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* Contact information:
lalbert@email.arizona.edu

# Leaf demography and physiology of the Tapajós National Forest: could phenology cause a forest-level increase in gross primary productivity during the dry season?

**Loren Albert[1*], Jin Wu[1], Neill Prohaska[1], Plinio Barbosa de Camargo[2], Raimundo Cosme Jr.[3], Travis E Huxman[4] and Scott R Saleska[1]**

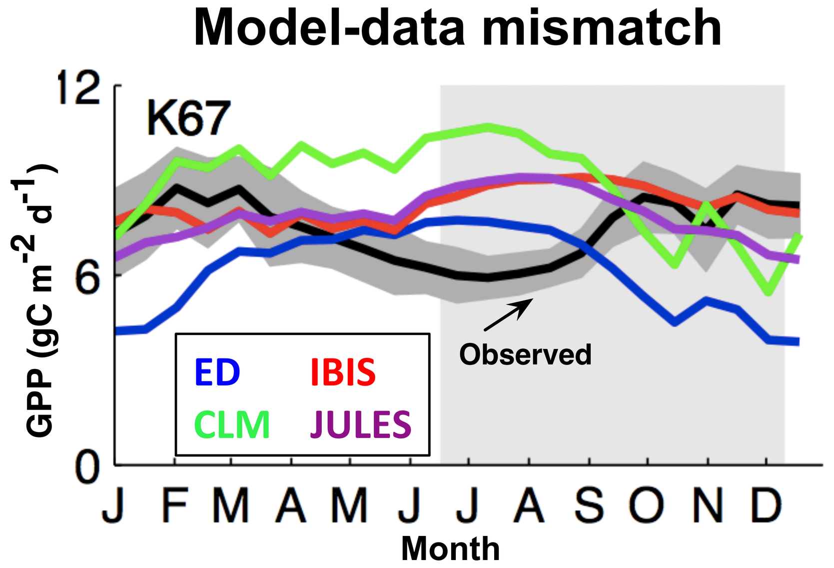
(1)University of Arizona, Tucson, AZ, United States, (2)University of Sao Paulo, Sao Paulo, United States, (3)EMBRAPA Brazilian Agricultural Research Corportation, Campinas, Brazil, (4)University of California, Irvine, Irvine, CA, United States

## 1. Tropical forests have seasons too: wet/dry seasonality in Amazonia

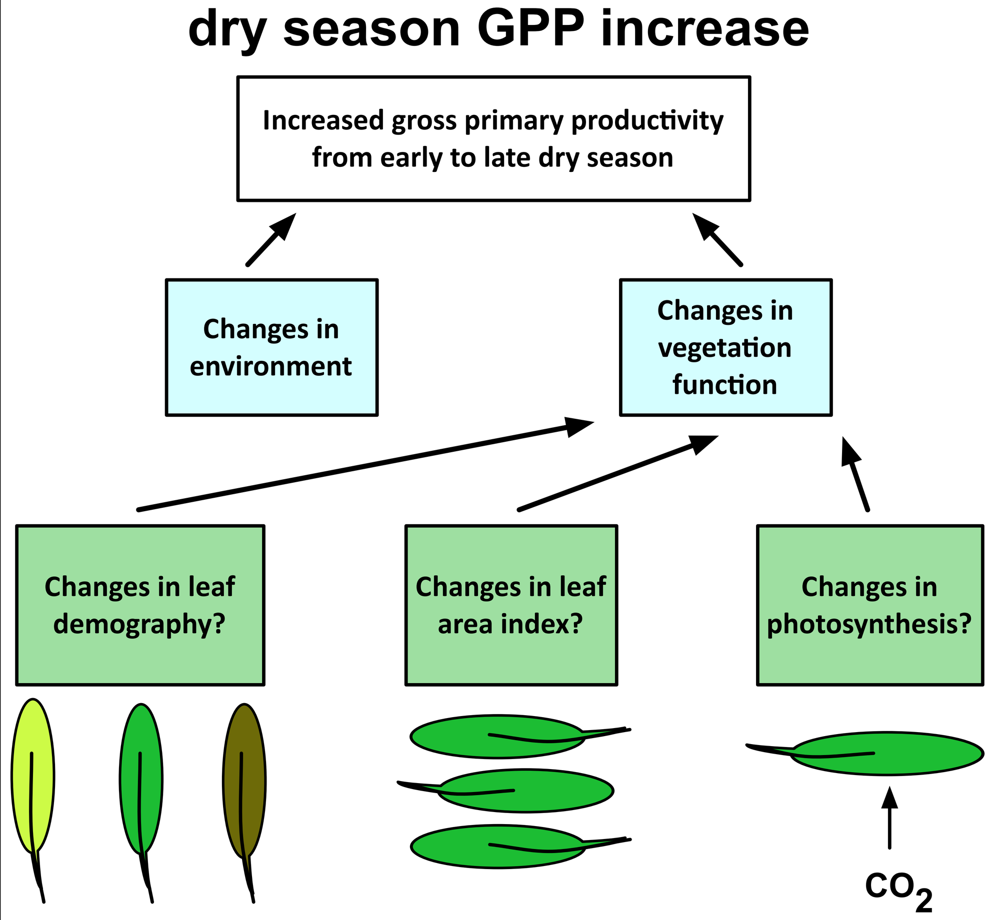
Tropical forests such as the forests of the Amazon basin are a significant component of the earth's carbon budget (1), yet how these forests respond to seasonal changes in weather, and the extent to which tree biology synchronizes with seasonal cycles, are poorly understood.

