



Adult beech and spruce under experimental drought – linking leaf physiology, phloem transport and tree rings by stable C and O isotopes

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Stable carbon (C) and oxygen (O) isotopes have become a widely used and powerful tool in tree ring research to infer tree physiological behavior. However, the strength of the link between leaf physiological processes on one side and stable isotopes in tree rings on the other side has been challenged in several recent reviews. For instance, transport along the phloem pathway may alter the signature of both C and O isotopes of the transported sucrose. While for C the link appears more direct, things get more complex in the case of O by e.g. exchange processes with source water during cellulose formation and methodological challenges during sample preparation. Hence, there is an urgent need for experimental studies on mature trees with parallel stable isotope information on both leaf physiology and tree rings to improve our understanding of the underlying processes.

This contribution largely presents findings from a throughfall-exclusion experiment on adult European beech (*Fagus sylvatica*) and Norway spruce (*Picea abies*). In addition, some related data from a natural precipitation gradient (PGR) in central European forests are presented, where C isotope signatures proved to be a more sensible indicator of tree responses to drought than stem diameter growth. Study objects are pure and mixed forest stands dominated by adult individuals of the two species (60 - 100-years old). At the throughfall-exclusion experiment (TEE), trees are readily accessible via canopy crane (Kranzberg Forest site, southern Germany), allowing for detailed assessments of leaf physiological processes. Impact by repeated summer droughts are assessed on about 100 trees assigned to a total of 12 plots (KROOF experiment). Experimental summer drought started in 2014 and was repeated throughout 2017. Precipitation throughfall was completely excluded from spring to late fall (i.e. March to November), resulting in significant drought effects in both species. For example, pre-dawn twig water potentials reached values as low as -2.5 MPa, resulting in reductions in stem diameter growth and rate of photosynthesis by up to 80% under drought, in particular in spruce. Moreover, phloem transport velocity tested through ¹³C-labeling of recent photoassimilates was significantly lowered with xylem water potentials. The link between photosynthesis and stem cellulose (DBH) was assessed based on natural abundance of isotope signatures. In the case of control trees under rather stable environmental conditions, phloem transport did not affect C and O isotope signatures of sucrose in both species. However under drought, mixing of recent photoassimilates with older carbohydrates during phloem transport affected isotopic signatures of transported sucrose, significantly diminishing and delaying impact of drought at the tree ring level. For example, $\delta^{13}\text{C}$ of spruce needles increased immediately in the first year of experimental drought (2014) by 1.5 ‰ whereas a similar increase in tree rings was not observed until 2016, the third year of drought. A quantitative relationship of this mixing effect (i.e. uncoupling of photosynthetic fractionation at the leaf level and isotopic signatures in stem cellulose) was established.