The role of stomatal acclimation in modelling tree adaptation to high CO₂

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Abstract
Carbon dioxide enrichment changes the balance of photosynthetic limitations due to water, nitrogen, and light. This paper examines the role of stomata in these changes by comparing enrichment responses predicted by an optimality-based tree growth model, DESPOT, using three alternative ‘setpoints’ for stomatal acclimation: leaf water potential (ψ_l-setpoint), the ratio of intercellular to ambient CO₂ mole fraction (c_i/c_a-setpoint), and the parameters in a simple model in which stomata are controlled by H₂O and CO₂ supply and demand (linked feedback). In each scenario, stomatal conductance (gₛ) and photosynthetic capacity (Vₘ) declined, productivity and leaf area index (LAI) increased, and c_i/c_a remained within 5% of its pre-enrichment value. Height growth preceded the LAI response in the ψ_l-setpoint and linked feedback scenarios, but not in the c_i/c_a-setpoint scenario. These trends were explained in terms of photosynthetic resource substitution using the equimarginal principle of production theory, which controls carbon allocation in DESPOT: enrichment initially increased the marginal product for light, driving substitution towards light; height growth also drove substitution towards N in the ψ_l and feedback scenarios, but the inflexibility of c_i/c_a prevented that substitution in the c_i/c_a-setpoint scenario, explaining the lack of height response. Each scenario, however, predicted similar behaviour for c_i/c_a and carbon and water flux. These results suggest that ‘setpoints’ may be robust tools for linking and constraining carbon and water fluxes, but that they should be used more cautiously in predicting or interpreting how those fluxes arise from changes in tree structure and physiology.

Key words: Carbon dioxide, climate change, photosynthesis, stomata, transpiration, water potential.

Introduction
A major challenge facing plant biologists today is the need for confident predictions about plant responses to climate change, based on sound theoretical understanding and supported by experiment where possible (Steffen and Canadell, 2005). This need is especially important for trees, because forests dominate the terrestrial biosphere, in terms of both carbon stocks and carbon fluxes. However, it is also especially difficult for trees, because the long lifespans of many species make it impossible to document experimentally the long-term effects of CO₂ enrichment above present-day levels. This makes long-term forecasting of tree growth and gas exchange heavily dependent on assumptions about the character of adaptive growth regulation.

One hallmark of plant growth is the strong co-ordination between structural development and physiological functioning, often described as ‘functional balance’, for example, between sapwood and leaf area (Shinozaki et al., 1964a, b) or roots and shoots (Davidson, 1969; Thornley, 1972a, b). Many growth models incorporate functional balance as a central constraint to predict carbon allocation and thus structural adjustment (Valentine, 1985, 1999; Mäkelä, 1986, 1997, 1999; Hilbert and Reynolds, 1991; Deleuze and Houllier, 1995; Luan et al., 1996; Grote, 1998; Lo et al., 2001; Battaglia et al., 2004). The dynamic regulation of leaf gas exchange is also characterized by functional balance: stomatal behaviour co-ordinates CO₂ supply with photosynthetic demand and evaporative...
demand with hydraulic supply, leading to virtually homeo-
static control of both \( c_i/c_a \) (intercellular/ambient \([\text{CO}_2]\))
and leaf water potential, \( \psi_l \) (Wong et al., 1979, 1985a, b; Farquhar and
Sharkey, 1982; Jones, 1990; Tardieu, 1993; Saliendra et al., 1995) (a list of
symbols with definitions and dimensions is given in Table 1). These functional
balancing acts—of structural adaptation and stomatal
regulation—are deeply entangled with one another. Homeo-
balancing acts—of structural adaptation and stomatal
and dimensions is given in Table 1). These functional
responses to the leaf environment, because those structural
features determine the relative supplies of nitrogen, water,
and light needed for photosynthesis.

Very little is known, however, about how the ‘setpoints’
for \( \psi_l \) and \( c_i/c_a \) are controlled, or about their potential to
change systematically over long time scales in relation to
the environmental and structural effectors of photosyn-
thetic resource balance (Farquhar et al., 1989; Ehleringer
and Cerling, 1995; Miller et al., 2001; Miller, 2002). The
data that are available paint a varied and often contradic-
tory picture. For example, Barnard and Ryan (2003) found
that the hydraulic burdens created by height growth in
Eucalyptus saligna were compensated by structural ad-
justment of sapwood:leaf area ratio and down-regulation
of the \( \psi_l \)-setpoint, which sustained stomatal conductance,
\( g_s \), with the result that the \( c_i/c_a \)-setpoint was not lower in
taller, older trees (it was slightly higher, in fact). In
contrast, Phillips et al. (2003) found large reductions in \( g_s \),

 Condition the response of mature trees to a step increase in ambient
\( \text{CO}_2 \) mole fraction (\( c_a \)) from 370 ppm to 570 ppm was
simulated. This was meant to mimic FACE experiments,
to allow the early stages of simulated responses to be
compared with empirical data. A tree growth model called
DESPOT (Buckley and Roberts, 2006a), in which carbon allocation is governed by
the equimarginal principal of production theory, and
carbon gain is calculated from a big-leaf Farquhar
(1980) model with stomatal conductance prescribed by
a priori empirical constraints. Instead, they emerge from a sequence
of carbon allocation decisions that are chosen by

