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Unpredictable responses to interactions between climatic drivers: Impact of warming, elevated CO₂, drought and their combinations on photosynthesis and growth patterns of heath plants

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The impact of elevated CO₂ [CO₂], warming [T] and drought [D] on heath ecosystem processes are investigated in the CLIMAITE project in which the modelled climatic scenario for Denmark in year 2075 are simulated [1]. The experiment is unique as it evaluates the interactions between drivers on ecosystem processes across scales ranging from ecosystem to leaf gas-exchange, primary production and biodiversity, in order to unravel the complex multi-factor impacts on water, carbon and nitrogen cycles.

Here we focus on the responses in growth pattern and photosynthesis for the evergreen dwarf shrub *Calluna vulgaris* during most of a growing season. From mid April, the first shoot growth phase of *Calluna* was characterized by shoot extension and increased leaf area per unit biomass, and also the leaf C/N ratio increased. The photosynthetic capacity was unchanged, as maximal electron transport rate (J_{\max}) and maximal velocity of Rubisco carboxylation (V_{\max}) showed little variation between May and July. However, the rates of photosynthesis and transpiration were stepwise decreased during this phase in parallel with decreasing water availability. After flowering a second phase of shoot growth from August to October was characterized by shoot extension and increase in leaf area per biomass, high leaf nitrogen concentration and increasing green-to-brown biomass ratio. The photosynthetic capacity was higher and no indications of senescence were significant even in late October. Hence, the photosynthetic rates increased and transpiration levels were high, in parallel with increasing amounts of precipitation and extraordinary warm autumn temperatures. From this growth pattern we hypothesize *Calluna* to have the potential to benefit from an extended growing season in response to [T] and also to benefit from CO₂ fertilization in response to [CO₂]. In addition, *Calluna* is expected to exhibit drought tolerance in response to [D].

Across the season [CO₂] did not induce any down regulation of V_{\max} or J_{\max} but increased net photosynthesis directly via increased intercellular CO₂ concentration. [T] caused an earlier start of the growing season via shift in phenology but *per se* [T] did not pose strong effects on photosynthesis and transpiration. However, the increased water consumption led to water shortage when combined with [D] resulting in a significant [T*D] and [T*CO₂] interaction during the experimental drought. In late autumn the [T] increased the green to brown biomass ratio and photosynthesis, but only in combination with [CO₂], which caused a significant [T*CO₂] interaction in October. In addition to the natural drought, the experimental drought decreased the soil water content even further and extended drought conditions for several weeks. The decrease in soil water content had negative impact on the plant water potential and transpiration in [D]. This led to decreased photosynthetic capacity via decreased J_{\max} and V_{\max} , and photosynthesis was reduced in response to [D]. In parallel, growth and green-to-brown biomass ratio were decreased in response to [D] and [T] during the experimental drought period.

The response patterns clearly demonstrate an earlier start up caused by warming, promoting water shortage and decreased net photosynthesis during the experimental drought period. Elevated CO₂ increased the net photosynthesis during the growing season, and to a larger degree than expected when combined with warming. [D] has a negative effect on water relations and decreased photosynthesis, and more than expected when combined with either warming or elevated CO₂. These findings could not be deduced from single factor experiments. Therefore, the multifactor experimental approach does indeed contribute to our understanding of the impact of climatic change on ecosystems.

[1] T.N. Mikkelsen *et al.*, *Functional Ecology*, 2008, 22(1), 185-195.