length ($L$) dependent. We assume $L_{sun} = L_{shade}$ and $K$ is proportional to $L$.

(ii) Optimization of $K$ while $N_{sun}$ and $N_{shade}$ are held constant and equal to $N_T/2$.

(iii) Co-optimization of $K$ and $N$.

We calculated the optimal partitioning of $K$ and/or $N$, and resulting sun and shade values of $A$, $\Psi_L$ and $g_s$. We examined the effect of varying the total $I_T$, as well as the partitioning of $I_T$...
between the plant leaves, $I_{\text{shade}} : I_{\text{sun}}$. Other environmental variables and model parameters were held fixed (Table 1).

Optimizations were performed in R (R Development Core Team 2010) using the `optimize` function for cases 1 and 2, and `optim` for case 3, which had two parameters. The Nelder–Mead algorithm was used in both cases.

**Results**

**Modelled response of leaf photosynthesis to light, nitrogen and hydraulic conductance**

The leaf-level photosynthesis model (Eqs. (1)–(4)) captured the main responses of $A$ to $N$, $K$ and PPFD (Figure 1). With increasing PPFD, $A$ shows a saturating response, and reaches higher light-saturated values when $K$ and $N$ are increased. The model also gives realistic responses to other environmental variables such as $D$ and $T$ (not shown), but in this study we were only concerned with average response of $A$ to the distribution of $N$ and $K$ among shaded and sunlit leaves.

**Total photosynthesis does not depend on PPFD distribution in optimal canopies**

Total plant photosynthesis ($A_T$), the sum of the two leaves, was optimized by distributing $N$ and/or $K$ between the two leaves. We repeated this analysis for a range of $I_{\text{shade}} : I_{\text{sun}}$, the ratio of PPFD on the shaded leaf to that on the sunlit leaf. For all optimization cases where either $N$ or $K$ was constrained, $A_T$ decreased at low values of $I_{\text{shade}} : I_{\text{sun}}$ (Figure 2), indicating that $A_T$ was constrained by the ability of the plant to distribute

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Table 1. Default parameter settings.

<table>
<thead>
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<th>Variable</th>
<th>Default value</th>
<th>Units</th>
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<td>ppm</td>
</tr>
<tr>
<td>$g_0$</td>
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<td>mol m$^{-2}$ s$^{-1}$</td>
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<tr>
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</tr>
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<td>$J_{\text{max}}$</td>
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</tr>
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<td>$V_{c_{\text{max}}}$</td>
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<td>mol m$^{-2}$ s$^{-1}$ MPa$^{-1}$</td>
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<td>g N m$^{-2}$</td>
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<td>$I_{\text{shade}} : I_{\text{sun}}$</td>
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</tr>
<tr>
<td>$R_d$</td>
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<td>°C</td>
</tr>
<tr>
<td>$\Psi_S$</td>
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<td>MPa</td>
</tr>
</tbody>
</table>

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Figure 1. Predictions of the dependence of leaf-level net photosynthesis rate ($A$) by the coupled model (Eqs. (1)–(4)) on PPFD, leaf-specific hydraulic conductance ($K$, mmol m$^{-2}$ s$^{-1}$) and leaf nitrogen content ($N$, g m$^{-2}$). For all other parameters, default values were used (see Table 1).

Figure 2. Maximized total plant photosynthesis ($A_T$) as a function of the PPFD on the shaded leaf ($I_{\text{shade}}$) relative to that on the sunlit leaf ($I_{\text{sun}}$). For each combination of $I_{\text{shade}} : I_{\text{sun}}$, $A_T$ was maximized by allowing $K$, $N$ or both to vary between the two leaves. The grey line shows $A_T$ when both $K$ and $N$ were held constant, and the small dots when $N$ was optimized but $K$ was path length dependent. Note that when both $K$ and $N$ are optimized, $A_T$ does not depend on the ratio $I_{\text{shade}} : I_{\text{sun}}$. 

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resources \((N \text{ and } K)\) among plant leaves. When \(N\) and \(K\) were both optimized (thick line in Figure 2), \(A_t\) did not depend on \(I_{\text{shade}} : I_{\text{sun}}\) because resources could be efficiently redistributed. This was also the case when the \(K\) constraint was removed (by setting it to infinity, large solid dots in Figure 2).