### Table 1. List of symbols used in this paper, in order of appearance

<table>
<thead>
<tr>
<th>Name</th>
<th>Symbol</th>
<th>Dimensions</th>
</tr>
</thead>
<tbody>
<tr>
<td>Intercellular ( \text{CO}_2 ) mole fraction</td>
<td>( c_i )</td>
<td>ppm</td>
</tr>
<tr>
<td>Ambient ( \text{CO}_2 ) mole fraction</td>
<td>( c_a )</td>
<td>ppm</td>
</tr>
<tr>
<td>Bulk leaf water potential</td>
<td>( \psi_l )</td>
<td>MPa</td>
</tr>
<tr>
<td>Stomatal conductance to ( \text{H}_2\text{O} )</td>
<td>( g_s )</td>
<td>mol \text{air m}^{-2} \text{s}^{-1}</td>
</tr>
<tr>
<td>Leaf net assimilation rate</td>
<td>( A )</td>
<td>( \mu \text{mol CO}_2 \text{ m}^{-2} \text{s}^{-1} )</td>
</tr>
<tr>
<td>Leaf-level transpiration rate</td>
<td>( E )</td>
<td>( \text{mmol H}_2\text{O m}^{-2} \text{s}^{-1} )</td>
</tr>
<tr>
<td>Leaf photosynthetic nitrogen content</td>
<td>( N )</td>
<td>( \text{mmol N m}^{-2} )</td>
</tr>
<tr>
<td>Leaf-level incident irradiance (PPFD)</td>
<td>( I )</td>
<td>( \mu \text{E m}^{-2} \text{s}^{-1} )</td>
</tr>
<tr>
<td>Marginal product for water</td>
<td>( \mu_e )</td>
<td>( \mu \text{mol CO}_2 \text{ mmol}^{-1} \text{H}_2\text{O} )</td>
</tr>
<tr>
<td>Marginal product for nitrogen</td>
<td>( \mu_n )</td>
<td>( \mu \text{mol CO}_2 \text{ mmol}^{-1} \text{N} )</td>
</tr>
<tr>
<td>Marginal product for light</td>
<td>( \mu_l )</td>
<td>( \mu \text{mol CO}_2 \text{ mmol}^{-1} )</td>
</tr>
<tr>
<td>Electron transport capacity</td>
<td>( I_m )</td>
<td>( \mu \text{mol} \text{ e} \text{ m}^{-2} \text{s}^{-1} )</td>
</tr>
<tr>
<td>Carboxylation capacity</td>
<td>( V_m )</td>
<td>( \mu \text{mol CO}_2 \text{ m}^{-2} \text{s}^{-1} )</td>
</tr>
<tr>
<td>Leaf-specific hydraulic conductance</td>
<td>( K_L )</td>
<td>( \text{mmol H}_2\text{O m}^{-2} \text{s}^{-1} \text{MPa}^{-1} )</td>
</tr>
<tr>
<td>Leaf-air ( \text{H}_2\text{O} ) vapour mole fraction difference</td>
<td>( D )</td>
<td>( \text{mmol H}_2\text{O mol}^{-1} \text{air} )</td>
</tr>
<tr>
<td>Residual photosynthetic capacity</td>
<td>( A_i )</td>
<td>( \mu \text{mol CO}_2 \text{ m}^{-2} \text{s}^{-1} )</td>
</tr>
<tr>
<td>Leaf turgor pressure</td>
<td>( P )</td>
<td>MPa</td>
</tr>
<tr>
<td>Sensitivity of ( g_s ) to product of ( P ) and ( A_i )</td>
<td>( F )</td>
<td>( \mu \text{mol} \text{ air MPa}^{-1} \text{mmol}^{-1} \text{CO}_2 )</td>
</tr>
<tr>
<td>Maximum leaf turgor pressure</td>
<td>( P_m )</td>
<td>MPa</td>
</tr>
<tr>
<td>Leaf area index</td>
<td>( LAI )</td>
<td>( \text{m}^2 \text{m}^{-2} )</td>
</tr>
<tr>
<td>Net primary productivity</td>
<td>( NPP )</td>
<td>( \text{kg} \text{ C m}^{-2} \text{s}^{-1} )</td>
</tr>
</tbody>
</table>
a numerical algorithm to satisfy a single goal function, which is to maximize carbon gain in the next time step.

**How DESPOT responds to CO₂ enrichment**

A large step increase of atmospheric CO₂ initiates a cascade of adaptive responses in leaf physiology and plant structure. In order for this adaptive cascade to make the best use of the extra CO₂, in the sense of maximizing the response of net carbon gain, it must satisfy a rule known as the equimarginal principle (see any microeconomics text). This principle states that the ratio of marginal product (the sensitivity of carbon gain to a given limiting resource, such as water) to marginal cost (the additional carbon investment needed to procure more of that limiting resource) should be the same for each photosynthetic resource, provided the responses of carbon gain to each resource, and of each resource to C investment, are convex. The marginal products are defined by Equation 1:

\[
\mu_e = \frac{\partial A}{\partial E}, \quad \mu_N = \frac{\partial A}{\partial N}, \quad \mu_I = \frac{\partial A}{\partial I}
\]

where A is net CO₂ assimilation rate and E, N, and I are transpiration rate, photosynthetic N content, and incident irradiance, respectively. DESPOT uses a big-leaf approach, so the \( \mu \) are identical for leaf and canopy level variables. Adaptation to CO₂ enrichment in DESPOT is directed by the equimarginal principle. Because this principle is based on co-ordinating marginal products and marginal costs, which in turn emerge from the optimization of carbon allocation with respect to carbon gain.

