Rethinking tropical phenology: insights from long-term monitoring and novel analytical methods

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ABSTRACT

Here we introduce the Special Section (SS) on long-term monitoring and new analytical methods in tropical phenology. The SS puts together nine original papers plus a synthesis, bringing significant advances and new insights to our understanding of tropical phenology across Africa and tropical America. The papers address environmental cues, methodological shortcomings, and provide innovative analytical approaches, opening new pathways, perspectives and applications of tropical phenology, for forest management and environmental monitoring. The SS is a substantial step towards a more comprehensive overview of trends in tropical phenology, since seven out of nine studies evaluate >10 yr datasets applying new methods of analysis such as hierarchical Bayesian models, generalized additive models and Fourier analysis. We argue that it is essential to maintain ongoing monitoring programs and build a tropical phenology network at least for long-term (>10 yr) study sites, providing the means for national and international financial support. Cross-continental comparisons are now a primary goal, as we work towards a global vision of trends and shifts in tropical phenology in the Anthropocene.

Key words: America; climate change; cross-continental comparison; flowering; fruiting; leafing; savanna; tropical long-term patterns; tropical Africa.

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MOST SERVICEABLY DESCRIBED BY LIETH (1974) AS, "… the study of the timing of recurrent biological events, the causes of their timing with regard to biotic and abiotic forces, and the interrelation among phases of the same or different species", phenology had become a key integrative discipline for global change research by the end of the last century. Here we summarize the nine papers resulting from the 2016 Association for Tropical Biology and Conservation (ATBC) Symposium on 'Long-term trends of tropical plant phenology: consequences for plants and consumers'. The present Special Section (SS) focuses on long-term tropical datasets and specifically on ground-based, directly observed or indirectly (plant litter traps) recorded phenology and the drivers of changes. We therefore do not present work on remote-sensed land surface proxies for leaf phenology or the recent technologies for near-remote phenology using digital camera repeated photography (Morellato *et al.* 2016, Alberton *et al.*, 2014, 2017) but these are addressed in our synthesis chapter (Abernethy *et al.* 2018). The studies in this SS bring significant new insights to our understanding of trends and patterns for tropical phenology across Africa and tropical America, based on the first comprehensive collection of long-term data sets spanning from five to more than 30 yr-long. The nine studies assembled address environmental cues, methodological shortcomings, and offer new analytical methods, along with potential pathways, perspectives and applications of phenology for forest management and environmental monitoring in the Anthropocene.

The papers by Wright and Calderón (2018) and Chapman *et al.* (2018) address the issue of environmental cues considering the variability of irradiance, rainfall and the occurrence of El Niño-Southern Oscillation (ENSO) as triggers for flowering and fruiting of tropical trees and

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lianas. Wright and Calderón (2018) test the relationships between irradiance, the timing and intensity of rainfall and flowering times over 30 yr of weekly trap censuses for 19 tree and liana species from Barro Colorado Island (BCI), Panama. They demonstrate that periods of rapidly increasing irradiance are likely to be the proximate cue for flowering in 10 of the tree species studied in this seasonal forest. Chapman *et al.* (2018) demonstrate that irradiance and the occurrence of El Niño are the strongest positive predictors of fruiting in a 16 yr long phenology record from Kibale National Park, Uganda. The study by Dunham *et al.* (2018) has a similar focus on environmental cues, also addressing the effects of rainfall, using 12 yr fruiting phenology for 69 tree species in a southeastern Madagascar rain forest. Fruit production increased in wetter years, with increased rain in the dry season affecting fruit production more strongly than increased rain in the rainy season, adding more evidence for the potential influence of climate change on tree phenology and associated frugivores.

Based on a unique 24 yr long record of community-wide flowering and fruiting phenology of 2526 trees in 206 plots at the Budongo Forest Reserve in western Uganda, Babweteera *et al.* (2018) determine that trees with faster growth rates and higher canopy exposure to light are increasing their flowering and fruiting frequencies, while fruit production declined over time. This study period coincided with increasing mean annual temperatures, though there was no evidence of a causal relationship between phenology and climate change at this site. The detailed investigations of many factors in this study, such as growth rate, canopy position, dispersal type, fruit production, tree size and liana infestation, enlighten the

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identification of the many variables defining phenology patterns at different scales in tropical forests (Babweteera *et al*. 2018).