**Contribution of individual leaves to total plant photosynthesis**

The distribution of \(A\) among the two leaves was not only a function of the relative PPFD incident on the two leaves but also on the total incident PPFD. To illustrate this dependency, we set \(I_{\text{shade}} : I_{\text{sun}} = 0.5\) (twice the PPFD on the sunlit leaf), and found the maximized \(A_t\), \(A_{\text{sun}}\) and \(A_{\text{shade}}\) across a range of total incident PPFD (Figure 3). As expected, maximized \(A_t\) showed a strong dependence on PPFD (Figure 3), much like the leaf level dependence (Figure 1). Maximized \(A_t\) was highest when both \(N\) and \(K\) were optimized. The distribution of \(A\) among the two leaves depended strongly on whether \(K\), \(N\) or both were optimized. When both \(K\) and \(N\) were optimized, \(A_{\text{shade}} : A_{\text{sun}}\) was the same as the ratio of PPFD on the two leaves \(I_{\text{shade}} : I_{\text{sun}}\), which was set to 0.5 in this simulation. When either \(K\) or \(N\) was fixed (i.e., not optimized), this ratio varied with PPFD, and the difference between \(A_{\text{sun}}\) and \(A_{\text{shade}}\) was much smaller than when \(K\) and \(N\) were co-optimized (particularly at high PPFD).

**Co-optimal \(K\) and \(N\) follow PPFD distribution and sub-optimal \(K\) distribution explains shallow \(N\) gradients in canopies**

The optimized distributions of \(A\), \(K\) and \(N\) with varying relative PPFD \(I_{\text{shade}} : I_{\text{sun}}\) are shown in Figure 4, for four of the optimization cases. When \(K\) was equal (i.e., the same for the shaded and sunlit leaves), or dependent on path length (so that \(K_{\text{shade}} > K_{\text{sun}}\), \(A_{\text{shade}} : A_{\text{sun}}\) and \(N_{\text{shade}} : N_{\text{sun}}\) were higher than the ratio \(I_{\text{shade}} : I_{\text{sun}}\). That is, the gradient in \(A\) and \(N\) was less steep than the gradient in PPFD within the canopy when \(K\) was fixed. This result was most pronounced for the case where \(K\) was path length dependent. In this case, the canopy gradient in \(K\) could even be reversed, resulting in higher \(N\) allocation to the shade leaf, when the \(I_{\text{shade}} : I_{\text{sun}}\) ratio was relatively high (>80%). When both \(N\) and \(K\) are optimized, all three variables, \(A\), \(K\) and \(N\), are proportional to \(I_{\text{shade}} : I_{\text{sun}}\) (thick solid line in Figure 4). That is, the gradients in \(N\) and \(K\) both follow the gradient in PPFD. These results were not sensitive to the total \(N\) and total \(K\) available to allocate to leaves, nor were they sensitive to uniform changes in temperature, \(\text{CO}_2\), VPD or soil water potential throughout the canopy (not shown).

**Implications for leaf water potential gradients**

When \(K\) was held constant for the two leaves, or dependent on path length, the simulated leaf water potential \(\Psi\) reached more negative values for the sunlit leaves (Figure 5). This indicates that, when \(K\) was not distributed optimally between the leaves, the sunlit leaves experienced greater water stress, because higher PPFD leads to higher rates of leaf transpiration (and thus lower \(\Psi\), Eq. (3)). In contrast, when \(K\) was optimized, the difference in \(\Psi_L\) between the sunlit and shaded leaves was much smaller, and led to somewhat more negative \(\Psi_L\) for the shaded leaf (particularly at very low values of \(I_{\text{shade}} : I_{\text{sun}}\) and when \(N\) was also optimized).

**Discussion**

We explored optimal co-allocation of nitrogen \((N)\) and hydraulic conductance \((K)\) within plant canopies, and asked whether hydraulic constraints can explain shallow \(N\) gradients in canopies. Our results showed that if the plant is constrained in its ability to construct higher \(K\) to sun-exposed leaves, the optimal \(N\) distribution does not follow the gradient in PPFD within canopies, but instead follows a shallower gradient.

Previous work on optimization of leaf nitrogen \((N)\) profiles in canopies has not explicitly considered water transport limitations (Field 1983, 1988, Sands 1995, Badeck 1995). Like these previous studies, our model results also showed that when \(N\) is allocated optimally within canopies, it is proportional to PPFD. In addition, we showed that this was only the case when \(K\) was also optimized. When both \(N\) and \(K\) were optimized, we found that both \(N\) and \(K\) were proportional to the gradient of PPFD in the canopy (Figure 4), and thus proportional to each other. It is not surprising that in an optimal plant, higher \(N\) (and thus photosynthetic capacity) is accompanied by higher water transport capacity \((K)\), because higher \(K\) has a greater pay-off where PPFD and \(N\) are higher (Figure 1).
result poses the question, however, whether plants are able to adjust \( K \) in response to the local light climate within the canopy.

