Cohort-specific tuning of foliage physiology to interacting stresses in evergreens

Ülo Niinemets

1,2,3

1Estonian University of Life Sciences, Kreutzwaldi 1, 51014 Tartu, Estonia; 2Estonian Academy of Sciences, Kohtu 6, 10130 Tallinn, Estonia; 3Corresponding author (ylo.niinemets@emu.ee)

Received October 6, 2014; accepted October 16, 2014; published online November 25, 2014; handling Editor Danielle Way

How the timing of leaf flush affects foliage functioning

Leaf economics spectrum is the basic concept linking leaf carbon gain strategies, fast vs slow turnover, to foliage functional traits (Wright et al. 2004). At the heart of the economics spectrum is the reverse correlation among traits responsible for leaf longevity and physiological activity; thus, high leaf longevity in evergreens is associated with traits improving leaf robustness such as high leaf dry mass per unit area and density reflecting enhanced biomass investment in support biomass (Wright et al. 2004). Increased support investments inevitably result in low photosynthetic capacity per dry mass placing evergreens towards the slow return end of the leaf economics spectrum (Wright et al. 2004, Reich 2014). The economics spectrum describes the basic co-variation patterns among leaf functional traits across plant functional types, but it does not implicitly consider several potentially confounding sources of variation such as leaf age (e.g., Niinemets 2014).

Evergreens characteristically support multiple leaf age classes with potentially contrasting structural, chemical and physiological characteristics, but due to practical reasons, often only the leaves from the newest fully mature leaf flush are included in analyses involving evergreens. However, older leaves contribute a major proportion of total canopy leaf area in many evergreens (Whitehead et al. 1994, Niinemets et al. 2005), implying that age-specific differences in foliage performance play a major role in whole canopy carbon gain. While the basic age-dependent modifications in foliage functional traits have been studied in evergreens (Kitajima et al. 1997a, Radoglou and Teskey 1997, Ellsworth 2000, Niinemets and Lukjanova 2003, McGarvey et al. 2004, Niinemets et al. 2005), there is limited information on responses of different-aged leaves to environmental stresses with a few exceptions (e.g., Mulkey et al. 1992, Ogaya and Peñuelas 2006).

Many evergreen species also have a complex phenology of foliage development characterized by multiple foliage flushes during the same growing season. In this issue of Tree Physiology, the study of Morales et al. (2014) conducted in a Chilean temperate rain forest with the evergreen relatively shade-intolerant species Eucryphia cordifolia Cav. demonstrates that seasonality in environmental conditions can strongly affect foliage growth and development as well as physiological potentials of fully mature leaves. They observed major differences in leaf structural, chemical and physiological traits among leaf flushes produced during a given growing season (Figure 1, Morales et al. 2014). Such flush-specific differences in foliage characteristics have been observed in several warm temperate and subtropical conifers (Whitehead et al. 1994, Teskey 1997, Niinemets et al. 2002, McGarvey et al. 2004) and in evergreen angiosperms in climates with seasonal distribution of precipitation (Mulkey et al. 1992, Kitajima et al. 1997b), and collectively emphasize the importance of the timing of leaf flush in foliage functioning.

The study of Morales et al. (2014) further found that differences among leaf cohorts in E. cordifolia were amplified in the low-light environment and under water stress (Figure 1). Although stress led to immediate physiological adjustments such as changes in stomatal conductance, the scaling among foliage physiological potentials (maximum carboxylase activity of Rubisco) and leaf nitrogen content was also altered (Figure 1). Such modifications in foliage functioning to stress during foliage growth suggest that the timing of leaf flush is an important driver altering the leaf economics spectrum in...
evergreens. Overall, stress-dependent phenotypic changes in leaf structure–function relationships have received little attention (Gotsch et al. 2010), but given that plants do frequently encounter single and multiple stresses in the field (Valladares and Pearcy 2002, Valladares et al. 2005, Niinemets 2010), such modifications, and their interaction with leaf age clearly constitute a high priority research target for future studies.

The severity of light and water availability treatments applied in the study of Morales et al. (2014) was well within the ‘normal’ stress range encountered under seasonal and year-to-year variations in environmental conditions in the field in Chilean temperate rainforests. Thus, clearly the observations of this study provide the major insight into understanding of the functioning of vegetation under the current situation. In light of the predictions that precipitation seasonality will be enhanced in future environments and the frequency of extreme weather conditions is likely increasing (Giorgi 2006, Kirtman et al. 2013), functional differences among leaf flushes formed at different times during the growing season are expected to become particularly large under global change.

**Incorporating trait phenological controls in models**

Apart from modification of the generality of leaf trait relationships, the finding that the timing of leaf formation can influence the plant photosynthetic response to drought and shade has important implications for studies intending to quantitatively scale up plant physiological responses in evergreen species. Potential differences in carbon gain characteristics (Figure 1) among leaf flushes are large enough that flush-specific physiological differentiation in evergreens needs to be incorporated in quantitative models of carbon gain.