This leaves two degrees of freedom in the calculations of carbon gain, however: the ratio of electron transport capacity to carboxylation capacity \( J_m/V_m \) and stomatal conductance. To reduce the analysis presented here to a single degree of freedom, \( J_m/V_m \) will be treated as a constant — acknowledging that enrichment often alters this ratio (Ainsworth and Long, 2005), but leaving analysis of those effects for further work and focusing instead on stomatal control. Three alternative assumptions for constraining stomatal conductance will be explored in the present study:

- (i) \( \psi_t \)-setpoint: leaf water potential is assumed invariant over growth time scales. Transpiration is calculated from soil–leaf water potential gradient, given the leaf-specific hydraulic conductance \( K_L \), which is calculated from structural properties such as sapwood area, fine root biomass, and tree height. \( g_s \) is calculated from the transpiration rate assuming fixed evaporative demand \( D \). The published form of DESPOT used this assumption, on the grounds that \( \psi_t \) is physically bounded in the negative direction by the threshold for runaway xylem embolism. However, the direct stomatal response to CO₂ enrichment reduces water loss, potentially shifting \( \psi_t \) in the positive direction and thus weakening the rationale for using a fixed \( \psi_t \) to constrain stomatal control in the case of CO₂ enrichment responses. Two other alternatives are outlined below.

- (ii) \( c/I_c \)-setpoint: the ratio \( c/I_c \) is assumed to be constant. The assimilation rate, \( A \), is calculated from \( c_i \) given \( c_a \) and structurally determined values for irradiance \( E \) (calculated from leaf area index (LAI) using Beer’s Law) and photosynthetic capacity \( A_r \) (based on canopy N content, which is simulated dynamically based on uptake by fine roots, N requirements for tissues other than leaves, and senescence losses). \( g_s \) is then calculated from \( A \), \( c_i \), and \( c_a \).

- (iii) Linked feedback: stomata respond directly to the balance of both CO₂ and H₂O supply and demand through linked feedback responses, as postulated in the models of Jarvis and Davies (1998) and Buckley et al. (2003). Simple measures of the balance of CO₂ and H₂O supply and demand are, respectively, the residual photosynthetic capacity, \( A_r \) (the amount \( A \) would increase if \( c_i \) equaled \( c_a \)), and leaf turgor pressure, \( P \). Assuming \( g_s = FPA_r \), where \( F \) is a parameter, and using \( P = P_m - E/K_L = P_m - g_s D/K_L \), where \( P_m \) is maximum leaf turgor (osmotic pressure plus soil water potential), this implies

\[
g_s = \frac{P_m F K_L A_r}{K_L + D F A_r}
\]

In this scenario, the parameters \( P_m \) and \( F \) are assumed to be conserved by long-term stomatal acclimation, so they are analogous to the ‘setpoints’ in the other scenarios. Note that the parameter \( F \) incorporates both stomatal density and the sensitivity of guard cell osmotic pressure to \( P \) and \( A_r \).

Simulations were performed in DESPOT using each of these alternatives, with the following values for each setpoint in their respective simulations: for the \( \psi_t \)-setpoint scenario, \( \psi_t = -1.0 \text{ MPa} \) (the value used in the original publication of DESPOT); for the \( c/I_c \)-setpoint scenario, \( c/I_c = 0.65 \) (the value from the \( \psi_t \)-setpoint scenario at the time of CO₂ enrichment); and for the linked-feedback scenario, \( P_m = 1.2 \text{ MPa} \) and \( F = 1.0 \) mol air MPa⁻¹ μmol⁻¹ CO₂ (these values were chosen to produce pre-enrichment values of \( \psi_t \) and \( c/I_c \) similar to those in the other two scenarios). \( \psi_t \), \( c/I_c \), \( P_m \), and \( F \) were calculated in each scenario, to determine how these quantities vary when one of them is held constant by assumption. The marginal...
products (Eqn 1) were also calculated to illustrate how the economic landscape of tree growth differs under each stomatal acclimation scenario.

Results

Figures 1–5 show the effects predicted by DESPOT for a step increase in atmospheric CO₂ mole fraction \((c_a)\) from 370 ppm to 570 ppm. The initial response is dominated by an increase in height growth (Fig. 1a) in the \(\psi_l\)-setpoint and linked-feedback scenarios, but by an increase in LAI (Fig. 1b) in the \(c_i/c_a\)-setpoint scenario. LAI declines in the first year after enrichment in the \(\psi_l\) and feedback scenarios, then increases steadily, whereas height growth never responds significantly in the \(c_i/c_a\) scenario. All three scenarios predict decreased allocation to fine roots, whether expressed relative to leaf carbon (Fig. 1c) or sapwood C (Fig. 1d).