### Distribution of hydraulic conductance within canopies

The determinants of leaf-specific hydraulic conductance \( (K) \) may be better understood by considering a simple one-dimensional flow model:

\[
K = \frac{A_S}{A} \frac{k_S}{h} \tag{5}
\]

where \( A_S/A \), the ratio of sapwood area to leaf area (i.e., the Huber value), \( k_S \) the sapwood permeability of the pathway to the leaf, \( h \) the length of the pathway and \( \eta \) the viscosity of water (Whitehead 1998). This equation shows that if xylem permeability is constant along the pathway from roots to leaves, \( K \) should simply be inversely proportional to path length \( (h) \), so that top canopy leaves would have lower \( K \) (Williams et al. 1996, Ryan and Yoder 1997). There are, however, ways that plants can overcome this path length effect, and even construct higher \( K \) to sun-exposed leaves at the top of the canopy. Firstly, xylem conductivity varies greatly within plants, so that small twigs near the end of the transport path have much lower conductivity (Zimmermann 1978, McCulloh and Sperry 2005). The reason for this pattern is that vessel diameter gradually decreases from the trunk base to the twigs (vessel tapering) (Mencuccini et al. 2007, Petit et al. 2010). This tapering can nearly completely compensate for the direct path length effect because most of the resistance occurs in small diameter vessels in distal twigs (Becker et al. 2000).

Furthermore, it has been shown empirically that sun branches can have higher leaf-specific conductivity \( (k_S/\eta) \) in Eq. (5)), indicating plastic responses of xylem anatomy to the light environment (Cochard et al. 1999, Lemoine et al. 2002a, 2002b).

Third, the Huber value has been observed to be higher towards the top of the canopy in \textit{Pinus sylvestris} L. (Berninger and Nikinmaa 1994, Mäkelä and Vanninen 2001), \textit{Pinus banksiana} Lamb. (Schneider et al. 2011), and four out of six angiosperm species studied by Sack et al. (2006). Interestingly, Sack et al. (2006) reported that the Huber value showed a more plastic response to within-canopy PPFD gradients than more well-studied traits like the specific leaf area.

Thus, there is evidence that plants can adjust their water transport capacity to the local light environment in canopies. However, it is unclear as to whether \( K \) can be proportional to PPFD within canopies, as predicted by our model. At the moment, very few datasets exist that can be used to test this hypothesis. Lemoine et al. (2002a) showed that leaf-specific hydraulic conductivity was nearly proportional to PPFD within a
beech canopy, but this does not necessarily imply that \( K \) was proportional to PPFD. There are likely constraints to the degree of plasticity of \( K \) within canopies. As an example of the trade-off in efficiency and safety of xylem, Domec et al. (2008) found gradual changes in pit anatomy with increased path length in very tall Douglas-fir (Pseudotsuga menziesii (Mirb.) Franco), associated with higher tolerance of low water potentials at great heights, but at a cost of reduced hydraulic conductivity with increasing height within the canopy.

Indirect evidence for variation in \( K \) within canopies comes from leaf water potential gradients. Our simulations showed that, when \( N \) and \( K \) were optimized, \( \Psi_L \) was more negative for shaded leaves, but the difference in \( \Psi_L \) between sun and shade leaves was relatively small. This suggests there is close—although not perfect—coupling between the leaf transpiration rate (\( E \)) and \( K \) within canopies. Measurements of gradients in \( \Psi_L \) in real canopies can thus be used to test our main hypothesis, that \( K \) is not optimally distributed within canopies, which leads to shallower \( N \) gradients. In a Betula pendula Roth crown, Sellin and Kupper (2005) observed much higher \( K \) in the sun canopy than the shade canopy. However, sun leaves did have lower \( \Psi_L \), suggesting that in their study, \( K \) was not proportional to PPFD. Other studies have also reported lower \( \Psi_L \) in sun leaves (Lemoine et al. 2002a), which imply that there are limitations on how \( K \) can be allocated.