Currently, such leaf phenology-dependent sources of variation are difficult to predict and include in models. On the basis of the concept of shoot autonomy (Sprugel et al. 1991), prevailing environmental conditions during shoot development should constitute the primary factor responsible for differences in foliage characteristics among subsequent leaf flushes. Shoot shading experiments have provided some evidence on shoot autonomy (Cregg et al. 1993), but there is apparently no full autonomy, implying that preceding shoot flushes alter the structure and physiology of the subsequent leaf flush, presumably through modifications in ‘old’ carbon availability during new shoot development (Stoll and Schmid 1998, Sprugel 2002, Ogaya and Peñuelas 2006). In addition, much of the nitrogen used for growth of the new leaf flush is remobilized from the older foliage (Weikert et al. 1989, Wendler et al. 1995). Thus, even if the subsequent leaf flush is developed under favorable environmental conditions, the size of the carbohydrate storage and the carbon fixation potentials of the foliage formed in the past as well as the rate and extent of nitrogen remobilization from the older shoots can lead to important ‘memory’ effects. Such endogenous effects are expected to gain in importance when new shoots develop under stressful conditions such as shade and/or drought leading to low availability of ‘new’ immediately synthesized carbon as observed in the study of Morales et al. (2014).

Other pertinent questions for simulating carbon gain in evergreens are how environmental and endogenous factors regulate the number of leaf flushes formed during a given season and what determines the timing of each individual leaf flush. Under more severe shading, the number of leaf cohorts produced during the growing season itself can be reduced, especially in young plants (Osada et al. 2002, Morales et al. 2014). Reduced flushing intensity in the shade is consistent with the hypothesis that the overall carbohydrate pool size determines the frequency of leaf flushing. In addition, the timing of leaf flushing across evergreen forests tends to be synchronized with the peak of solar irradiance when carbon supply from photosynthesis is potentially enhanced (van Schaik et al. 1993). The control of flushing by carbohydrate supply is also supported by increases in the number of leaf flushes under elevated [CO₂] treatment (Tissue et al. 1996).

Increasing severity of drought also reduces the number of leaf flushes produced or reduces the share of leaf area produced by flushes developing under well-watered vs drought-stressed conditions (Singh and Kushwaha 2005b, Nanda et
2013, Morales et al. 2014). Availability of soil water reserves to support leaf growth seems to be the key factor responsible for the number of leaf flushes produced, but shoot sugar concentrations also importantly change through the drought cycle (Newell et al. 2002). In addition, drought can increase leaf mortality to reduce plant water loss (Singh and Kushwaha 2005b, Ogaya and Peñuelas 2006). At the extreme, evergreen species in wetter habitats can become semi-deciduous or deciduous in seasonally drier environments (Singh and Kushwaha 2005b, Souza et al. 2009, Gotsch et al. 2010). Both the controls by atmospheric [CO₂] and soil water availability on foliage flushing suggest that global change drivers could importantly alter foliage formation in future climates.

However, there is a large species variability in the importance of environmental vs endogenous controls on the onset of leaf flushing (Reich 1995). In seasonally dry ecosystems, leaf flushing of several species may occur actually at the end of the dry period when the soil water availability is the lowest (van Schaik et al. 1993, Franco et al. 2005, Singh and Kushwaha 2005a, Elliott et al. 2006, Rojas-Jiménez et al. 2007). This ‘aggressive’ flushing strategy potentially enhances the length of the growth period as the plants can take advantage of the onset of the rainy period immediately when it starts. However, it has the risk of losing the entire developing leaf cohort when the onset of the wet period is delayed (Vico et al. 2014). This is a significant risk as there is a large interannual variation in the growing season length in many subtropical and tropical ecosystems with seasonal water availability (Yoshifuji et al. 2006, Archibald and Scholes 2007). A safer strategy of leafing out after the onset of the rainy period does not carry such a risk, but it effectively reduces the length of the growth season due to delays associated with new flush formation. Inclusion of leafing strategies in carbon gain models clearly requires a better understanding of endogenous vs environmental controls on the timing of leaf flush as well as game theoretical approaches assessing the risk of delayed rain events on the potential share of early vs late flushers under particular climatic conditions. Extension of these models to future conditions will further require improved understanding of the possible changes in rain onset and interannual variability under global change.

Overall, the findings of Morales et al. (2014) and past evidence highlight an important source of foliage physiological differentiation, timing of leaf flushing, in evergreens that has not yet given due consideration. Future studies are needed to gain insight into the generality of observed leaf flush-dependent modifications in foliage structure–function relationships and stress responses across evergreen species. Globally changing conditions can importantly modify the magnitude and significance of flush-specific physiologies, emphasizing that ‘phenological phenotypes’ of leaf structure and physiology along with environmental and endogenous controls on leaf flushing need to be included in predictive carbon gain models.

**Conflict of interest**

None declared.

**Funding**

The research of Ü.N. on plant structure–function relationships is supported by the Estonian Ministry of Science and Education (institutional grant IUT-8-3), and the European Commission through the European Regional Fund (Center of Excellence in Environmental Adaptation).

**References**


