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Adaptations of quaking aspen (*Populus tremuloides* Michx.) for defense against herbivores

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ABSTRACT

Quaking aspen (*Populus tremuloides*) is a quintessential "foundation species" in early-successional forest ecosystems throughout much of North America. Although subject to damage by hundreds of species of herbivores, aspen has persisted in these environments due largely to a suite of defense strategies: resistance (traits that deter herbivores), tolerance (traits that facilitate recovery from damage) and escape (traits that reduce exposure to herbivores). Here, we review the current state of knowledge about aspen defense against herbivores, with particular focus on montane habitats of western North America.

The principal chemical defenses of aspen are phenylpropanoid-derived compounds, including phenolic glycosides (salicinoids) and condensed tannins. Phenolic glycosides reduce feeding, growth and survival of insect herbivores and deter feeding by mammalian herbivores. Expression of chemical defense traits is strongly influenced by genotype, development, environment (biotic and abiotic) and interactions among those factors, and high levels of defense exact a cost to growth. The value of tolerance as a defense strategy likely increases with tree age. Both tolerance and escape via vertical growth are also highly genetically variable in aspen.

The efficacy of aspen defense systems is context-dependent. Under conditions of low to moderate herbivore pressure, chemical defenses serve as effective deterrents, and well-defended genotypes are selectively favored. Under conditions of high herbivore pressure – whether insect or mammal – resistance fails and trees sustain high levels of damage. Under these conditions, genotypes with high levels of tolerance are likely selectively favored.

Large-scale landscape modifiers, coupled with genetic, developmental and local environmental variation, produce temporal and spatial mosaics of defense across western landscapes. Competition with conifers, fire severity, and extreme climatic events all influence expression of defense and response to herbivore damage in aspen.

Aspen's extraordinary genetic variation and phenotypic plasticity are no match for the environmental stressors, particularly ungulate browsing, contributing to its decline in portions of the Interior West. Management approaches should capitalize on the genetic and environmental factors known to contribute to diverse expression of defense in aspen, while maintaining herbivore population densities below levels that overwhelm all combinations of defense traits.

1. Introduction

Quaking aspen (*Populus tremuloides*) is a species of superlatives: largest individual organism on Earth, individual genets with lifespans of thousands of years, broadest distributional range of all North American tree species, among the most genetically diverse plant species known to science (Mitton and Grant, 1996). It is a quintessential foundation species (Ellison et al., 2005) in forests throughout northern and western North America. In short, quaking aspen is, by many evolutionary and ecological measures, an extraordinarily "successful" species.

That success is now being challenged in the Interior West of the U.S.A., where expansive areas of aspen are in decline (Romme et al., 1995). Aspen decline is related to a complex of factors, including fire history, climate change, mammalian browsing, and their interactions (Kashian et al., 2007; Endress et al., 2012; Martin and Maron, 2012; Zegler et al., 2012). Although each of the factors is important, release from excessive browsing pressure by wild and domestic ungulates is essential for recruitment and long-term survival of aspen (Zegler et al., 2012).

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Historically, a key contributor to the success of aspen over large temporal and spatial scales has been its capacity to defend against a diversity of herbivores. Likewise, understanding the factors that may limit or compromise those defenses may provide insight into the mechanisms underlying current patterns of decline in western North America. Here, we present a review of the major defense systems in aspen and explore their relevance for aspen ecology in the Interior West. Several recent reviews (e.g., Philippe and Bohlmann, 2007; Chen et al., 2009; Constabel and Lindroth, 2010; Boeckler et al., 2011) have focused specifically on the biochemistry and genomics of defense in *Populus*, and should be consulted for further details on those topics.

1.1. Terminology of defense strategies

Various researchers accord different and even conflicting meanings to the words "defense," "resistance" and "tolerance." For clarity, we use the terminology of Karban and Baldwin (1997) and Strauss and Agrawal (1999). "Defense" is any plant trait that confers a fitness benefit to a plant in the presence of herbivores. Thus, defense is viewed from the plant perspective, and may or may not harm the herbivore. The major defense strategies employed by plants include resistance, tolerance, and escape. "Resistance" is any plant trait (e.g., toxins) that reduces performance or preference of herbivores. "Tolerance" is the degree to which plant fitness is affected by herbivory relative to fitness in the undamaged state. Tolerance reflects the plant's ability to sustain growth and reproduction following damage. "Escape" incorporates traits (e.g., architecture, phenology) that reduce exposure to herbivores.

1.2. Conceptual model: causes and consequences of phenotypic variation in defense

Our conceptual model of the causes and consequences of phenotypic variation in plant defense is illustrated in Fig. 1. Genetics, development and environment each contribute to shaping the expression of defense traits in plants. Moreover, those factors typically interact, giving rise to phenotypic plasticity in expression of defense: individual genotypes may have different defense profiles in different environments (gene × environment interactions) or at different developmental stages (gene × development interactions). Plant defense traits influence, and are influenced by, trophic interactions, community structure and ecosystem processes. Temporal variation in the magnitude of these interactions will influence plant population densities over ecological time scales, while variable impacts of these interactions on plant genotypes will alter the genetic structure of plant populations over evolutionary time scales.

