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^{13}Carbon allocated to the leaf growth zone of *Poa pratensis* reflects soil water and vapor pressure deficit

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Introduction

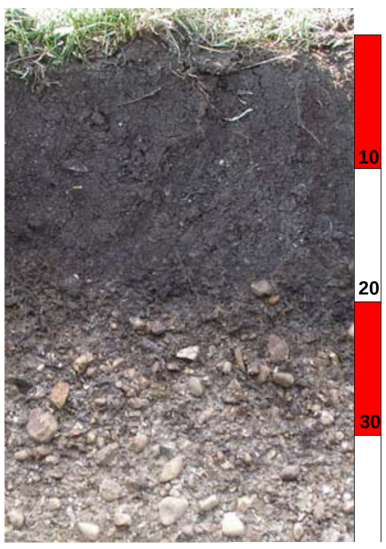
Water stress affects the relationship between stomatal conductance and photosynthetic capacity and modifies discrimination (Δ) of the heavier ^{13}C through the stomatal coupling of water vapor loss and CO_2 assimilation. Thus, water stress is recorded in the isotopic composition of the assimilates. The CO_2 concentration in the intercellular space relative to air (c_c/c_a) can then be estimated from Δ as

$$c_i / c_a = \frac{\Delta - a}{b - a}$$

where *a* is the fractionation due to diffusion in air (4.4 ‰) and *b* is the fractionation by carboxylation (~27 ‰) (Farquhar *et al*. 1989).

Schnyder *et al*. (2006) have shown that differences in water availability lead to an isotopic signal, which was transferred from herbage to grazer tissues. A much finer spatio-temporal resolution and hence more direct insight into the effects of water stress is achievable by analysis of the carbon isotope composition (δ^{13}C) of the leaf growth zone (LGZ), which is fed by recent assimilates and hence records water stress in the habitat of a plant at a daily resolution.

Water stress results from two drivers, the soil water content (SWC) and the atmospheric water vapor deficit (VPD). The δ^{13}C of the LGZ could allow quantification of the overall contribution of these drivers.



Here, we tested **the hypothesis** that the LGZ is a high-resolution recorder of water stress. We use this to quantify the influence of VPD and SWC within a wide range in natural conditions. To do this, we took advantage of fully drained peat soils overlaying gravel, which provided a wide range of rooting depths that were well defined due to a sharp discontinuity between peat and gravel. Other soil properties and grazing conditions were similar.

Materials & Methods

At the Grünschwaige Grassland Research Station, situated at the north end of the Munich Gravel Plain, Germany (435 m a.s.l.), the LGZ (lower half between the last nodium and the ligule) of *Poa pratensis* was sampled three times (early spring to mid summer) at 10-11 sites differing in soil water capacity to cover wide ranges in SWC and VPD. Volumetric SWC was determined by taking soil cores of the peat soil. The soils were well above the groundwater table during sampling.

Plant available water was modeled following Allen *et al*. (1998) and yielded r^2 = 0.8 with SWC. Both were largely determined by soil depth, which varied from 5 to 95 cm.

VPD was taken from a meteorological station at 3 km distance.

The δ^{13}C of the LGZ was measured and Δ was calculated by taking into account the seasonal variation of δ^{13}C in air CO_2 following Wittmer *et al*. (2008).

References

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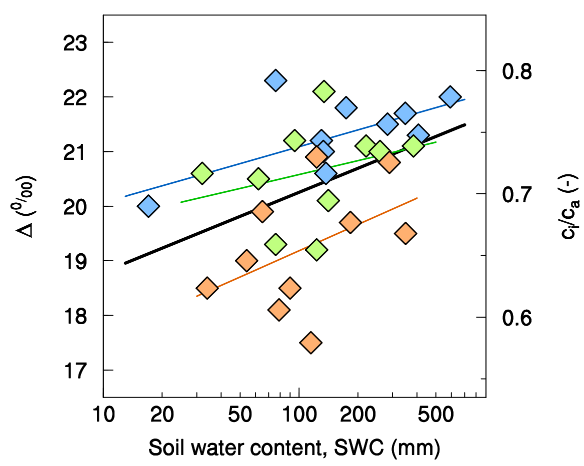
Conclusions

The leaf growth zone recorded the relationship between stomatal conductance and photosynthetic capacity as influenced by water stress with high temporal resolution. In this study, atmospheric vapor pressure deficit had a stronger effect than soil water content. Together both drivers changed CO_2 concentration in the intercellular space by 35%.

