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Commentary

Insect feeding location determines interactions between biotic and environmental stressors in trees

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Increasing summer temperatures are driving changes in both insect and tree phenology, especially in arctic regions. Tree growth and productivity have been in decline for many tree species in North America (van Mantgem et al. 2009). Warmer temperatures increase vapor pressure deficit (VPD) and water-use by trees, which may limit tree growth. Trophic interactions, however, can complicate the impacts of climate change on forests, making combined impacts difficult to predict (Rosenblatt and Schmitz 2016). Outbreaks of herbivorous insects have been shown to significantly affect plant performance (Yang 2012). The magnitude of these insect outbreaks can increase because of warmer winter temperatures that improve overwintering survivorship (Kreyling 2010) and warmer spring conditions that enhance herbivore reproduction (Ayres and Lombardero 2000). Furthermore, the damage caused by herbivores on plants can be magnified in the summer by increases in VPD due to increased temperatures and low water availability (Anderegg et al. 2015).

Here, we highlight research published by Wagner et al. (2019) that demonstrates the importance of biotic interactions in tree responses to VPD. This has implications for modeling of net primary productivity and our understanding of tree growth and development in both natural and agricultural environments. For trembling aspen (*Populus tremuloides* Michx.), reductions in growth have been observed resulting from increases in midsummer VPD (Trugman et al. 2018). Recent outbreaks of leaf miners have led to increased damage and reduced growth for aspen in the boreal forest (Boyd et al. 2019). Furthermore, adverse physiological responses of forest tree species to insect

damage can exacerbate reductions in growth associated with increases in VPD. These effects can have implications on species distribution and success, particularly for regions like the boreal forest that are experiencing more rapid changes (IPCC 2013). Wagner et al. (2019) present evidence that insect damage can magnify the impact of increases in VPD or drought on aspen physiology.

Trembling aspen is a deciduous tree that dominates North American boreal forests, which can be affected by severe attacks from the lepidopteran leaf miner *Phyllocnistis populiella*. This leaf miner feeds on epidermal tissue and reduces photosynthesis, which can have impacts on tree productivity and physiology that are at least comparable to, if not greater than, climatic effects like temperature and VPD (Boyd et al. 2019). Furthermore, the negative effect of feeding can affect the physiological response to high VPD conditions, but it depends on the feeding location of the leaf miner (Wagner et al. 2008). This damage can negatively affect the long-term performance of trembling aspen (Wagner and Doak 2013). The leaf miner has one generation per year and typically overwinters in spruce leaf litter, which provides a warmer and drier environment compared with ambient conditions, improving winter survival (Wagner et al. 2012). Because they have a single generation, population outbreaks likely are highly dependent on two environmental factors: the severity of winters, which influences overwinter survivorship, and spring temperatures, which, if warm, allow rapid reproduction. However, the leaf miners can feed either abaxially or adaxially and, as the authors found, the impact of these outbreaks on tree physiology and ability to withstand

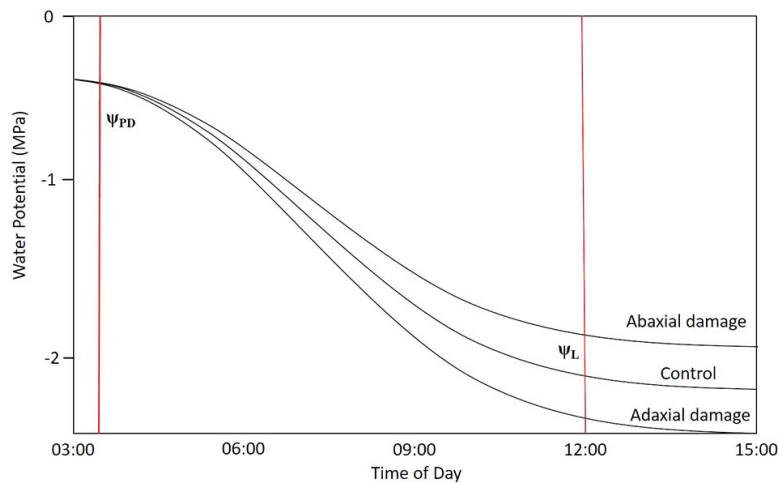


Figure 1. Schematic leaf water potential response curve reported in Wagner et al. 2019 for the effect of *Phyllocnistis populiella* (leaf miner) damage to either the abaxial or adaxial side of trembling aspen (*Populus tremuloides*) leaves compared with an undamaged control. Ψ_{PD} = pre-dawn water potential. Ψ_L = midday leaf water potential.

