

Models of photosynthesis need to and can be upgraded to include the effects of drought, phenological changes, sink activity and carbohydrate accumulation on the light exposure/photosynthetic capacity relationship

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Introduction

Biochemical models of leaf photosynthesis, based on the seminal work of Farquhar et al. (1980), have been widely used to compare photosynthetic performance among plant species and to analyse photosynthetic acclimation to high CO₂ concentrations or growth irradiance. Such functional models may also be coupled to radiation transfer models, which are structural models, to simulate photosynthesis at the canopy level. FSPM based on coupled models of leaf photosynthesis and radiation transfer are also used in global change modelling. Such coupled models are based on two key relationships, the first between the amount of leaf nitrogen per unit leaf area (N_a) and light exposure or leaf age, and the second between leaf photosynthetic capacity (essentially the light saturated rate of electron transport, J_{max} , and the maximal rate of carboxylation, V_{cmax}) and N_a . These fundamental relationships are implicitly assumed to be constants. Moreover it is generally assumed that V_{cmax}/J_{max} is stable.

Although there is an increasingly large body of evidence that drought impacts negatively photosynthetic capacity, these models do not include such effects, impairing our capacity to model photosynthesis in conditions of limiting water supply. Similarly, such models do not satisfy the specific needs of fruit production, mainly because they don't integrate the effects of phenology and cultural practices, with the exception of nitrogen fertilisation. In fruit production, the effects of flowering and fruiting, which modify source-sink relationships, cannot be overlooked. This is even more true in tropical fruit production, where the flowering and fruiting phases exceed six months at the individual tree scale, depending on climatic conditions. More specifically, little is known about the effects of source/sink balance, and the associated changes in carbon export rate from leaves and leaf carbohydrate concentration, like the ones resulting from the presence of developing fruits, on leaf nitrogen and photosynthetic capacity within the crown of field-growing trees. This can restrict our ability to accurately predict the spatial distribution of carbon gains and fruit growth within the canopy of fruit trees.

The objectives of this paper are: 1) to provide an overview of the effects of long-term drought, phenological changes and the associated variations in sink activity and carbohydrate accumulation on the key relationships of the coupled model of photosynthesis, and 2) to evaluate the prospects of improving these models. Data presented here were collected over more than seven years on two tropical trees, mango and lychee.

Effects of climatic changes, long-term drought, the proximity of inflorescences, low fruit load and starch accumulation in the presence or absence of sink activity

Observations on adult mango trees suggest that in the absence of drought, and provided that there are no phenological changes, mild climatic variations, like the ones occurring in tropical

conditions, do not affect the fundamental relationships between leaf nitrogen concentration and light exposure, and between photosynthetic capacity and leaf nitrogen concentration (Urban et al. 2006).

Long-term drought in two-year old lychee trees results in a decrease in leaf starch concentration expressed on an area basis $[\text{starch}]_a$, an increase in M_a and N_a , and a decrease in both J_{max} and J_{max}/N_a (Damour et al. 2007). $N_a = N_m M_a$ where N_m represents leaf nitrogen concentration expressed on a dry matter basis and M_a the leaf mass-to-area ratio.

The proximity of inflorescences does not affect $[\text{starch}]_a$ but results in a decrease in N_m and N_a , and a decrease in J_{max} and J_{max}/N_a (Urban et al. 2004a and 2007b). The proximity of inflorescences is moreover associated with a reversible decrease in mesophyll conductance and increase in photosynthetic electron fluxes towards alternative sinks (Urban et al. 2007b).

Starch accumulates while N_m and N_a decrease as a consequence of low fruit load. Photosynthetic capacity estimated from measurements of either maximum photosynthesis (A_{max}), V_{cmax} or J_{max} , decreases although it may be argued that A_{max} , V_{cmax} and J_{max} are underestimated in the presence of starch accumulation. Consequently, the decreases in A_{max}/N_a , V_{cmax}/N_a and J_{max}/N_a which were observed as a consequence of low fruit load may be considered with caution (Urban et al. 2004b, Urban and Léchaudel 2005). The $V_{\text{cmax}}/J_{\text{max}}$ ratio was found to be unaffected by starch accumulation.

Starch accumulation in the presence of sink activity results in a decrease in N_m and N_a like when fruit load is low (Urban et al. 2007a). However, in the absence of sink activity, N_m and N_a are not significantly affected. But then the absence of sink activity results in an increase in photoinhibition and a decrease in the apparent efficiency of light energy conversion (α), more pronounced than in the presence of sink activity.

Data basically show that the fundamental relationships between leaf nitrogen concentration and light exposure, and between photosynthetic capacity and leaf nitrogen concentrations cannot be considered as constants in the presence of long-term drought or phenological events, when sink activity is modified or carbohydrates accumulate. Our observations also show that the effect of starch accumulation on leaf nitrogen concentration depends on sink activity (Urban et al. 2007a), which seems to put an additional layer of complexity. Now the question is whether modelling is possible.

Prospects for modelling

As far as long-term drought is concerned, we are confident about our capacity to design very simple empirical models expressing N_a as a monomolecular and J_{max}/N_a as an exponential function of the predawn water potential (Damour et al. 2007). The complexity of the processes involved during the development of inflorescences leaves us with very little hope about the prospects for modelling (Urban et al. 2007b). The effect of starch accumulation, on the contrary, lends itself to modelling. Modelling the effect of starch accumulation on N_a may be achieved using a negative linear relationship (Urban and Léchaudel 2005, Urban et al. 2006). However, such relationships apply only in the presence of sink activity. In the absence of sink activity, N_a may simply be considered as a constant (Urban et al. 2007a). The most tricky part consists in modelling the effect of starch accumulation on J_{max}/N_a and V_{cmax}/N_a . Considering that J_{max} may be underestimated in the presence of starch accumulation and that α is negatively correlated to leaf starch concentration, we decided to consider J_{max}/N_a as a constant (as well as V_{cmax}/N_a and $V_{\text{cmax}}/J_{\text{max}}$) and to integrate the effect of starch in the biochemical model of leaf photosynthesis in the form of a global corrective factor C_{starch} applied to the rate of electron flow, J (Urban et al. 2007a):

$$J = C_{\text{starch}} \alpha \theta Q (1 + (\alpha \theta Q / J_{\text{max}})^2)^{-0.5}$$

where θ represents leaf absorptance and Q the photosynthetically active flux density.

$C_{\text{starch}} = e^{-0.0412[\text{starch}]_a}$ (in the absence of sink activity)

or $C_{\text{starch}}' = e^{-0.0398[\text{starch}]_a}$ (in the presence of sink activity)

Differences between C_{starch} and C_{starch}' are due to the fact that the absence of sink activity results in an increase in photoinhibition and a decrease in α . The model of the effect of starch accumulation on A_{net} in the presence of sink activity was tested on an independent set of data obtained from gas exchange measurements made on leaves from girdled branches with 10 and 100 leaves per fruit. The modified model of leaf photosynthesis of Urban et al. (2003) that incorporated the corrective factor C_{starch}' performed much better than the uncorrected model. The slope of the relationship between simulated and measured values of A_{net} was 1.03 for the modified model and 1.27 for the uncorrected model, resulting in an increase in r^2 from 0.32 to 0.76.

Conclusion

With the exception of the proximity of inflorescences, the effects of seasonal changes, including long-term drought, starch accumulation and variations in sink activity resulting from such phenological changes like fruiting can be easily handled to correct and adapt the biochemical model of Farquhar et al. (1980). One of the major challenge for the future will consist in coupling models of water relationships and models of starch accumulation, on one side, with models of photosynthesis, on the other side.

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