Importance of tannins for responses of aspen to anthropogenic nitrogen enrichment

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Abstract
Boreal forests are nitrogen (N) limited, but human activities are leading to increased N inputs, through atmospheric N deposition and forest fertilization. Nitrogen inputs can promote net primary productivity, increase enemy damage, shift plant species composition and community structure. Genetic diversity has been proposed to promote a plant species' stability within communities that experience environmental change. Within any population, specific traits can vary considerably among individuals, and a greater variation may increase chances for the persistence of at least some individuals, when environmental conditions change. Foliar condensed tannins (CTs) vary greatly among different genotypes (GTs), and have been suggested to affect plant performance by influencing growth, plant-herbivore and plant-pathogen interactions, and by affecting litter decomposition. To study how genotypic variation in CT production may mediate the effects of N enrichment on plant performance and litter decomposition, I did several experiments. Aspen GTs with contrasting abilities to produce CTs (i.e. low vs. high) were grown under 3 N conditions, representing ambient N (+0 kg ha^{-1}), upper level atmospheric N deposition (+15 kg ha^{-1}), and forest fertilization rates (+150 kg ha^{-1}). This general set-up was once established in a field-like environment, from which natural enemies were excluded, and in a field with enemies present. I investigated tissue chemistry and plant performance in both settings. CT levels decreased with added N in the enemy-free environment (**study I**), but increased with N when enemies were present (**study II**), which may have been due to differences in soil N availability in the two environments, or due to induction of CTs after enemy attack. Enemy damage increased in response to N, and was higher in low- than in high-tannin plants across all N levels. Growth of high-tannin plants was restricted at the ambient and low N addition level, likely due to a growth-defense trade-off. This growth constraint was weakened, when high amounts of N were added (**study I** and **II**), and when enemy levels were sufficiently high, so that benefits gained through defense could outweigh CT production costs (**study II**). Despite those general responses of low- and high-tannin plants, I also observed many individual responses of GTs to N addition, which sometimes were not connected to the intrinsic ability of the plants to produce CTs. In **study III**, gene expression levels and phenolic pools in plants grown in the enemy-free setting were studied. Gene control over the regulation of the phenylpropanoid pathway (PPP) was distributed across the entire pathway. PPP gene expression was higher in high- than in low-tannin GTs, particularly under ambient N. At the low N addition level, gene expressions declined for both low- and high-tannin plants, whereas at the high N addition level expression at the beginning and the end of the PPP was upregulated and difference between tannin groups disappeared. Phenolic pools were frequently uncorrelated, and only to some extent related to CT production and gene expression. In **study IV**, I assessed the decomposability of litter from the field plants. N enrichment decreased mass loss, but there was a strong GT effect, and GTs were differentially responsive to N. Condensed tannins only had a weak effect on decomposition, and other traits (e.g. SLA and lignin:N ratio) were better predictors for GT differences in mass loss. Nitrogen addition also caused a shift in which traits most strongly influenced mass loss. Collectively, my results highlight the importance of genetic diversity to promote the stability of species in environments that experience anthropogenic change.

Keywords
aspen, foliar condensed tannins, genetic variability, anthropogenic nitrogen enrichment, plant growth, plant defense, litter decomposition, *Populus tremula*

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