For evergreen forests in equatorial Amazon that experience dry seasons, eddy covariance observations and remote sensing assessments suggest a late-dry season increase in gross primary productivity (GPP) (2 However, most global vegetation models project a dry-season decrease in GPP (Fig. 1) (3).

**Model-data mismatch**




**Hypothesized drivers of late dry season GPP increase**



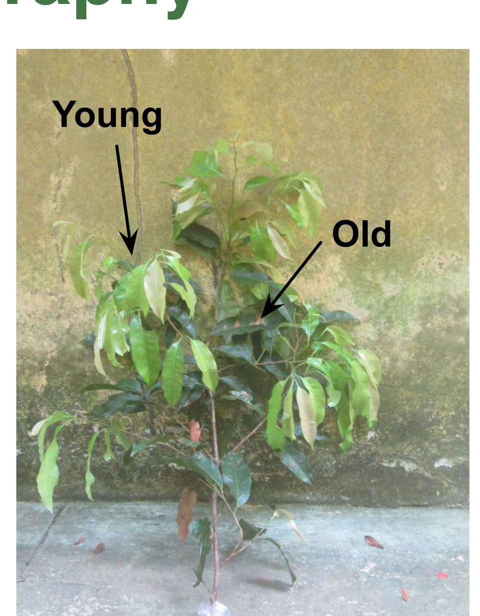

The observed seasonality of GPP could be due to seasonal changes in vegetation function associated with phenology (4), but phenology and leaf physiology of tropical evergreen forests is not well-characterized at sites with simultaneous eddy covariance observations. We measured leaf physiology for leaves of different ages, and surveyed leaf demography, at KM 67 in the Tapajôs National Forest, Brazil.

## 2. Methods: Leaf Physiology

* Five emergent trees and one understory tree.
* Measured photosynthesis (A/$C_i$ curves) of young, mature and old leaves with LI-6400.
* Sun and shade leaves
* Measurements performed *in situ* or with cut branches.


