Editor's Highlight: Adaptive responses of tropical savanna trees to frost

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The savanna biome, characterized by an open upper canopy, scattered trees, and abundant grasses in the ground layer, covers around 20% of the global land (Pennington et al. 2018). The structure of savanna vegetation is largely maintained by the interaction of climate, disturbance and plant life history traits, and whereas open tree canopies provide space for grasses, these in turn produce a loosely packed, highly flammable fuel bed that is the primary cause of the recurring fires (Pennington et al. 2006; Pennington et al. 2018; Bond 2008). Disturbance by fire and large herbivores can delay tree growth and recruitment, with the latter being generally greater under tree crowns (Hoffmann 1996).

Beyond fire and herbivory, the importance of other types of disturbances or their interaction is less understood in savanna ecosystems. For example, the effects of frost (below-freezing temperature) on trees are well characterized for temperate regions and in the northern hemisphere (e.g., Inouye 2000; Hufkens et al. 2012; Kreyling 2019). However, much less is known for the southern hemisphere, particularly at the limits of distribution of tropical savannas that together with forests are the dominant types of vegetation in seasonally dry tropical regions. Here we focus on tropical savanna trees, that can extend their distribution southwards towards regions that are subjected to frequent frost events during the dry cool winter months or are also found at higher elevations in lower latitudes, where frost events are not as frequent but can occur and have a major impact on savanna trees (Filgueiras and Pereira 1987).

Frost can be an important cause of top-kill (i.e., irreversible damage and loss of the tree crown regardless whether the plant recovers by resprouting from belowground or

aboveground buds) and tree death. These frost effects alter vegetation structure and composition and constrain the geographical expansion of plant populations of tropical origin towards higher latitudes or altitudes, where freeze events are more frequent or extreme (Brando and Durigan 2005; Bannister and Lord 2006; Bredenkamp et al. 2002; Bojórquez et al. 2019; Hoffmann et al. 2019). Because leaves and stems of many tropical woody plants are damaged or killed by temperatures of -4 to -1 °C (Sakai and Larcher 1987), frost events particularly rare episodes of intense frost can cause extensive dieback of savanna trees and shrubs on the fringes of the tropical region (Muller et al. 2016; Hoffmann et al. 2019) or in higher elevation areas within the tropical zone (Filgueiras and Pereira 1987). The small size of savanna woody seedlings that expose them to the colder temperatures near the ground during radiation frost events (Leuning and Cremer 1988) and the lower thermal mass of their thin stems make them particularly vulnerable to frost (Whitecross et al. 2012; Botha et al. 2020). Therefore, in addition to fire and herbivory, frost can also limit the recruitment of new individuals, which is a crucial process for maintenance and expansion of plant populations and recovery from perturbations. In fact, paleontological evidence suggests that changes from warm interglacial phases to cooler glacial maxima were mirrored by shifts from woodland savanna to open grassland in Africa (Partridge et al. 1993; Scott 1982). Pollen records suggest that grasslands covered large areas of southern Brazil during the most recent glacial maximum, which are now covered with tropical forest and savanna (Behling 2002). Paleo-niche models also suggest range contraction of neotropical savanna trees toward central Brazil and eastern Bolivia and to lower altitudes during the last glacial maximum likely related to decreased temperatures and precipitation and their expansion during the warmer and moister last interglacial and the Mid-Holocene (Bueno et al. 2017).

Frost can be expected to exert strong selective pressure on savanna tree populations thriving in these transitional regions and adaptive features that reduce the level of damage

