

# Stable isotopes from herbarium specimens reveal physiological responses of plants to global change

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Investigating the impacts of global environmental change on plants remains a challenge. Experiments that scale from leaf to ecosystem have provided important insights into the ways plants and ecosystems respond to changing environmental drivers. Yet, experiments are often short-lived and can not realistically simulate long-term environmental changes. Monitoring programs and historical observations are thus valuable alternatives for studying the impact of environmental change on plants. These are, however, unfortunately rare and often poorly suited to identify the mechanistic and physiological basis by which changes in the environment impact plant life. Analyses of biological collections and in particular herbarium materials could be a valuable complementary approach that allows assessing functional responses of plants to global environmental change.

Specifically the analysis of stable carbon and oxygen isotopes of archived plant material offers the exciting opportunity to reconstruct long-term physiological responses of plants to environmental change (Dawson et al. 2002). The carbon isotope composition of plant materials is a reliable proxy for leaf-level intrinsic water use efficiency (iWUE), which describes the ratio of net photosynthesis over stomatal conductance and thus combines two key plant physiological processes. The oxygen isotope composition of plant materials provides time-integrated information on leaf stomatal conductance. In combination, carbon and oxygen isotope measurements thus allow integrated values for net photosynthesis and stomatal conductance to be explicitly determined (Scheidegger et al. 2000).

The analysis and interpretation of the carbon isotope composition of plant materials is already well established in dendrochronology. Their analysis in tree ring archives have shown that iWUE in trees has generally increased since 1900 by 40 % and that these increases are mostly the result of increases in net photosynthesis in response to increasing atmospheric CO<sub>2</sub> (Mathias & Thomas 2021). In temperate ecosystems, the majority of plants are, however, herbaceous. These plants do not preserve annual growth rings that persist for decades, so isotope-based assessments of their physiological responses to global environmental change are much more difficult. Herbarium specimens fill this shortcoming and can provide valuable study material helping us to understand how global environmental change has been impacting non-woody plant species (Fig.1).

## Keywords

Botanical collections, Ecophysiology, Elevated CO<sub>2</sub>, Intrinsic water use efficiency, Time series

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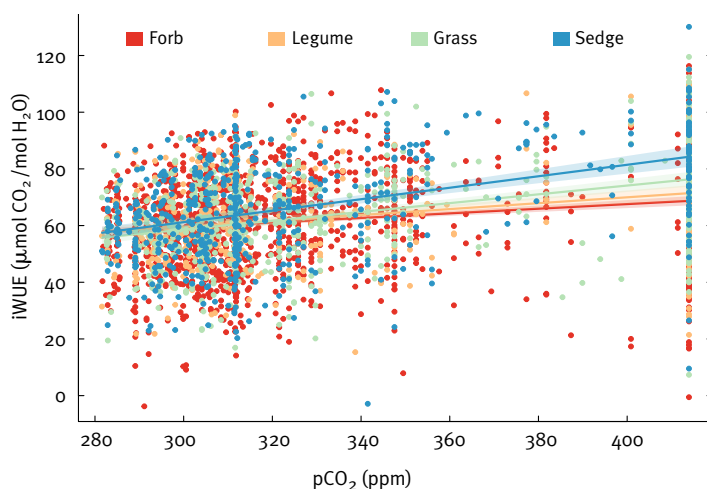
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**Fig. 1.** Collecting for the herbarium of the Basel Botanical Society (BASBG), a primary source of specimens for this study. Scheltenpass, BE, Switzerland, 22 June 2022. Photo Aurélie Grall

We analyzed the carbon isotope values ( $\delta^{13}\text{C}$ ) of over 3000 Swiss specimens from the Herbaria Basel (BAS/BASBG), representing 89 species and the years 1900–2020. Our analysis shows (Fig. 2) that herbaceous plants improved their iWUE over the past century. The increase in iWUE was, however, smaller than that of trees reported previously. Moreover, responses differed significantly among forbs, legumes, grasses and sedges. Future analysis of the oxygen isotope composition of these samples will help to identify if changes in the intrinsic water use efficiency in herbaceous plants are the result of higher net photosynthesis or the result of reduced stomatal conductance. Already, our study demonstrates that all plants, not just trees, respond sensitively to global environmental changes with possible implications for ecosystem carbon and water relations. Our study also shows that stable isotope analysis of herbarium materials is a powerful tool to address the effects of global environmental change on the physiology of a large range of plant species, and that important differences in these responses among plant functional groups exist.



**Fig. 2.** Changes in intrinsic water use efficiency (iWUE), which is the ratio of photosynthesis over stomatal conductance in response to increasing atmospheric  $\text{CO}_2$  concentrations revealed by the stable carbon isotope analysis of over 3000 herbarium specimen from 89 temperate herbaceous plant species collected in Switzerland between 1900 and 2020.

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