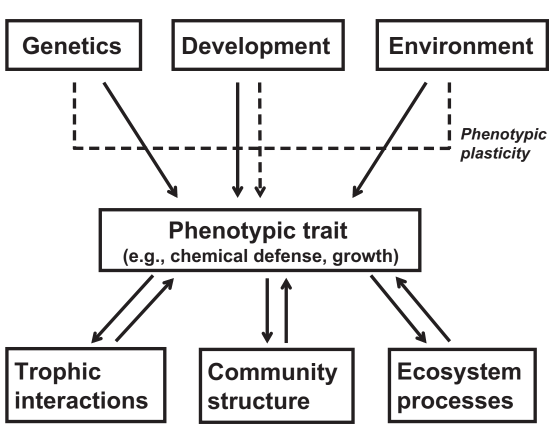

Fig. 1. Conceptual model of the major factors that shape phenotypic expression of defense traits, and ecological consequences thereof, in quaking aspen. Dashed lines represent interactions among factors.

2. Resistance mechanisms

2.1. Chemical defenses

The dominant secondary metabolites employed by aspen as defense against herbivores are products of the shikimic acid (=phenylpropanoid) pathway (Palo, 1984; Tsai et al., 2006; Constabel and Lindroth, 2010). The constituents with demonstrated impacts on herbivores include phenolic glycosides and condensed tannins, which occur in leaves, bark and roots, and coniferyl benzoate, which occurs in flower buds.

The signature defense compounds of aspen are a suite of simple phenolic glycosides, structurally related to salicylates ("salicinoids"; Boeckler et al., 2011). Quaking aspen produces four major phenolic glycosides (salicin, salicortin, tremuloidin, tremulacin; Lindroth et al., 1987) and trace amounts of others (Keefover-Ring and Lindroth, unpubl. results). Of these, salicortin and tremulacin, both of which contain a cyclohexenone carboxylic acid functional group, are the most biologically active. In aggregate, phenolic glycosides can comprise upwards of 25% dry weight in aspen leaves (Donaldson et al., 2006b) and 18% dry weight of woody twigs and root sprouts (Lindroth et al., 2007).

In *Populus*, condensed tannins are polymers of flavan-3-ol subunits with chain lengths that vary among species (Schweitzer et al., 2008). In quaking aspen, condensed tannins have relatively short chain lengths (9–12 units; Hagerman et al., unpubl. results) consisting of epicatechin, gallocatechin and epigallocatechin subunits (Schweitzer et al., 2008). As is the case for phenolic glycosides, levels of condensed tannins can be quite high, up to 25% leaf dry weight (Donaldson and Lindroth, 2008). Levels in woody tissues such as sapling twigs and root sprouts are generally low (1–3% dry weight; Lindroth et al., 2007).

Coniferyl benzoate is a simple phenlypropanoid ester. Relative to the wealth of information available for phenolic glycosides and condensed tannins in aspen, relatively little is known about coniferyl benzoate. The compound can comprise up to 7% dry weight of flower buds (Jakubas et al., 1993).

In addition to phenolic-based secondary metabolites, aspen may employ protein-based defenses against herbivores. Over the last decade, researchers have increasingly turned to genomic tools to explore novel herbivore defense systems in *Populus*. This work has shown that feeding by insects such as the forest tent caterpillar (*Malacosoma disstria*) induces genes that encode for a variety of putative defense proteins, such as protease inhibitors, chitinases and polyphenol oxidases (reviewed by Philippe and Bohlmann (2007) and Constabel and Lindroth (2010)). To date, however, little empirical evidence exists for the efficacy of these defense systems against herbivores of *Populus* in general, and aspen in particular.

Finally, *Populus* species produce a variety of other secondary metabolites, including a host of simple phenolic and terpenoid compounds (Tsai et al., 2006; Chen et al., 2009; Constabel and Lindroth, 2010). Upon mechanical or herbivore damage, *Populus* species release monoterpenes, sesquiterpenes and other green leaf volatiles (reviewed by Chen et al., 2009). These compounds may serve to attract natural enemies of herbivorous insects or to "prime" undamaged leaves for rapid chemical response to future attack. Herbivore-induced release of volatiles may benefit not only the damaged tree, but also neighboring conspecifics (Li et al., 2012). Although these chemically-mediated systems are intriguing, their utility as defenses against aspen herbivores remains largely unexplored.

2.1.1. Effects on herbivores

Interactions between aspen and both specialist and generalist insect herbivores are strongly influenced by defense compounds. Phenolic glycosides are particularly important: they shift feeding