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by frost (resistance traits) or that minimizes the negative fitness impacts of frost damage (tolerance traits) should be favored by natural selection (Agrawal et al. 2004). However, detailed studies of frost tolerance and resistance in tropical savannas are rare (e.g., Muller et al. 2016; Whitecross et al. 2012; Hoffmann et al. 2019), especially those using a functional approach that may deepen our understanding about how savanna trees respond to frost disturbance (Fig. 1). The study of De Antonio et al. (2021) in this issue of *Trees: Structure and Function*, contributes towards filling an important research gap for southern savanna systems that experience sporadic but severe frost. In this study, authors analyzed morphological and physiological responses of trees to frost events and to simulated low temperatures in two savanna sites in Southeastern Brazil. Since frost events are common and have a significant effect on savanna ecology, authors analyzed strategies of frost-resistant and frost-sensitive (tolerant species sensu Agrawal et al. 2004) trees in relation to the degree of bud protection, bark investment and resprouting strategies, as well the effects of low temperatures on leaf function (assessed by measurements of the maximum potential quantum efficiency of Photosystem II, $F_v:F_m$). They expected resistant plants to have thicker bark and greater bud protection in comparison with sensitive species, as well high values of photosynthetic capacity ($F_v:F_m$) even after exposure to sub-zero temperatures. They also expected that frost-sensitive species would recover their height and biomass

after a year of growth. Authors found that frost-sensitive and frost-resistant species differed in several morphological and physiological traits. Even though these trait differences were associated with contrasting responses to frost, both groups ultimately cope quite well with frost by resisting (resistant species) or quickly recovering by resprouting (tolerant species).

The co-occurrence of tolerant and resistant species is not unexpected because natural selection in frost-prone regions should favor either high resistance combined with low tolerance or low resistance coupled with high tolerance but not high or low levels of both traits simultaneously (Agrawal et al. 2004). Natural selection for resistance would result in low levels of damage, and hence reduced selection for tolerance. Conversely populations with high level of frost tolerance would not be expected to undergo selection for resistance because the inflicted damage would not reduce fitness. However, many tolerant species did show some level of protection for the epicormic buds and for the internal stem tissues that enable them to resprout from aboveground buds while many resistant species underwent some level of damage of the aboveground parts but were able to resprout from well-protected buds in these frost-prone savannas (Brando and Durigan 2005; De Antonio et al. 2021). Thus, plant functional typologies that represent variation along a continuum may better represent how savanna trees cope with frost.

Fig. 1 Examples of frost-tolerant (a, c–e) and frost-resistant (b) species in the savannas of South Brazil; **a** *Aegiphila verticillata* after a frost event in June 2016, **b** *Moquiniastrum polymorphum*, a frost-resistant species was not damaged while the vine (*Smilax* sp, dashed arrow) on top of it was killed by the frost event, **c** *Stryphnodendron obovatum* resprouting from buds located in side branches, **d** *Dimorphandra mollis* resprouting from the main stem (arrow) and **e** *Miconia albicans* resprouting from underground buds. More details can be found in De Antonio et al. (2021). Photographs taken by William A. Hoffmann (a, b) and Ariadne C. de Antonio (c, d, e)

The availability of mineral nutrient and carbon reserves will be essential for resprouting and for replenishing the new tissues following the sudden loss of foliage (Pearce 2001). Because of the high investment in new vegetative tissue, the resprouting individual may be, however, limited in terms of resource allocation to seed production (Stevens 2021). Thus, carbon starvation, mineral deficiency and their effects on reproductive output would be an increasing risk in regions undergoing frequent frost events that provoke top-kill or partial loss of aboveground tissues.

Frost is not the only disturbance factor provoking top-kill in frost-prone regions within the tropical belt. In fact, fire is the major cause of top-kill in tropical savanna ecosystems and these transitional regions are no exception. Frost and fire interact at the limits of the savanna biome and their synergistic effects can be particularly severe for savanna tree seedlings that thrive in open sites with little tree cover. Frost can exacerbate the effects of fire on vegetation structure by predominantly damaging trees in open environments and generating high loads of dead, flammable fuels (Hoffmann et al. 2019). Despite some evidence that savanna tree seedlings can survive single events of frost and fire (Botha et al. 2020), further studies are necessary to better evaluate the costs associated with frost resistance and tolerance in savanna trees and of long-term effects of repeated events of fire and frost, particularly for seedlings. Studies on frost effects on roots of savanna trees are also lacking. Roots are less exposed to near- or below-freezing temperature due to the insulation provided by the soil. They are, however, less frost hardy than the shoots and savanna tree seedlings generally do not develop a deep-rooted system during the initial growth period (Rizzini et al. 1965; Hoffmann et al. 2004). Frost mainly damages and kills fine roots, which are essential for the uptake of water and mineral nutrients (Ambroise et al. 2020).