The work by Adamescu *et al.* (2018) and Mendoza *et al.* (2018) focuses on timing and cycles rather than cues of tropical phenology. Using a continental comparison across Africa, Adamescu *et al.* (2018) investigate the long-standing question of whether tropical trees have annual cycles. They analyzed an unprecedented data set of flowering events for 5,446 trees from 196 species across 12 sites, and fruiting events for 4595 trees from 191 species, across 11 sites monitored over 6 to 29 yr. Applying a Fourier analysis, a class of spectral analysis based on sine and cosine waves used to quantitatively describe the cyclic nature of a time series (Bloomfield 2000), they demonstrate that annual cycles are the most common among African tropical forests, although variability occurs across sites, species, and individuals. Using a novel Bayesian model approach, Mendoza *et al.* (2018) define variation in the timing and quantity of fruit production at seasonal and inter-annual scales for a 10 yr data set from an Amazonian forest in Nouragues, French Guiana. They demonstrate that most species vary substantially across years in fruit production, although changes were greater in terms of quantity than of timing. Species ranged from continuously fruiting (11%) to those fruiting at two or more-year intervals (40%) or mast fruiting species.

Leaf exchange patterns are linked to a broad range of ecosystem processes, but only one study in this SS addresses leaf phenology, the 7-yr long observation of a cerrado savanna woody community by Camargo *et al.* (2018). They aim to determine whether there is inter-annual variability in the degree of deciduousness at the level of the species and the individual, to define the start of growing season, and to identify the relationships between leafing onset, leaf fall and climate drivers using general additive models. Their unique approach demonstrates large inter-annual variations in the degree of deciduousness among years and thus the importance of long-term observations to define the species leaf exchange strategies (Camargo *et al.* 2018). Inter-annual variations in rainfall and temperature affect deciduousness at species and individual levels and the general trends on leaf fall and leaf flush, suggesting a susceptibility to future climate change scenarios.

From a more practical standpoint, Bush and collaborators innovate by introducing the concept of observation uncertainty or how easily we can observe a phenological event and detect biases in phenology recording (Bush *et al.* 2018). Based on the unique Lopé, Gabon, 29 yr long phenology data set they demonstrate that time series length, phenophase visibility and duration are good predictors for the detection of regular phenological cycles. Their study is a crucial step towards a more effective phenological data collection and analyses. Finally, the Ouédraogo *et al.* (2018) study stands as an important practical application of long-term phenology data sets to forest management. They quantify the reproductive diameter for 31 major timber species across 11 sites in Cameroon, Congo, and Central African Republic, covering 5 to 8 yr of continuous observations. They demonstrate that long-term phenology monitoring is essential to detect and evaluate species reproductive thresholds for timber trees, questioning the minimum cutting diameter limits (MCDL) established by Forest Law in these countries, and stressing the importance of considering inter-site variability within species.

The SS gives ample evidence that long-term data sets are essential to define plant cycles, triggers and the responses to climate change, or to define large-trees reproductive thresholds, but highlights the elevated level of variability in tropical forest phenology. All these analyses are needed to support management policies and for biodiversity conservation actions and are discussed in a historical perspective in the closing synthesis article by Abernethy *et al.* (2018). The short-time span of many ground-based datasets on tropical phenology remains an obstacle for understanding the current velocity of change in tropical ecosystems (Chambers *et al*. 2013, Adole *et al.* 2016, Abernethy *et al.* 2018). Indeed, we have knowledge of only 12, 14 and 6 study sites with more than 10 yr of phenological monitoring in tropical America, Africa and Asia, respectively (see Fig. 2 in Abernethy *et al.* 2018).

Therefore, the testing of hypotheses using long-term datasets and innovative methodologies presented in this Special Section has opened new points of view for the future research on tropical phenology. Moreover, the insights gained indicate it is essential to maintain the ongoing long-term tropical phenology monitoring programs and build a network at least for those studies, providing the means for national and international financial support. Site-based understanding of the links between climate and phenology, and the ecosystem interaction consequences of phenological change are now within reach due to the growing number of long datasets and marked improvements in analytical methods. Cross-continental comparisons are presently a primary goal, as we work towards a global overview of trends and shifts in tropical phenology in the Anthropocene.

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