Results & Discussion

The air temperature at the time of sampling varied between 10 and 25 °C, VPD varied between 0.5 and 1.2 kPa. SWC varied between 15 and 500 mm between sites and dates while plant available water differed between 10 and >200 mm.

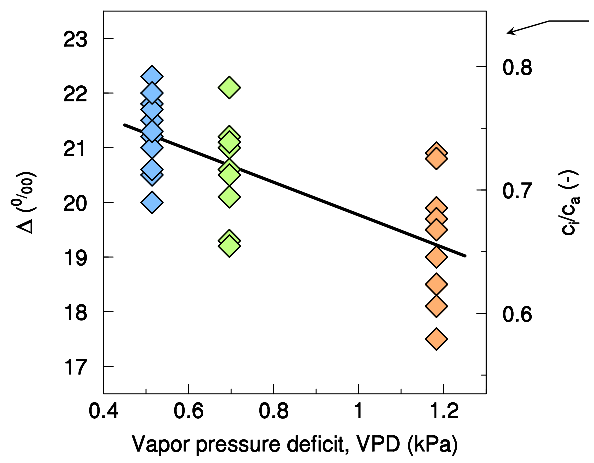


Legend:
blue = April, green = May, orange = July;
thin lines = monthly regressions,
thick line = overall regression.

Δ varied by ~ 5 ‰ and increased with increasing **SWC** while CO_2 concentration in the intercellular space increased by 35% from c_i/c_a = 0.58 to 0.79.

The influence of SWC was sub-proportional (logarithmic) indicating that an increase in water supply had a stronger effect if the initial SWC was low than on an initially wet soil. Furthermore, the influence of SWC seemed to be smaller (r^2 = 0.18, P < 0.05) than that of VPD (r^2 = 0.48, P < 0.001) although VPD differed only by a factor of three, while SWC differed by two orders of magnitude.

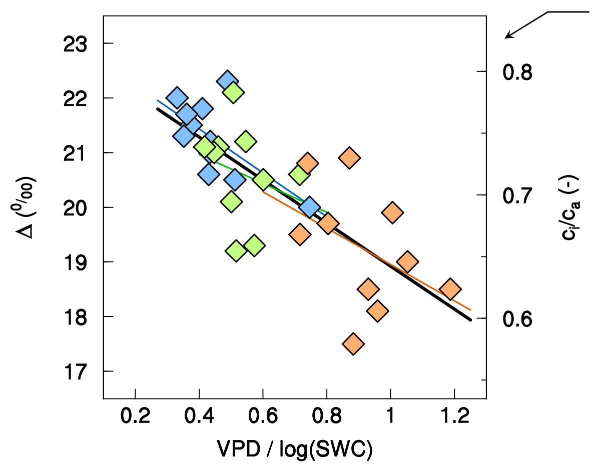
The regressions were shifted between months, but, interestingly, the slope of Δ towards SWC did not differ with month (= different VPD). This indicated that the influence of SWC was independent from VPD, although at low VPD also SWC usually had a smaller range than at high VPD (the standard deviation of SWC was 175 mm at VPD = 0.5 kPa, while it was 105 mm at VPD = 1.2 kPa).



Δ strongly decreased with increasing **VPD**. The influence of VPD was more pronounced than that of SWC. However, a high VPD was generally associated with a low SWC. The seasonal trend of VPD hence also included some seasonal variation in SWC.

This also implied that the influence of soil water availability on stomatal opening, discrimination and water use efficiency thus not only depended on the soil properties in the rooting zone of a particular plant but also on soil properties on a larger scale, which is large enough to influence VPD substantially.

In consequence, the influence of SWC must become more important on a larger spatial scale, which integrates over the mosaic of soils, and on a larger temporal scale, because daily fluctuations in VPD level out while the effects of the slowly changing SWC accumulate. This agrees with the finding by Schnyder *et al*. (2006) that the variation in discrimination between pastures and between years was closely related to the variation in SWC on the pasture scale.



Combining both counteracting influences in **a ratio VPD/log(SWC)** then explained 58% of the Δ variation (root mean squared error: 1.25 ‰). More importantly, the regressions for the individual dates did not deviate from the overall regression, indicating that VPD/log(SWC) fully accounted for both influences.

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