## 3. Methods: Leaf Demography

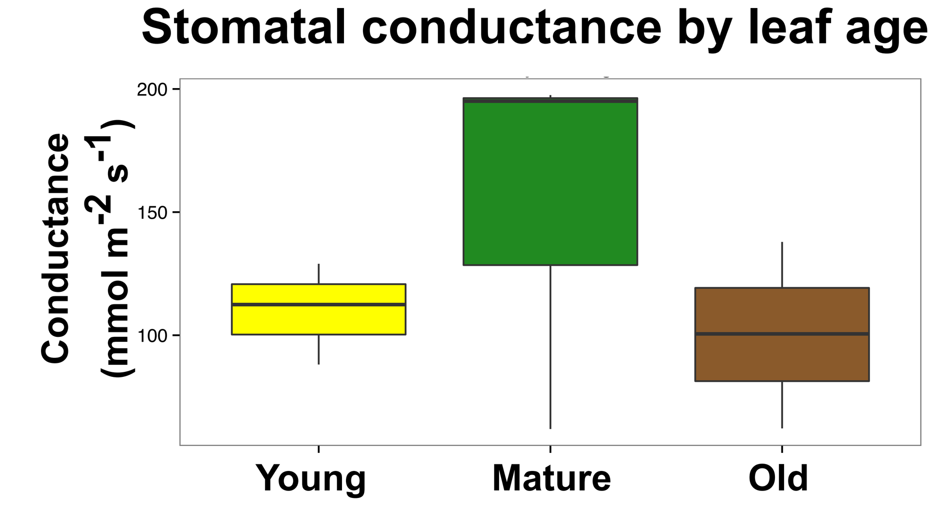
* Six emergent trees and fourteen understory trees.
* Collected one meter branches multiple times throughout the dry season (following 5, 6).
* Sun and shade microenvironments within the tree
* Counted young, mature and old leaves on sampled branches.




## 4. Physiology & Leaf Demography Results

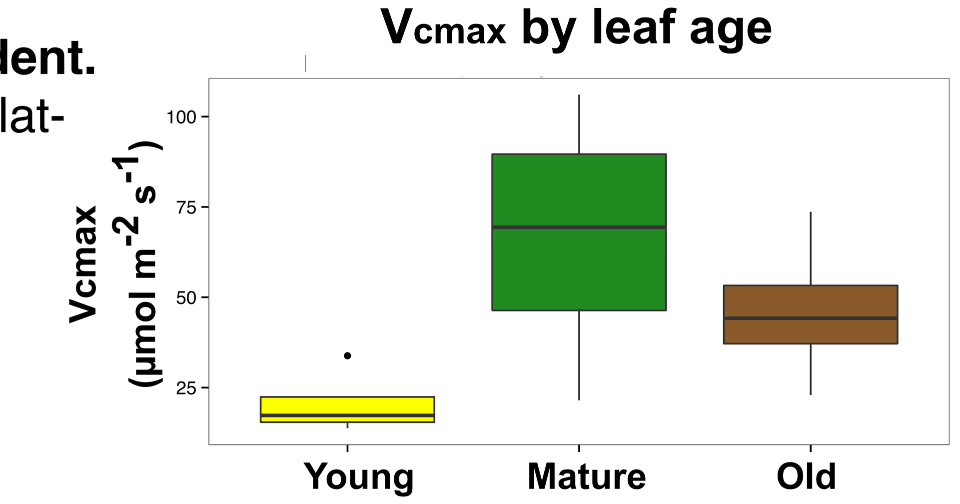
**Stomatal conductance for mature leaves is higher than for young or old leaves.** Box plots of the stomatal conductance (mean conductanceby leaf age for three trees), show that conductance is dependent upon leaf age.

**Stomatal conductance by leaf age**



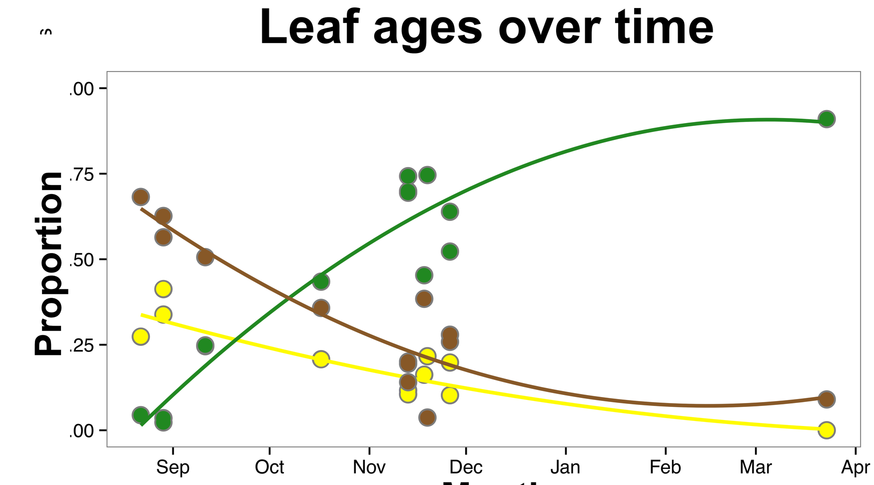

**$V_{cmax}$ is also leaf-age dependent.** Box plots of maximum carboxylation rate ($V_{cmax}$) by leaf age (mean $V_{cmax}$ by leaf age for four trees) suggest that mature leaves have the highest $V_{cmax}$.

