Commentary

Tree competition and defense against herbivores: currency matters when counting the cost

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Browsing by herbivores profoundly affects the nature and extent of woody plant communities through a variety of mechanisms, including alterations to disturbance regimes (such as fire frequency), indirect effects on nutrient cycling and soil fertility, and changes to net primary production (Hobbs 1996). Plants have evolved myriad ways to avoid being eaten, ranging from the development of spiny, unpalatable foliage to the production of secondary metabolites as defense compounds (Bennett and Wallsgrove 1994). In analyzing the responses of plants to herbivory and the consequences of these responses for plant–plant competition, there has often been an implicit assumption that such defense strategies come at a cost to the individual (more defense means less growth or reproduction), thereby providing the basis for fundamental ecological and evolutionary hypotheses about allocation of limited resources (Strauss et al. 2002).

Several hypotheses have been used as a framework for investigating the patterns and trade-offs of plant defense against herbivores (Stamp 2003), especially in the ecological literature. These hypotheses have been used singularly, or even in combination, to try and produce a unifying theory of plant–herbivore ecology and evolution. All of these hypotheses have been criticized in the literature. Although there are many instances when hypotheses have predicted empirical observations correctly, there are also many instances when either they have not, or they have been misinterpreted (Stamp 2003). One of these hypotheses, the carbon/nutrient balance (CNB) hypothesis, was originally developed to explain the influence of soil nutrients and shade on plant defense chemistry (Bryant et al. 1983). The CNB hypothesis suggests that species adapted to fertile sites (such as early-successional species) will respond to herbivory by utilizing stored resources for compensatory growth, while slower-growing species adapted to relatively infertile soils will instead protect their leaves by investing more carbon in anti-herbivory defense compounds. Such a hypothesis is appealing, as it makes specific predictions about patterns of allocation to plant secondary metabolite production, which have often been confirmed by empirical observation (reviewed by Stamp 2003). However, the CNB hypothesis has also been criticized, as there are many instances when predictions do not match observations (e.g., Hamilton et al. 2001, Koricheva 2002).

In this issue, Calder et al. (2011) report that conifer expansion reduces the competitive ability of *Populus tremuloides* (trembling aspen). The transition from aspen to conifer forests in western North America often coincides with a transition to soils with lower pH and lower nitrogen concentrations (Jerabkova et al. 2006), at least partly mediated by the chemical composition of conifer needles being added to the litter. The loss of early-successional species, such as aspen, in these systems over time has been attributed to their physiological preference for nitrogen uptake as NO_3^-, which may become less available in soils as conifer dominance increases (Kronzucker et al. 1997, Min et al. 1998, Kronzucker et al. 2003). While changes in nutrient availability may partly explain this successional trajectory, the canopies of evergreen conifers and deciduous broad-leaf trees also provide very different light environments for seedlings. Calder et al. (2011) show that by reducing light availability and altering soil characteristics, a conifer species (*Abies lasiocarpa*, subalpine fir) inhibited the growth of competing aspen trees. However, these abiotic changes induced by conifer dominance had another effect: they led to lower concentrations of phenolic glycosides (PGs) and condensed tannins (CTs) in aspen leaves, two groups of

chemicals that deter herbivory. The CNB hypothesis would appear to predict many of the results of Calder et al. (2011). First, aspen growing in the shade, where carbon fixation should be more limited, produced fewer foliar defenses than aspen in high-light environments. Second, the fast-growing, early-successional aspen also produced fewer foliar defenses than the shade-tolerant and slower-growing fir trees. However, this second finding is not necessarily related to carbon physiology *per se*. While the CNB hypothesis assumes that tree function can be explained using a cost/benefit analysis with carbon as the basic currency (e.g., Mooney and Gulmon 1982), there is growing evidence that tree growth and functioning are seldom carbon limited (Körner 2003, Millard et al. 2007), even if they have been browsed repeatedly by herbivores (Palacio et al. 2008). So is this underlying assumption of the CNB hypothesis correct? Orians et al. (2010) found no trade-off between chemical defense and growth in willow seedlings after only 6 weeks of growth, perhaps because they already had a surplus of carbon.