All three scenarios also predict declines in stomatal conductance \((g_s, \text{Fig. 2a})\) and photosynthetic capacity [carboxylation capacity, \(V_m, \text{Fig. 2b}\)] (electron transport capacity, \(J_m\), is not independent of \(V_m\) in this model). Incident photosynthetic irradiance per unit leaf area \((I, \text{Fig. 2c})\) declines immediately in the \(c_i/c_a\) scenario, but initially rises in the \(\psi_l\) and feedback scenarios as a result of the initial drop in LAI; irradiance eventually drops below pre-enrichment values in the \(\psi_l\) and feedback cases, but by a smaller amount than \(g_s\) or \(V_m\). In all cases, net primary productivity \((\text{NPP, Fig. 3a})\) increases strongly at first before declining somewhat and eventually settling at a stimulation of \(\sim 18–21\%\). Stand-level transpiration (Fig. 3b) declines by \(25\%\) in all scenarios after 10 years, before diverging somewhat after 20 years and then converging again such that the net decline after 100 years is \(21\%\) for the \(\psi_l\) and \(c_i/c_a\) scenarios, and \(24\%\) for the feedback scenario (Fig. 3b).

Trajectories for \(\psi_l, c_i/c_a, P_m, \text{ and } F\) are presented in Fig. 4a–d, respectively; in each panel, one trajectory is simply a horizontal line, representing the simulation in which that parameter was treated as a constant. Leaf water potential increases (moves towards zero) by \(5\%\) in the linked-feedback scenario (dashed line in Fig. 4a), or by \(\sim 25\%\) in the \(c_i/c_a\)-setpoint scenario (dotted line in Fig. 4a). \(c_i/c_a\) fluctuates somewhat in the \(\psi_l\)-setpoint scenario before increasing by \(3\%\) after 50 years (solid line in Fig. 4a); in the linked-feedback scenario, \(c_i/c_a\) declines by \(5\%\) after 30 years, but then slowly increases to within \(3\%\) of its pre-enrichment value after 50 years. To maintain a fixed set-point for either \(\psi_l\) or \(c_i/c_a\) after enrichment, one of the parameters of the linked-feedback model (Eqn 2) would have to decline: the \(\psi_l\)-setpoint scenario requires either a \(6\%\) decline in \(P_m\) or a \(16\%\) decline in \(F\) after 50 years (solid lines in Fig. 4b and c, respectively), whereas the \(c_i/c_a\)-setpoint scenario requires declines of \(22–29\%\) in \(P_m\) or of \(50–60\%\) in \(F\) (dotted lines in Fig. 4b and c, respectively).

Figure 5 shows trajectories predicted for the marginal products for water, nitrogen, and light \((\mu_w, \mu_n, \text{ and } \mu_l)\); solid, dashed, and dotted lines in Fig. 5, respectively; Eqn 1), under each stomatal acclimation scenario. The general trend is identical in each scenario: \(\mu_l\) increases strongly at first, then drops to near its initial value, while
and \( l_1 \) but remain elevated. The eventual relative increase is greatest for \( l_n \), followed by \( l_e \) and \( l_i \). In the \( c_i/c_a \)-setpoint scenario (Fig. 5b), \( l_e \) and \( l_n \) do not change after the initial response to enrichment, whereas \( \mu_e \) and \( \mu_n \) both fluctuate after enrichment in the \( \psi_1 \) and feedback scenarios (Fig. 5a and c, respectively), with \( \mu_n \) decreasing and \( \mu_e \) gradually increasing during height growth.

**Discussion**

No significant change in the ratio of \( c_i/c_a \) was predicted by DESPOT after several years of CO\(_2\) enrichment, for any of the three alternative 'setpoint' assumptions used to constrain stomatal acclimation—\( c_i/c_a, \psi_1 \), or the parameters of the linked hydraulic–biochemical feedback model for \( g_s \) (Eqn 2). This result is consistent with many data showing that the co-ordination of stomatal conductance and photosynthesis is usually not substantially altered by CO\(_2\) enrichment (Ellsworth, 1999; Medlyn et al., 2001; Schafer et al., 2003; Herrick et al., 2004; Ainsworth and Long, 2005). Several other predictions common to all three scenarios are also consistent with most observations from FACE experiments on trees (Ainsworth and Long, 2005): a decline in photosynthetic capacity \( (V_m) \), a somewhat larger decline in \( g_s \), an eventual increase in LAI, and an enhancement of NPP that is greatest in the first year or two after enrichment, but which persists indefinitely at 14–21% above pre-enrichment values (Table 2).

Another prediction common to all three scenarios, that allocation to fine roots decreases relative to allocation to leaves or to sapwood, contradicts some results (Hyvonen et al., 2007). One possible explanation for this is the lack of a mechanism for negative feedback between increased growth and nutrient availability in the model used here. However, reported enrichment responses for below-ground allocation are highly variable, with strong responses typically found in nutrient-limited conditions (Norby et al., 2004) and small and ambiguous responses in the absence of container effects or prior nutrient limitations (Norby et al., 1999; Tingey et al., 2000; Hyvonen et al., 2007). The fact that similar trends were predicted by each acclimation scenario for fine root allocation and NPP does suggest, at any rate, that variation in below-ground allocation responses is not related to variation in the character of stomatal acclimation, and that
none of the physiological constraints built into DESPOT should inherently prevent a sustained productivity enhancement of the same order as that observed in several forest FACE experiments (23 ± 2%) (Norby et al., 2005).