**$V_{cmax}$ by leaf age**




**For many trees, the number of mature leaves increased as the dry season progressed.** The example on the right shows how the proportion of young, mature and old leaves changed across time (data compiled from 2012, 2013 and 2014). However, there was variation between trees.

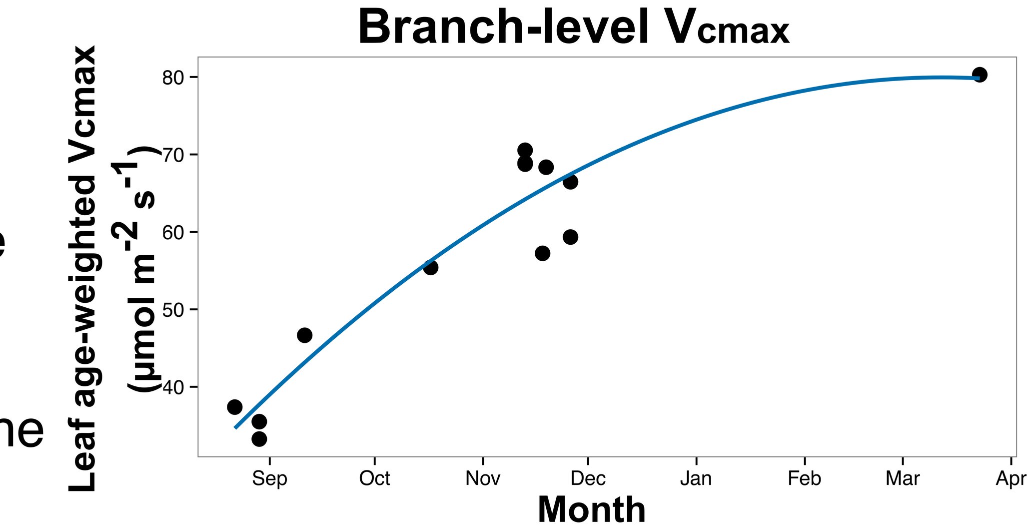
**Leaf ages over time**




## 5. Physiology & Leaf Demography Results

**Estimating $V_{cmax}$ at the branch level** reveals that shifts in leaf demography plus the effects of leaf age on leaf function could combine to increase GPP during the dry season at the KM67 site.

**Branch-level $V_{cmax}$**




$V_{cmax}$ estimated at the branch level is simply the proportion of leaves from each leaf age category multiplied by mean $V_{cmax}$ for that leaf age category. The example above shows estimated branch-level $V_{cmax}$ for *Erisma uncinatum.*

## 6. Discussion

1) Our results show that photosynthetic capacity (e.g. Vcmax) is higher for leaves that matured during the most recent dry season than for older leaves from previous periods of growth.

2) For many trees, leaf demography shifted during the dry season such that recently matured leaves replaced old leaves. For instance, leaf demography of an *Erisma uncinatum*, the most abundant canopy tree species at our site, had significantly more recently matured leaves, and significantly fewer old leaves, during surveys late in the dry season (after mid-October) than early in the dry season (prior to mid-September).

3) Together, shifts in leaf demography and the effects of leaf age on leaf function could increase GPP during the dry season at the KM67 site. Thus, leaf phenology may be a critical driver of GPP seasonality in moist tropical forests of the equatorial Amazon.

4) Most current vegetation models do not include vegetative phenology for broadleaf evergreen forests. Incorporating leaf age and vegetation into the models may improve match between vegetation models and observed eddy flux data (3,4). This study reveals patterns of leaf-age dependent physiology and vegetation phenology that can help with future model parameterization.

## References

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