

Comments from Anonymous Referee #1

This paper presents an analysis of how leaf N per area (N_a) varies with climate in terms of its structural and functional (photosynthetic) components. The effects are attributed to inter-specific variation and within species adaptation, and the results are interpreted in a leaf optimization framework. I find this study to be extraordinary in going all the way from leaf sampling to modeling, producing empirical evidence, theoretical progress, and new components for predictive models in one paper. It is a rarely seen example of how to combine observations and theory to make real quantitative progress, beyond the usual "significant or not" testing of ecological hypotheses. In conclusion, I find this an very useful contribution to the research area.

Response: we thank the referee for this appreciative comment.

In the discussion, p.10 l. 19, the least cost hypothesis is explained as reducing c_i/c_a in drier environment due to the need for increased water transport capacity for a given rate of assimilation. Why this happens is not obvious to me. I would have thought that in drier environments water limitation would force the plants to increase water use efficiency by increasing assimilation capacity (A_{max}) per water use? Maybe an additional line of explanation could help here.

Response: nitrogen and water use are substitutable for each other, according to the least-cost hypothesis. The marginal cost of water transport is relatively high, compared to that of nitrogen use, in drier environments. Thus, plants adapt to a drier environment by reducing water loss by adopting a lower c_i/c_a ratio, while increasing carbon fixation capacity (V_{cmax}).

This reasoning follows from an economic perspective on plant adaptation, which replaces the concept of 'limitation' with the concept of relative costs and benefits. However, the outcome is fully consistent with the referee's suggestion, because lower c_i/c_a implies increased water use efficiency (assimilation per unit water use).

To make this clearer, we propose to amend the text as follows:

"The least-cost hypothesis (Wright et al. 2003; Prentice et al. 2014) predicts lower $c_i:c_a$ in drier environments. This is because the drier the atmosphere, the greater the flux of water required to support a given rate of assimilation; which in turn shifts the balance of costs and benefits towards investment in photosynthetic capacity (V_{cmax}) and away from water transport capacity."

Then in the final comments it is suggested that V_{cmax} should be plotted on the X axis against leaf N instead of the usual opposite way. I think I get the point of this, but at the same time, isn't N in proteins a key part of the machinery or structure that performs the "function V_{cmax} ". I think both ways of plotting could be equally valid also from an plant centered perspective.

Response: N in proteins is indeed a key part of the machinery that supports V_{cmax} . However, we think our slightly provocative point is worth making, because when the two variables are plotted in the usual way, it is easy to infer (as is very commonly done, in both empirical and modelling studies) that the N content of the leaf is an independent ‘cause’ of its V_{cmax} . We are suggesting the reverse: that the metabolic N content of the leaf is a consequence of the V_{cmax} adopted by the leaf.

It is also too easy, and incorrect, to regard leaf N simply as a proxy for V_{cmax} . As our analysis suggested, the non-photosynthetic component of leaf N can be large in plants with high LMA. Adams et al. (2016) have shown that photosynthetic capacity is not related to N_{area} in N-fixing plants, and pointed out that leaf N can also perform other functions such as defence against herbivory. There is also evidence that the predominant effect of artificially increasing N availability by fertilizer addition is increased canopy size (see e.g. Rosati et al., 2000 and references therein). Although a full review would be beyond the scope of this paper, there seem to be several lines of evidence suggesting that the common modelling approach, whereby N supply regulates photosynthetic capacity, needs replacing.

We propose to expand our discussion of this point, and to refer to Adams et al. (2016) in support of our argument and revised the text as followed in the discussion:

“As both LMA (Wright et al. 2005) and $c_i:c_a$ (Prentice et al. 2014) show relationships to environment, our results suggest a possible route towards a general adaptive scheme for the prediction of major leaf traits in DGVMs, which would be an improvement on models that assume a one-to-one relationship between photosynthetic capacity and N_{area} (see e.g. Adams et al. 2016, who showed that there is considerable variation in N_{area} among N-fixers that is unrelated to photosynthetic capacity).”

References:

- Adams, M. A., Turnbull, T. L., Sprent, J. I., and Buchmann, N.: Legumes are different: Leaf nitrogen, photosynthesis, and water use efficiency, Proceedings of the National Academy of Sciences, 113, 4098-4103, 2016.
- Rosati, A., Day, K. R., and DeJong, T. M.: Distribution of leaf mass per unit area and leaf nitrogen concentration determine partitioning of leaf nitrogen within tree canopies, Tree Physiology, 20, 271-276, 2000.