The adaptive character of these responses can be interpreted in terms of changes in the sensitivities of carbon gain to water, nitrogen, and light (the marginal products \( \mu_w, \mu_n, \) and \( \mu_l \), respectively; Eqn 1 and Fig. 5), by reference to the equimarginal principle of production theory, which governs carbon allocation in the growth model used here. This principle states that the ratio of marginal product to marginal carbon cost should be the same for each photosynthetic resource. CO2 enrichment initially causes a very large increase in \( \mu_l \) relative to \( \mu_e \) and \( \mu_n \) (Fig. 5). Therefore, equimarginality requires either a shift in carbon allocation towards light capture, which would increase the marginal carbon cost of light, or an increase in leaf-level irradiance relative to \( V_m \) and \( g_s \), which would reduce the marginal product for light relative to those for nitrogen and water. The increase in LAI (Fig. 1b) increases light capture, which works towards the first objective, and the reductions in \( V_m \) and \( g_s \) (Fig. 2a, b) both work towards the second objective. Enrichment also increases \( \mu_n \) more than
explains why nitrogen for water—or equivalently, of CO2 demand for the equimarginal principle requires substitution of light and/or order for height growth to be economically efficient, the height growth preferentially increases the marginal car-

growth followed by an increase in LAI, whereas the scenarios predicted a strong initial response of height respond in the feedback scenarios. The reason height growth did not cement—are driven by the initial increase in Both of these responses—height growth and LAI enhan-

<table>
<thead>
<tr>
<th>Response to CO2 enrichment (%)</th>
<th>g_s</th>
<th>V_m</th>
<th>LAI</th>
<th>NPP</th>
<th>c_i/c_a</th>
</tr>
</thead>
<tbody>
<tr>
<td>Observedc</td>
<td>All tree species</td>
<td>-15.6</td>
<td>-6.1</td>
<td>+21.0</td>
<td>+28.0b</td>
</tr>
<tr>
<td>Duke forest</td>
<td>-17.1</td>
<td>-5.9</td>
<td>0d</td>
<td>+24e</td>
<td>0f</td>
</tr>
<tr>
<td>Predicted by DESPOTψ1-setpoint scenario</td>
<td>2 years</td>
<td>-17.3</td>
<td>-4.4</td>
<td>-7.7</td>
<td>+27.5</td>
</tr>
<tr>
<td></td>
<td>5 years</td>
<td>-19.1</td>
<td>-12.0</td>
<td>-4.9</td>
<td>+22.3</td>
</tr>
<tr>
<td></td>
<td>10 years</td>
<td>-22.6</td>
<td>-14.6</td>
<td>-2.2</td>
<td>+19.4</td>
</tr>
<tr>
<td></td>
<td>50 years</td>
<td>-29.7</td>
<td>-28.3</td>
<td>+14.9</td>
<td>+21.0</td>
</tr>
<tr>
<td>c_i/c_a-setpoint scenario</td>
<td>2 years</td>
<td>-30.4</td>
<td>-23.0</td>
<td>+22.9</td>
<td>+35.8</td>
</tr>
<tr>
<td></td>
<td>5 years</td>
<td>-38.1</td>
<td>-31.5</td>
<td>+12.8</td>
<td>+6.7</td>
</tr>
<tr>
<td></td>
<td>10 years</td>
<td>-35.3</td>
<td>-28.4</td>
<td>+14.4</td>
<td>+15.0</td>
</tr>
<tr>
<td></td>
<td>50 years</td>
<td>-37.9</td>
<td>-31.3</td>
<td>+22.6</td>
<td>+19.8</td>
</tr>
<tr>
<td>Linked-feedback scenario</td>
<td>2 years</td>
<td>-18.6</td>
<td>-5.4</td>
<td>-6.8</td>
<td>+26.1</td>
</tr>
<tr>
<td></td>
<td>5 years</td>
<td>-18.8</td>
<td>-13.2</td>
<td>-5.6</td>
<td>+20.2</td>
</tr>
<tr>
<td></td>
<td>10 years</td>
<td>-20.5</td>
<td>-14.8</td>
<td>-4.8</td>
<td>+16.6</td>
</tr>
<tr>
<td></td>
<td>50 years</td>
<td>-30.6</td>
<td>-23.0</td>
<td>+8.2</td>
<td>+18.2</td>
</tr>
</tbody>
</table>

a Averages reported by Ainsworth and Long (2005) (AL), except which are from Schafer et al. (2003). b Reported by Ainsworth and Long (2005) as dry matter production. c A separate value was not reported by Ainsworth and Long (2005) for tree species; this is the value for all functional types. 2, 5, 10, and 50 years refer to values after enrichment began.

| Table 2. Comparison of enrichment responses observed for tree species in FACE experiments and those predicted by DESPOT using three different assumptions to constrain long-term stomatal acclimation |

μ_s; this dictates an increase in V_m relative to g_s, which explains why g_s declines more than V_m (Fig. 2a, b).