Drought interacts with fire and frost, which makes it more difficult to examine the role of frost as a relevant selective force or as a single major abiotic factor imposing a limit for range expansion of tropical savanna trees. Several traits such as thick bark (Schafer et al. 2015), well-protected buds (Charles-Dominique et al. 2015), resprouting ability, belowground storage organs (Maurin et al. 2014) are not specific adaptive responses to frost but would also be favored in fire- and drought-prone environments. Interestingly, many genes are responsive to both drought and cold stress, suggesting that some plant tolerance mechanisms or adaptations to drought may be advantageous for enduring frost (Guy 2003). For example, frost-hardy plants tend to have thick leaves, high investment in palisade parenchyma (Palta and Li 1979), high leaf water repellency due to waxy cuticles or pubescence (Aryal and Neuner 2010), which are also typical of savanna trees (Bieras 2009; Ferreira 2015). Drought exposure can increase cold acclimation of leaves

(e.g., Medeiros and Pockman 2011), however, results of a study of four savanna trees native to Southern Africa suggests that effects of water-limited conditions on sensitivity to nighttime freeze events are species dependent (O’Keefe et al. 2016).

Maintenance of the integrity of the vascular system by selection of a suite of traits that increase hydraulic safety and mitigate the negative impacts of frost-induced xylem cavitation is essential to sustain successful epicormic resprouting after top-kill. Drought, fire and frost differ in how they affect xylem structure and functioning, and in many cases, post-stress effects have also an important impact (Dickison 2000; Lucas et al. 2013; West et al. 2016; Yin et al. 2018). Traits that minimize the effects of frost-induced embolism and cavitation, such as narrow vessels and hydraulic segmentation, refilling or production of new xylem before resprouting are also considered adaptations to fire and drought-induced cavitation. Resprouting from aboveground buds depends on the preservation of the vascular tissues even if the plant undergoes top-kill during a frost event. In this regard, the structural properties of the bark are instrumental in protecting and insulating the vascular tissues during frost episodes for plants that resprout epicormically after top-kill (Bond and Midgley 2001; Clarke et al. 2013; De Antonio et al. 2020). The inner and the outer bark have different ecological functions and respond differently to fire, water stress and frost. Water storage and transport are related to properties of the inner bark, which also affects thermal insulation of the vascular tissues, while variations in the outer bark, particularly outer bark thickness is strongly related to fire resistance (Rosell 2016; De Antonio et al. 2020; Loram-Lourenço et al. 2020). Deciduousness during the winter months, a trait that has been selected in woody clades that successfully colonized freezing-prone environments (Zanne et al. 2014), would also reduce the risk of tree death by drought or fire in savannas subjected to cold and dry winters. In terms of plant functional responses to frost in tropical savanna ecosystems, we have yet to identify the suit of coordinated morphological, physiological and phenological traits linked to tree resistance and tolerance to frost that further evidence functional type differentiation and major specialization trends.

Fewer cold events are expected in the coming decades due to global warming. Still, rare cold extremes will continue to occur over some temperate and tropical regions (IPCC 2014). The importance of these events for ecosystems within the tropical belt is clearer when looking at the maintenance of boundaries between tropical savannas and forests (Hoffmann et al. 2019) or between savannas and shrublands (Muller et al. 2016). Furthermore, the study by De Antonio et al. (2021) suggests that tropical savannas may be resilient to recurrent frosts and this resilience is also likely related to species adaptations to drought and fire. Both resistant and tolerant species are present in the savanna ecosystem and

although frequency and intensity of frost events might favor one strategy over the other, the savanna may continue to be resilient in the context of the framework outlined by Hodgson et al. (2015), where resilience is achieved either through resisting or recovering from frost disturbance. In this case, the predominant resilience mechanism will likely depend on the dominant species strategy (resistant vs. tolerant species) and the potential interactive effects of drought, fire and frost.

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Declarations

Conflict of interest The authors have no conflicts of interest to declare that are relevant to the content of this article.

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