More direct experimental exploration of our hypothesis is warranted. Our results suggest that an explanation for the frequently observed shallow \( N \) gradients is that the distribution of \( K \) is not optimal, due to constraints on the distribution of \( K \) within canopies. This hypothesis lends itself very well to an empirical test in real canopies. Gradients in \( N \) and \( K \) can be measured, and the difference from the optimal distribution quantified, to gain an understanding of how within-canopy distribution of water transport and nitrogen is co-ordinated. For example, if we assume that \( K \) is equal in both leaves, the model gives an optimal \( N \)-distribution that follows an approximately exponential decline with canopy depth with a decay coefficient \( (k_N) \) of between 65 and 75% of the light-extinction coefficient. For a light extinction coefficient of 0.5, predicted \( k_N \) is thus in the range 0.32–0.38. For comparison, Lloyd et al. (2010) review experimentally measured gradients of \( V_{\text{max}} \) in canopies, and found decay coefficients in the range 0.12–0.25, shallower than we predicted for \( k_N \) under the assumption of equal \( K \). Note however that in our model, assuming a path length dependent \( K \) reversed the canopy gradient in \( N \). Experimental measurements of both \( K \) and \( N \) gradients are needed to gain an understanding of how within-canopy distribution of water transport and nitrogen is co-ordinated and constrained.

It may also be necessary to take into account variation in other environmental drivers within canopies when interpreting co-variation in \( A \), \( N \), \( \Psi_L \), and \( K \), in particular VPD, air temperature and net radiation in cases where the boundary layer conductance is low (Roberts et al. 1990). In our simple toy model, we assumed that environmental drivers were constant through the canopy. We also assumed that leaf-level relationships, such as the sensitivity of \( g_L \) to \( \Psi_L \), were similar throughout the canopy. An empirical test of the hypothesis may need to quantify and account for any differences in these relationships with canopy height.

**Consequences for the ‘big-leaf’ model of canopy photosynthesis**

If total canopy nitrogen (\( N_t \)) is fixed, then the optimal allocation of \( N \) along the light gradient that maximizes total canopy \( A (A_t) \) occurs when \( dA/dN = \lambda \) everywhere in the canopy (Field 1983, Farquhar 1989). This condition follows from calculus of variations (e.g., Hildebrand 1965), and it states that \( A_t \) is reached when the marginal cost of moving \( N \) from any leaf in the canopy to another yields a decrease of \( dA_t \) in leaf 1 but an increase of the same magnitude in leaf 2, i.e., \( dA_t = -dA_t \). The optimal allocation of \( N \) follows PPFD when the light-response function is a homogeneous function, i.e., \( A(t, tN) = tA(t, N) \) (Farquhar 1989, Badeck 1995). For example, the commonly used non-rectangular hyperbola is a homogeneous function, but more complex models may not be. Calculus of variations applied to the \( N \) allocation problem can be extended to co-allocation of any number of resources (e.g., Hildebrand 1965). In our case, it yields two simultaneously operating conditions \( dA/dN = \lambda \) and \( dA/dk = \gamma \), both of which need to be satisfied to reach maximum \( A_t \). When models are more complex, they are less likely to be homogeneous functions of all limiting resources, so that a numerical solution becomes necessary. The emergence of close 1 : 1 relationships for both \( K \) and \( N \) with PPFD was surprising, considering the various non-linear functions in the model (see the Appendix). This result suggests that our coupled model is nearly homogeneous in both \( K \) and \( N \). As a result, if \( N \) and \( K \) are both assumed to be optimally distributed, canopy photosynthetic rates can be modelled using a ‘big-leaf’ approximation, similar to existing ‘big-leaf’ models of canopy photosynthesis (e.g., Sellers et al. 1996). Such a simplified implementation of the water transport limitation would be valuable for predicting forest production and carbon and water exchange. However, further empirical research is needed to quantify how far from optimal is the distribution of \( K \) within canopies, and whether optimal distributions of \( N \) and \( K \) are suitable assumptions when predicting canopy photosynthesis.

**Conclusions**

Our study showed that the optimal \( N \) distribution within plant canopies is proportional to the irradiance distribution only if hydraulic conductance, \( K \), is also optimally distributed (or if \( K \) is infinite). The optimal distribution of \( K \) is that where \( K \), \( N \) and incident irradiance \( I \) are proportional to each other. We
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hypothesize that measured deviations from the predicted optimal distribution of \( N \) could be explained by constraints on the distribution of \( K \) within canopies. Further empirical research on the allocation of \( N \) within canopies should focus on constraints to photosynthesis arising via allocation of other resources, such as water transport capacity.

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Conflict of interest

None declared.