There was one fundamental difference in the enrichment responses predicted for the alternative scenarios for stomatal acclimation. The ψ_l-setpoint and linked-feedback scenarios predicted a strong initial response of height growth followed by an increase in LAI, whereas the c_i/c_a-setpoint scenario predicted an immediate increase in LAI with no associated height growth response (Fig. 1a, b). Both of these responses—height growth and LAI enhancement—are driven by the initial increase in μ_s, which increases the profitability of light capture. Height growth eventually becomes less profitable due to increasing hydraulic burdens and respiratory costs, so allocation eventually shifts to leaf area production in the ψ_l and feedback scenarios. The reason height growth did not respond in the c_i/c_a-setpoint scenario involves the effect on economic flexibility of treating c_i/c_a as a rigid setpoint. Height growth preferentially increases the marginal carbon cost of water (Buckley and Roberts, 2006b) so, in order for height growth to be economically efficient, the equimarginal principle requires substitution of light and/or nitrogen for water—or equivalently, of CO2 demand for CO2 supply. Treating c_i/c_a as a rigid setpoint precludes the required plasticity in CO2 supply and demand. This makes height growth inherently less efficient in the c_i/c_a-setpoint scenario, so DESPOT’s optimization routine chooses to enhance leaf area rather than height growth in that scenario. The economic effect of this constraint is illustrated by the fact that μ_a and μ_e remain constant in the c_i/c_a scenario (Fig. 5b), whereas they change with respect to one another in relation to height growth dynamics in the ψ_l and feedback scenarios (Fig. 5a, c).

This does not imply that the c_i/c_a-setpoint scenario is less representative of how real trees adapt to CO2 enrichment, however. Reported LAI responses to enrichment in tree species are variable, with larger responses typically found for young trees in open stands (Kellomaki and Wang, 1997) or for mature stands with lower LAI (Norby et al., 2005), and little or no response in mature forests with high LAI (Norby et al., 2003; Schafer et al., 2003). The present analysis suggests this variation may relate to plasticity in height growth, such that the initial responses of LAI and height to enrichment are anti-

correlated among species. There are reasons to suspect that DESPOT’s assumption of total plasticity in carbon allocation fractions overestimates the responsiveness of height growth to environmental change, particularly in mature trees. First, small reductions in either the flexibility or the precision of DESPOT’s allocation algorithm cause NPP to decline with age, which the model does not otherwise predict (Buckley and Roberts, 2006a)—hinting that the model may indeed overestimate the plasticity of growth form in older trees. Secondly, McDowell et al. (2005) reported that carbon isotope discrimination was less sensitive to environmental change in tall Douglas-fir (Pseudotsuga menziesii) trees than in short trees, which they suggested may reduce the sensitivity of tall or otherwise hydraulically burdened trees to climate change.

Changes in stomatal function required to maintain ψ_l or c_i/c_a-setpoints

The alternative setpoints can also be compared on the basis of their implications for stomatal physiology, because specific changes in the anatomical determinants of stomatal function are required to maintain fixed setpoints for either ψ_l or c_i/c_a as tree structure and physiology adapt to CO2 enrichment. A model based on the premise that stomatal control involves direct feedback responses to leaf turgor pressure and residual photosynthetic capacity (the ‘linked-feedback’ scenario, Eqn 2) (Jarvis and Davies, 1998; Buckley and Mott, 2002; Buckley, 2005) was used to infer how the parameters of those putative feedback responses—maximum turgor (P_m) and stomatal sensitivity (F) to the effectors of guard cell osmotic pressure—must vary during enrichment responses to preserve setpoints for ψ_l or c_i/c_a. The parameter F captures changes in both stomatal density and the gain of guard cell signal transduction. The ψ_l-setpoint scenario requires a 3–6% decline in P_m or a 9–16% decline in F,
whereas the $c_l/c_a$-setpoint scenario requires a 25% decline in $P_m$ or a 75% decline in $F$ (Fig. 4b, c).

These predictions are difficult to validate or refute empirically, because little is known about the long-term acclimation in parameters that describe processes or properties directly involved in stomatal control. Stomatal density (embedded in $F$) is well known to decline in response to increasing $c_a$ during growth; however, that response appears to saturate close to present-day ambient levels, and FACE experiments typically show little or no change in stomatal density (Medlyn et al., 2001; Herrick et al., 2004; Tricker et al., 2005). Similarly, Herrick et al. (2004) found no effect of enrichment on the sensitivity of $g_s$ to soil moisture or evaporative gradient in sweetgum ($Liquidambar styraciflua$) trees in the Duke FACE experiment, and Leakey et al. (2006) found that short-term stomatal responses in enriched soybean ($Glycine max$) plants were accurately described using the Ball–Berry model with pre-enrichment parameter values. These results suggest, but by no means prove, that the reduced parameters of stomatal function are not strongly sensitive to CO2 enrichment above present-day levels.

This supports the linked-feedback scenario, which assumes that $P_m$ and $F$ do not respond to enrichment. In contrast, the $\psi_l$ and $c_l/c_a$-setpoint scenarios both require either $P_m$ or $F$ to change after enrichment. The required change is smaller for $P_m$ than for $F$ in both cases, suggesting that either setpoint scenario is more likely to involve osmotic down-regulation (i.e. reductions in maximum leaf turgor, $P_m$) than reductions in stomatal density or guard cell metabolic sensitivity. Additionally, much smaller changes in $P_m$ and $F$ are required to preserve a constant setpoint for $\psi_l$ than for $c_l/c_a$. The matter could be clarified by characterizing in greater detail how enrichment affects stomatal properties in trees, ideally in the language of a process-based model. It is interesting to note that the linked-feedback scenario (fixed $P_m$ and $F$) predicts trajectories for both $\psi_l$ and $c_l/c_a$ that remain within $\pm 5\%$ of their pre-enrichment values (Fig. 5a, b). This prediction is intriguing because it shows that conservative behaviour in the apparent hydraulic and biochemical setpoints of stomatal control can emerge passively from local feedback regulation—without the need for any systemic co-ordination or acclimation of stomatal physiology, and even after a 200 ppm increase in $c_a$.

