



## **Trade-offs between growth, constitutive and induced defense: beyond the carbon source-sink balance**

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Trees are sessile organisms that cannot escape biotic attack but have to build up chemical defences via allocation of resources like carbohydrates. During environmental stress (e.g., drought and shade) trees face a particular dilemma where sparse resources have to be partitioned among competing carbon sinks, including defence but also growth and storage. Our current understanding is that resource allocation to defence is determined by the balance between carbon supply from photosynthesis and carbon demand from growth. However, recent evidence suggests that trees can tightly control a functional equilibrium between growth and defence, particularly upon herbivore attack. Here, we tested whether allocation to inducible defence can occur at the expense of storage and growth during carbon limitation.

To induce carbon limitation we exposed Norway spruce (*Picea abies*) to five weeks of complete darkness followed by a spray-application of methyl jasmonate (MeJA) to simulate insect attacks. We measured biomass, non-structural carbohydrate (NSC) storage, and secondary metabolites (SMs) both constitutive and induced (flavan-3-ols, stilbenes, and diverse terpenoids) either stored in different organs or emitted from the canopy.

Our results showed that shade-induced carbon limitation decreased biomass and concentrations of NSC and constitutive SMs only in young organs, along with a compositional change in SMs relevant for tree defence. Spraying MeJA induced the production of terpenoids and flavan-3-ols independent of organ age, the induction was, however, suppressed by local sugars availability in young needles but not in young branches under shading. Emissions of both constitutive and induced mono- and sesquiterpenes and of methyl salicylate were strongly suppressed after five weeks exposure to complete darkness. After one hour of re-illumination, monoterpenes hydrocarbons rapidly recovered and independent of CO<sub>2</sub> supply, likely due in part to the evaporation of resin monoterpenes through light-induced stomatal openness; by contrast, emissions of linalool and sesquiterpenes did not recover after short re-illumination, indicating that their de novo synthesis may have been suppressed by low carbon availability.

We provide evidence for trade-offs in carbon allocation patterns, defence strategies and metabolic diversity that cannot be explained only by the simple carbon source-sink balance. Allocation to inducible defence was prioritized over growth, storage and constitutive defence. Future studies should investigate how such trade-offs may influence antagonistic relationships with different biotic agents.