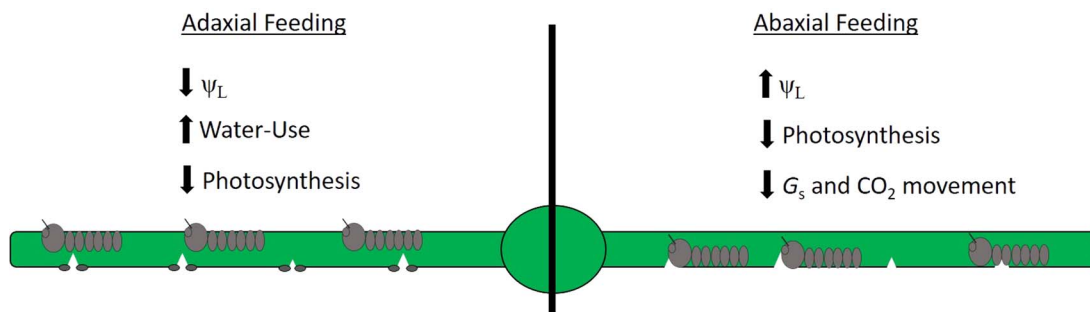


Figure 2. Schematic representation of the contrasting effects of adaxial and abaxial damage from *Phyllocnistis populiella* (leaf miner) to trembling aspen (*Populus tremuloides*) leaves showing increased water stress from adaxial feeding and increased carbon starvation from abaxial feeding. Caterpillars represent damage to leaves. Ψ_L = midday leaf water potential. G_s = stomatal conductance.

drought conditions could depend on which surface of the leaf is damaged.

Wagner et al. (2019) report the effects of insect damage on whole-tree productivity and physiological responses of trembling aspen to their environment. Through a combination of three separate controlled field and laboratory experiments, they were able to clearly identify how leaf miner feeding location affected water-use and carbon relations. Adaxial damage reduced photosynthesis and increased water stress through reduced water content and possible damage to the leaf cuticle (Figure 1). Abaxial damage reduced stomatal function, impairing gas exchange and limiting carbon fixation, and had the opposite effect on water potential. The authors present direct evidence that abaxial damage from leaf miners reduces stomatal function and net gas exchange, which was consistent with results reported in Wagner et al. (2008). Furthermore, adaxial leaf miner damage has been linked with increased water loss under greater midday VPD (Figure 2). These contrasting effects have implications for how the location of insect damage can affect tree responses to a changing environment.

The combined effects of abiotic and biotic stresses can have profound impacts on growth and productivity of perennial woody species (Andregg et al. 2015). Wagner et al. (2019) report the impact of leaf miners on the photosynthetic capacity and water status of trembling aspen in the natural environment where leaf miners were controlled, compared with untreated trees. Furthermore, a simple change in preferred feeding location by herbivores under controlled conditions had dramatic physiological impacts, which may alter tree survival in a changing climate. For this study (Wagner et al. 2019) and a previous study (Wagner et al. 2008), adaxial to abaxial feeding ratios were similar but there was some variation across years and sampling locations. These results highlight further opportunities to understand whether feeding location naturally varies according to pest pressure and the impact this has on tree responses under natural conditions. These same effects may also be observed for other biotic stresses including both pathogenic and insect damage in natural forests, as well as horticultural woody perennial species (Jactel et al. 2012). Modeling the impact of climate change on net primary productivity and tree health needs to

carefully consider indirect effects from biotic factors as well as direct effects of the environment on tree physiology and growth.

Conflict of interest

None declared.

Contributions

L.K. and T.N. wrote and edited the manuscript. L.K. developed the conceptual figures.

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