Commentary

Phenological and structural linkages to seasonality inform productivity relationships in the Amazon Rainforest

The Amazon Rainforest accounts for *c.* 15% of global terrestrial photosynthesis (Malhi *et al.*, 2008). Yet, estimates of primary productivity in these forests carry the greatest uncertainties due to the seasonality of productivity as a function of dry season length, and interannual climate variability – including responses to El Niño Southern Oscillation (ENSO). Empirical observations and model predictions diverge concerning the seasonality of photosynthesis (Restrepo-Coupe *et al.*, 2017). Vegetation models show declines in gross primary productivity (GPP) during the dry season, while field and satellite observations show increases (Albert *et al.*, 2018). It has been hypothesized that these differences may be due to environmental cues such as change in day length or solar zenith angle (i.e. 'phenological clock'); however, there are indications that seasonal changes in vegetation structure and function within the canopy, as well as leaf demography, exert strong controls on carbon and water fluxes (Albert *et al.*, 2018). Within the Amazon, leaf area (measured as leaf area index or LAI) may remain fairly constant across the year (Wu *et al.*, 2016) yet show seasonal differences in its vertical distribution within the canopy (Tang & Dubayah, 2017). In this issue of *New Phytologist*, Smith *et al.* (pp. 1284–1297) link these seasonal changes in the vertical distribution of LAI to the seasonality of Amazonian forest productivity. This is done using terrestrial LiDAR (light detection and ranging) data collected in the Tapajós National Forest (2°51′S, 54°58′W) from three different time periods spanning from 2010 to 2017, including three non-El Niño years (2010, 2012, and 2016–2017) and one El Niño drought year (2015–2016). Importantly, this study shows differences in vegetation structure, both within and across seasons, that have been obscured in previous studies, thus highlighting the importance of fine-scale canopy measurements through time to address structure–function relationships.

In Smith *et al.*, vegetation structure is quantified using a ground-based LiDAR system that samples a vertical plane of the canopy along a transect. LiDAR pulse returns are converted to estimates of leaf area density (LAD) and LAI (Stark *et al.*, 2012) allowing for characterization of the vertical and horizontal distribution of vegetation. This method creates more integrated descriptors of the canopy that have been linked to productivity (Hardiman *et al.*, 2011; Stark *et al.*, 2012), resource use efficiencies (Hardiman *et al.*, 2011), and light acquisition (Stark *et al.*, 2015; Atkins *et al.*, 2018b).

This article is a Commentary on Smith *et al.*, **222**: 1284–1297.

Smith *et al.* linked canopy structure to productivity by comparing annual ranges of total LAI, as well as LAI in upper and lower canopy strata (e.g. where LAI occurs vertically), among seasons and years, and found that LAI increased during the dry season but decreased following the onset of the wet season. The upper canopy gained leaf area during the dry season, while the lower canopy lost leaf area. These relationships reversed during the wet season – an inverse correlation between canopy strata that has not been shown previously. The ENSO drought year further enhanced these seasonal differences.

> *'The question arises then by what mechanism does leaf area seasonality differ in synchronicity between lower and upper canopy strata?'*

The question arises then by what mechanism does leaf area seasonality differ in synchronicity between lower and upper canopy strata? Smith *et al.* detail two possibilities. That a phenological clock determines patterns in the upper canopy, while light limitation, as a function of shading from the upper canopy, drive slower canopy stratum patterns. However, relationships among all strata and solar zenith angle are similar, indicating that all strata may be 'following a phenological clock'. Conversely, it is hypothesized that tree size and functional differences may drive seasonal patterns between layers. Smith *et al.* note: 'The upper canopy likely corresponds to late successional, well illuminated emergent and tall trees . . . the lower canopy surface to light-demanding early and mid-successional trees, and the understory comprises short shade tolerants, canopy sub-adults . . . . Our results thus support the hypothesis that tree size and functional groups exhibit divergent phenological responses arrayed over environmental heterogeneity spanning light gaps to deep shade.'

The enhanced seasonality of canopy structure due to water limitation informs a multitude of future research avenues. With basin-wide drying and more frequent and severe droughts projected across Amazonia (Malhi *et al.*, 2008), it is critical to understand root-to-canopy structural and functional responses to water limitation. This is non-trivial as understanding how forest structure, demography, and water and light availability interact to influence productivity requires a multi-pronged approach (Leitold *et al.*, 2018; Brum *et al.*, 2019). As Smith *et al.* suggest, complex linkages between a diversity of hydrological and phenological strategies may mediate forest drought response. This work illustrates the different temporal scales of the drought response – that canopy strata may be affected independently both in time and magnitude. While previous work has generally focused on the vulnerability of larger canopy trees to water limitation, these effects are first observed in lower-strata individuals. Trees with roots in shallow soil layers experience the early onset of water limitation, and as such, require means to avoid complete hydraulic failure and mortality. While some species favor xylem structural integrity (e.g. resistance to cavitation), others potentially compensate by dropping leaves to become more drought tolerant. Conversely, large canopy trees are typically more hydraulically vulnerable over the long-term but compensate in the short-term by accessing deeper soil water reserves. Changing patterns of evapotranspiration and precipitation in the Amazon (Xu *et al.*, 2019) point towards the necessity for understanding linkages among structure, phenology, and hydraulic strategies to mediate drought response.

Smith *et al.* also show that satellite-derived vegetation indices, such as enhanced vegetation index (EVI) or near-infrared (NIR) reflectance, are more strongly correlated to leaf demography than leaf area – indicating that these measures may not fully infer productivity or biomass. This highlights the necessity to harmonize ground-based measurements of vegetation structure to those estimated from airborne and satellite platforms to adequately scale, model, and understand productivity and function across Amazonia and the globe. Yet, this is an exciting time. New methodologies are being created to better use LiDAR and remote sensing data (Atkins *et al.*, 2018a; Shao *et al.*, 2019; Silva, 2019) while technological advances such as NASA's Global Ecosystem Dynamics Investigation (GEDI) create unique opportunities to view forest structure from space. GEDI, a full waveform LiDAR system mounted on the International Space Station, will provide highly detailed, consistent measurements of forest canopy height and structure for a wide swath of the globe – particularly for equatorial regions such as Amazonia where optical remote sensing (e.g. Landsat) use has been hindered by dense cloud cover. These advances are critical as forecasting the future response of the Amazon Rainforest to changing drought regimes will require mesoscale and macroscale remote sensing coupled with fundamental understanding of the linkages among structure, phenology, and plant hydraulic strategies including coupling belowground and aboveground processes from the roots to the canopy.

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