**Recommendations for model-based prediction and analysis**

The analysis presented above leads to two conclusions relevant to the choice of stomatal constraints in models used to interpret or simulate tree responses to CO2 enrichment. First, the adaptive landscape on which growth and gas exchange are regulated is strongly affected by *a priori* constraints on the phenomenological outcomes of structural and physiological adaptation. A constant ratio of $c_l/c_a$, for example, precludes resource substitution between nitrogen and water, which in turn leads to very different predictions for both the timing and magnitude of climatory adjustments in LAI and tree height to enrichment. Secondly, if constraints are based on the regulatory processes that are hypothesized to give rise to homeostatic setpoints, rather than on the assumption that those setpoints will be preserved, the long-term behaviour that emerges for those setpoints turns out to be quite conservative anyway. The recommendation arising from these conclusions depends on the reason for which one is simulating tree responses to CO2 in the first place. Any process-based model, even the simple conceptual ‘linked-feedback’ model used here, increases computational time and complexity, and the results of this study suggest that the phenomenology that emerges from such models is very similar to that embedded in setpoint assumptions anyway. Therefore, when the purpose of modelling is simply to project gas exchange dynamics under high CO2, this study offers no reason to abandon the simplicity and computational efficiency offered by setpoint assumptions. If, on the other hand, the purpose of modelling is to understand the interplay between physiological and structural responses to CO2 enrichment—particularly from an adaptive or economic perspective—a more wary approach to ‘setpoints’ is warranted. Understanding of these issues could be improved by experiments designed to characterize stomatal acclimation in terms of reduced properties related to the processes involved in stomatal control, and by experiments designed to quantify the plasticity of carbon allocation, particularly height growth, with respect to the drivers of photosynthetic resource balance.

**Conclusions**

Adaptive tree responses to a step increase in ambient CO2 from 370 ppm to 570 ppm were simulated with an optimality-based growth model, using three alternative ‘setpoints’ for stomatal acclimation: leaf water potential ($\psi_l$), the ratio of intercellular to ambient CO2 mole fraction ($c_l/c_a$), or the parameters of a simple feedback model for stomatal control (Eqn 2). None of the scenarios predicted large changes in the co-ordination of stomatal conductance with photosynthesis (as $c_l/c_a$) in the first decade after enrichment. All scenarios predicted declines in $g_s$ and $V_m$, and increases in NPP and LAI as reported in FACE experiments. The LAI response was initially offset by diversion of carbon for height growth in the $\psi_l$ and feedback scenarios, but not in the $c_l/c_a$ scenario. Both responses (LAI and height growth) served to re-establish equimarginality by shifting photosynthetic resource balance towards light, after the CO2 enrichment-induced jump in the marginal product for light. Height growth also requires
substitution of N for water, which is impossible if c_l/c_w is fixed, explaining the lack of height response in the c_l/c_w scenario. Conservative behaviour for c_l/c_w was predicted in the ψ_l-setpoint and feedback scenarios, and all scenarios predicted similar long-term behaviour for stand-level carbon and water fluxes and above- versus below-ground partitioning. These results suggest that c_l/c_w or ψ_l could be used as setpoints for constraining flux projections. However, they also highlight the importance of a priori constraints on allocation and coordination in determining patterns of structural and physiological adjustment. This suggests that the adaptive or physiological basis of those patterns cannot be fully understood without a better understanding of the process basis of stomatal acclimation itself.

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Appendix

Gas exchange model

The calculations described in this paper, including those embedded in the DESPOT model, were based on the photosynthesis model of Farquhar et al. (1980), combined with simplified Fick’s Law-based diffusion models for CO₂ and water vapour flux between leaves and the atmosphere. Net CO₂ assimilation rate is defined by the intersection of mesophyll demand (A_d) and stomatal diffusion (supply, A_s):

\[ A = A_d \cap A_s \]  \hspace{1cm} (A1)

\[ A_s = g(c_a - c_l) \] \hspace{1cm} (A2)

\[ A_d = \text{minh}(A_v, A_j, \theta_A) \] \hspace{1cm} (A3)

where g is total conductance to CO₂, minh(y,z,θ) is defined as the lesser solution X of 0(X²−(y+z)X+yz=0, and A_v and A_j are RuBP carboxylation- and regeneration-limited assimilation rates, respectively:

\[ A_v = \frac{V_m(c_l - \Gamma_s)}{c_l + K_r} - R_d \] \hspace{1cm} (A4)

\[ A_j = \frac{1}{4} \frac{J(c_l - \Gamma_s)}{c_l + 2\Gamma_s} - R_d \] \hspace{1cm} (A5)

