

Carbon limitation reveals allocation priority to defense compounds in peppermint

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Studies of carbon partitioning during insect or pathogen infestation reveal high carbon investment into induced chemical defenses to deter the biotic agent (Baldwin, 1998). However, little is known how carbon investment into chemical defenses changes under abiotic stress such as drought. Drought forces plants to close their stomata to prevent water loss through transpiration while decreasing the amount of assimilated carbon. Furthermore drought hampers carbohydrates translocation due to declining plant hydration and reduced phloem functioning (McDowell, 2011; Hartmann et al., 2013; Sevanto, 2014). Hence long lasting drought can force plants into carbon starvation. The aim of our study was to disentangle carbon allocation priorities between growth, maintenance metabolism, storage and production of defense compounds under carbon limiting conditions using peppermint as our model plant. Drought is not the only method how to manipulate plant carbon metabolism and photosynthetic yield. Exposing plants to reduced $[CO_2]$ air is a promising tool simulating drought induced carbon limitation without affecting phloem functioning and so carbohydrate translocation (Hartmann et al., 2015). We exposed peppermint plants to drought (50% of the control irrigation) and to low $[CO_2]$ (progressive decrease from 350 ppm to 20 ppm) to disentangle hydraulic failure from carbon starvation effects on carbon allocation. Drought was applied as a cross-treatment yielding four treatments: watered and high $[CO_2]$ (W+ CO_2), drought and high $[CO_2]$ (D+ CO_2), water and low $[CO_2]$ (W- CO_2), drought and low $[CO_2]$ (D- CO_2). We analyzed the most abundant terpenoid defense compounds (α -Pinene, sabinene, myrcene, limonene, menthone, menthol and pulegone) and used continuous $^{13}CO_2$ labelling to trace allocation pattern of new and old assimilated carbon in the four carbon sinks (structural biomass, water soluble sugars, starch and terpenoid defense compounds) in young expanding leaf tissue. This leaf tissue grew after the start of treatments and after the onset of the $^{13}CO_2$ labelling. Under the control treatment (W+ CO_2) the relative proportion of new carbon in the four carbon sinks was very similar whereas under the three stress treatments (D+ CO_2 , W- CO_2 , D- CO_2) new carbon was preferentially invested into terpenoid defense compounds. This indicates that also under abiotic stress plants need to invest carbon into defense and so protect immature leaf tissue to secure long-term photosynthetic activity (Massad et al., 2014). Even though the concentration of water soluble sugars under both low $[CO_2]$ treatments dramatically dropped, concentration of terpenoid compounds correspondingly change only under the combination of drought and low $[CO_2]$ (D- CO_2), which was the harshest treatment. Drought alone (D+ CO_2) caused high investment of old carbon and concentration increase of water soluble sugars as well as starch compared to other treatments. This carbohydrates increase could be explained by the use of water soluble sugars as osmoprotectants (Dichio et al., 2009) and by the fast growth decline as the main carbon sink (Muller et al., 2011).