An alternative interpretation of the results of Calder et al. (2011) can be made using nitrogen as the basic currency instead of carbon. Most trees rely upon remobilization of stored nitrogen to meet their annual demand for new growth, especially in the spring (Millard 1994) and to a greater extent under nutrient-limited rather than replete conditions (Millard and Grelet 2010). Millard et al. (2001) suggested that as an alternative to the CNB hypothesis, anti-herbivory compounds serve primarily to protect the nutrients stored within leaves, rather than the leaves *per se*. Evergreen conifers, such as sub-alpine fir, store nitrogen in their foliage, while broad-leafed, deciduous species, such as aspen, tend to store nitrogen in their trunk and roots (Millard and Grelet 2010). Therefore, the nitrogen stored by the aspen is less susceptible to loss by herbivory and elicits the production of fewer foliar defense compounds. For example, the nitrogen physiology of another deciduous tree, *Betula pubescens*, which also stores nitrogen away from aboveground herbivores, was more affected by competition than by browsing, since competition (but not browsing) reduced both the sink strength for leaf nitrogen withdrawal in the autumn and the source strength for nitrogen remobilization in the spring (Millet et al. 2005). In contrast, the ability of *B. pubescens* saplings for compensatory growth in response to browsing (due to their leaf phenology) maintained source and sink strengths for internal nitrogen cycling and therefore also removed any potential effect of herbivory on tree nitrogen dynamics (Millard et al. 2001, Millet et al. 2005).

Although Calder et al. (2011) saw little difference in aspen concentrations of PGs and CTs between soil types, low nitrogen availability and competition can affect PG concentrations in trembling aspen (Donaldson et al. 2006). Under resource-limited conditions, trembling aspen seedlings demonstrated a trade-off between growth and defense, whereby slower growth correlated with greater investment in defense, the response that would be predicted by the CNB hypothesis (Donaldson et al. 2006). However, a key exception to the predictions of the CNB hypothesis occurred: the increased production of CTs under limited resource availability appeared to exact a cost (slower growth), implying that the extra CTs had not been produced by 'excess' carbon (Donaldson et al. 2006). Given that leaves were sampled in early autumn when nitrogen starts to be withdrawn for winter storage, the extra carbon may have been allocated to defend potential nitrogen stores, in keeping with the use of nitrogen as the currency of concern.

While trees experience a complex range of interacting stresses in the field, we often study them separately to better frame our questions. But by linking processes such as succession, competition and herbivory, we can develop a richer and more realistic view of tree responses to their environment (Bazzaz et al. 1987). Increased competition reduces growth through many of the same mechanisms used to predict herbivore chemical defense strategies (Figure 1). So, while the succession from deciduous-dominated forests to evergreen stands may thus be explained by how conifers change nutrient cycling and light availability in ways that inhibit aspen growth, these
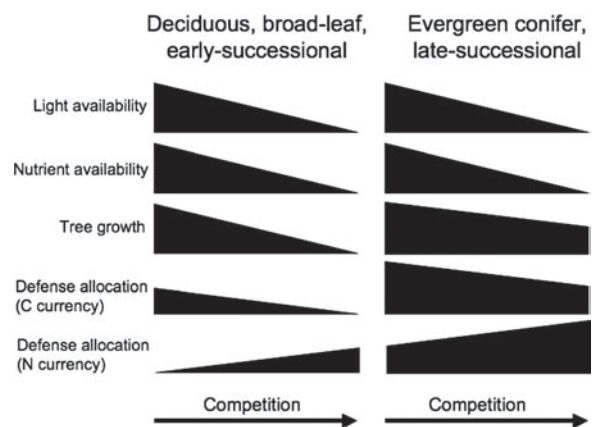

Figure 1. A conceptual relationship of how competition affects the abiotic environment of trees from the different functional groups in Calder et al. (2011), and how those changes affect herbivore defense allocation under schemes where the currency for defense investment is either carbon (C currency) or nitrogen (N currency). Although increasing competition reduces light and nutrient availability in both deciduous broad-leaved species and evergreen conifers, these changes affect growth in early-successional deciduous species such as aspen more strongly than in late-successional evergreen species such as fir. While excess carbon from high-light environments may increase defense allocation in both tree groups when carbon is the currency for defense, the long lifespan of evergreen leaves leads to greater investment in defense than in deciduous species. Alternatively, if nitrogen is the currency considered, greater defenses should be invested as nitrogen becomes scarce (i.e., increasing competition), while deciduous species storing nitrogen in trunks and roots have less need to invest in defense than evergreens that store nitrogen in accessible leaves.

changes also affect the deciduous species' herbivory defenses in a way that should further reduce its competitive ability. As well, the decreases in light and nutrient availability associated with greater competition affect leaf structure in ways that reduce not only growth rates, but also susceptibility to herbivores physically: species that are tolerant of resource-limited conditions often have long-lived, sclerophyllous leaves with a high C:N ratio (Reich et al. 2003) that are less susceptible to herbivory, regardless of additional investment in specialized defense chemicals. Establishing how the costs of defense change with increasing competition and what currency drives defense allocation in competing deciduous and evergreen groups will therefore give us a better accounting of both competition and defense. But given the intimate relationship between carbon and nitrogen dynamics in trees, especially over long time spans, the goal of defining a single theory of defense allocation and a single currency that account for all situations may be unreachable. Future experiments investigating the intersection of competition and herbivory should aim to define not only the costs to trees, but also the limits of using both carbon and nitrogen as currencies for those costs.

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