where \( V_m \) is maximum carboxylation velocity, \( R_d \) is the rate of mitochondrial respiration that continues in the dark (assumed equal to 0.01\( \times V_m \)), \( K_r \) is the effective Michaelis constant for carboxylation by Rubisco, \( \Gamma_r \) is the photorespiratory compensation point, and \( J \) is the potential electron transport rate, given by \( J = \min(\sqrt{J_m}, \phi I, \theta_I) \); \( J_m \) is the maximum potential electron transport rate, \( I \) is incident PPFD, \( \phi \) is effective maximum quantum yield of electron transport from incident PPFD, \( \Gamma_r \) is a curvature parameter (0.9). \( V_m \) and \( J_m \) are considered proportional to leaf N content, \( N \) (\( V_m = \chi_r N \) and \( J_m = \chi_r N \)), which in turn is the ratio of canopy N content to leaf area (\( N = N_i/L \)). In DESPOT, \( \chi_r = 1.9 \mu \text{mol e}^- \text{mmol}^{-1} \) N and \( \chi_r = \chi_r / (2.1 \text{ e}^-/\text{CO}_2) \). Incident PPFD, \( I \), is annual canopy PPFD capture divided by leaf area and by a time integration factor \( Y \) [\( Y \) represents, in essence, the number of seconds of positive photosynthesis each year; see Buckley and Roberts (2006a) for details] (\( I = I_L/L \)). g is annual canopy transpiration (\( E_d \)) divided by leaf area, \( Y \) and 1.6\( \times \)D [\( g = E_d / (1.6 \times D_L Y) \)], where D is leaf–air H₂O mole fraction difference and 1.6 converts from H₂O to CO₂ diffusivity. Note that this assumes negligible boundary layer resistance. Calculating \( E, N, \) and \( I \) from \( E_d, N_i, \) and \( I_i \) in this way is equivalent to a ‘big-leaf’ assumption, i.e. the gas exchange model is assumed to be scale-invariant (Farquhar, 1989; Field, 1991).

Note that for \( \theta_A < 1 \), the intersection of Eqs A2 and A3 creates a quartic expression for \( c_l \), which can be solved directly as described in any mathematics text. It would be simpler to calculate the intersections of \( A_v \) with \( A_j \) and \( A_d \) separately and then take the minimum; however, this is strictly incorrect if \( \theta_A < 1 \), and it creates discontinuous marginal products if \( \theta_A \) is assumed equal to 1. In reality, there will always be some co-limitation, however small, between carboxylation and regeneration, and although accommodating \( \theta_A < 1 \) is more difficult computationally, meaningful analysis of photosynthetic resource economics is otherwise impossible. In the present study \( \theta_A \) was assumed to be equal to 0.9.

Marginal products

The marginal products from water, nitrogen, and light (transpiration, photosynthetic leaf N content, and incident PPFD, to be precise) can be calculated from the gas exchange model described above. Only the final expressions are given here; see Buckley et al. (2002) for complete derivations. The marginal product from water use is

\[ \mu_w = \frac{\partial A}{\partial E} \left( \frac{A}{E} \right) \left( \frac{k}{g + k} \right) \] \hspace{1cm} (A6)

where k is the slope of the photosynthetic demand curve, calculated as described below (Eqs A12–A14). Note that, like the gas exchange model itself, Eqn A6 assumes that the canopy is well coupled to the atmosphere. This avoids complications arising from the different ratios of
diffusivities for H₂O and CO₂ for diffusion and bulk flow, and from effects of changes in leaf temperature on VPD and photosynthetic parameters. Expressions that accommodate such effects are given by Buckley et al. (2002). The marginal product from photosynthetic N use is a function of two values, $\mu_{n,v}$ and $\mu_{n,j}$, representing carboxylation- and regeneration-limited conditions, respectively:

$$
\mu_n = \frac{\mu_{n,j} (A - A_v) + \mu_{n,v} (A - A_j)}{20 \sigma A - A_v - A_j}
$$

(A7)

\[
\frac{\partial A_i}{\partial N} = \frac{g}{g+k} \left[ \frac{\left( A_j + R_d \right)}{J} \right] \left[ \frac{J - \phi I}{20 J - J_m - \phi I} \right] \chi_j - 0.01 \chi_v
\]

(A8)

$$
\frac{\partial A_v}{\partial N} = \frac{g}{g+k} \left( \frac{A_v}{N} \right)
$$

(A9)

Equation A7 is found by implicitly differentiating the $minh$ function. The marginal product from PPFD requires a similar calculation, except that the value corresponding to carboxylation-limited conditions is simply zero ($\mu_{n,v}=0$):

$$
\mu_i = \frac{\mu_{i,j} (A - A_v)}{20 \sigma A - A_v - A_j}
$$

(A10)

$$
\frac{\partial A_j}{\partial I} = \frac{g}{g+k} \left( \frac{A_j + R_d}{J} \right) \left[ \frac{J - J_m}{20 J - J_m - \phi I} \right] \phi
$$

(A11)

Finally, the slope of the demand curve, $k$, is calculated in similar fashion, from values ($k_v$ and $k_j$) representing the different limitations:

$$
\frac{\partial A}{\partial c_1} = \frac{\partial A_i}{\partial c_1} = \frac{k_i (A - A_v) + k_v (A - A_j)}{20 \sigma A - A_v - A_j}
$$

(A12)

$$
V_m (K' + \Gamma*)
$$

\[ (c_1 + K')^2 \]

(A13)

$$
\frac{3}{4} \frac{J \Gamma *}{(c_1 + 2 \Gamma*)^2}
$$

(A14)

References


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