References


**Appendix**

**Model description and numerical solution**

Leaf transpiration rate ($E$) is calculated with the vapour pressure deficit ($D$), and stomatal conductance ($g_s$) assuming saturated water vapour within the leaf:

\[ E = 1.6g_sD \]  

(A.1)

The coefficient 1.6 in the equation arises from differences in diffusivities of water vapour and CO₂. The water supply was estimated based on the soil and leaf water potential difference ($\Psi_s - \Psi_f$), and the leaf-specific conductance of the soil to leaf pathway ($K$).

\[ E = K(\Psi_s - \Psi_f) \]  

(A.2)
The dependence of the leaf CO₂ assimilation rate \( (A) \) on the intercellular CO₂ concentration \( (C_i) \) was based on the photosynthesis model of Farquhar et al. (1980):

\[
A_c = V_{\text{max}} \frac{C_i - \Gamma^*}{C_i + K_M} \quad (A.3)
\]

\[
A_j = V_j \frac{C_i - \Gamma^*}{C_i + 2\Gamma^*} \quad (A.4)
\]

\( A_c \) is the CO₂-limited rate limited by maximum RubP rate of carboxylation \( V_{\text{max}} \), \( \Gamma^* \) is the CO₂ compensation point in the absence of dark respiration \( R_d \), \( K_M \) is the effective Michaelis–Menten coefficient of Rubisco activity. These parameters were calculated following Medlyn et al. (2002).

The dependence of the potential electron transport rate \( (V_j) \) on irradiance was calculated according to

\[
V_j = \frac{1}{4} A_{\text{Q}} J_{\text{max}} - \frac{\sqrt{(A_{\text{Q}} J_{\text{max}}})^2 - 4 A_{\text{Q}} J_{\text{max}}}{2\theta} \quad (A.5)
\]

where \( A_{\text{Q}} \) is the quantum yield, \( J_{\text{max}} \) is the light-saturated rate of electron transport, \( \theta \) is the PPFD and \( \theta \) is a curvature parameter. \( V_{\text{max}}, J_{\text{max}} \) and \( R_d \) were assumed to be linearly dependent on the leaf \( N \) content:

\[
X = \frac{N}{N_{\text{ref}}} X_{\text{ref}} \quad (A.6)
\]

where \( X \) is \( V_{\text{max}}, J_{\text{max}} \) or \( R_d \) and \( X_{\text{ref}} \) the reference value at \( N_{\text{ref}} \).

Net photosynthesis was estimated as the hyperbolic minimum of \( A_c \) and \( A_j \) in order to remove discontinuity from moving light and electron transport-limited photosynthesis to Rubisco-limited photosynthesis:

\[
A_b = A_c + \frac{A_j - \sqrt{(A_c + A_j)^2 - 4 A_c A_j}}{2h} \quad (A.7)
\]

where \( h \) was set to 0.99. Net photosynthesis \( A \) was obtained by

\[
A = A_b - R_d \quad (A.8)
\]

Net photosynthesis and stomatal conductance are coupled by the basic diffusion equation:

\[
A = g_s (c_a - c_i) \quad (A.9)
\]

where \( g_s \) is the stomatal conductance estimated with the Tuzet model (Tuzet et al. 2003):

\[
g_s = g_0 + \frac{g_1 A_{\text{Q}}}{c_a - \Gamma} \left( 1 + e^{h \Psi L} \right) \quad (A.10)
\]

where \( g_0 \) is a ‘residual’ \( g_s \) (that includes cuticular conductance and stomatal leakiness), \( g_1 \) a parameter, \( C_a \) is the atmospheric CO₂ concentration (ppm), \( \Gamma \) is the CO₂ compensation point in the presence of dark respiration and the effect of \( \Psi L \) on \( g_s \) is depicted with an S-shaped curve, which has parameters \( s_f \), which controls the steepness of the s-shape, and \( \Psi f \), that controls the location of the bend. We replaced \( c_i \) appearing in the original Tuzet et al. (2003) model with \( c_a \) as it appears in most other stomatal conductance models, as we found no strong support for using \( c_i \) instead \( c_a \) and the equation is more readily solvable.

Equations (A.1), (A.2), (A.8), (A.9) and (A.10) represent five equations for five unknown variables \( (E, \Psi L, A, c_i \) and \( g_s) \), while the remainder of the parameters can be considered constant or simple functions of leaf temperature. The leaf water potential \( (\Psi L) \) was solved by numerical optimization from analytically solved \( E, A, c_i \) and \( g_s \) so that all five equations were satisfied.