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## Balancing the risks of hydraulic failure and carbon starvation: a twig scale analysis in declining Scots pine

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## Abstract:

Understanding physiological processes involved in drought-induced mortality is important for predicting the future of forests and for modelling the carbon and water cycles. Recent research has highlighted the variable risks of carbon starvation and hydraulic failure in drought-exposed trees. However, little is known about the specific responses of leaves and supporting twigs, despite their critical role in balancing carbon acquisition and water loss. Comparing healthy (non-defoliated) and unhealthy (defoliated) Scots pine at the same site, we measured physiological variables involved in regulating carbon and water resources. Defoliated trees showed different responses to summer drought compared to non-defoliated trees. Defoliated trees maintained gas-exchange while non-defoliated trees reduced photosynthesis and transpiration during the drought period. At the branch scale, very few differences were observed in non-structural carbohydrate concentrations between health classes. However, defoliated trees tended to have lower water potentials and smaller hydraulic safety margins. While nondefoliated trees showed a typical response to drought for an isohydric species, the physiology appears to be driven in defoliated trees by the need to maintain carbon resources in twigs. These responses put defoliated trees at higher risk of branch hydraulic failure and help to explain the interaction between carbon-starvation and hydraulic failure in dying trees.