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Habitat responses of fossil plant species to palaeoclimate – Possible interference with CO_2?

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ABSTRACT

One important tool for palaeoclimate reconstruction uses climate space data of extant species representing the Nearest Living Relatives of fossil taxa, under the assumption of taxon-specific climate demands remaining unchanged through time. This is problematic because the calibration of these proxies is based on current vegetation that has grown under current CO_2. Atmospheric CO_2 may interfere with taxon-specific climate demands, particularly water availability, because stomatal conductance is negatively correlated with CO_2. In order to assess direct effects of CO_2 on gas exchange, results of numerous experimental studies are available to provide benchmark data. Experiments will, however, always provide data which are restricted to response ranges that living plants are able to express. Simulation models of plant gas exchange offer additional possibilities to explore the influence of CO_2 on gas exchange and to consider evolutionary adaptation to gas exchange.

In this study, the potential effects of a changing CO_2 level on photosynthesis performance under simultaneously changing water availability and temperature is evaluated by using a model based on optimized gas exchange, including different scenarios of photosynthesis regulation that may result from evolutionary adaptation. The results illustrate the impact of changing CO_2 on water and temperature demands under these various conditions, indicating 1) a particularly substantial influence of CO_2 under low CO_2 (<380 ppm); 2) for higher levels of CO_2 (>380 ppm) a decreasing influence under further increasing CO_2, and 3) the relevance of possible evolutionary adaptation of the photosynthetic machinery to a changing CO_2 level. Downregulation of photosynthesis, for instance, leads to a distinctly enhanced response of gas exchange to increasing CO_2, particularly under low to moderate levels (180 ppm–380 ppm). Changes in atmospheric CO_2 therefore adds an additional source of uncertainty to those already considered for NLR based methods. It may, however, also offer new possibilities for palaeoecophysiological research.

1. Introduction: why CO_2 matters when using fossil plants as palaeoclimate archive

Assessing terrestrial palaeoclimate from fossil vegetation is a widely established tool, with a fairly long history (Heer, 1855, 1856, 1859; see also Mai, 1999; Utescher et al., 2014). The concept is based on deriving past climates from modern relationships between plant species/traits and environment. Species-based methods rely on the Nearest Living Relative (NLR) concept, presuming that climatic ranges of lineages remain more or less constant over time. Additionally, it is assumed that the more closely related a fossil and a recent species are, the more similar should be their environmental demands. Modern NLR based methods, such as the Coexistence Approach (CA) (Mosbrugger and Utescher, 1997; Utescher et al., 2014), the Climatic Amplitude method (Fauquette et al., 1998), or the Probability Mutual Climatic Spheres (Pross et al., 2000) aim at obtaining quantitative climate parameters from fossil vegetation that also allow for comparison with climate data from other methods, such as climate simulations.

Undoubtedly, concepts exploiting fossil vegetation for palaeoclimate reconstruction are extremely valuable and have provided a wealth of data thus far (Utescher et al., 2014). There are, however, concerns with respect to palaeoclimate situations which have no modern counterpart, termed “no-modern analogue climate” (Jackson and Overpeck, 2000; Jackson and Williams, 2004).

One example is the situation of “warm” polar regions under greenhouse conditions that allowed for the existence of forests in high latitudes which are nowadays covered in ice and largely barren (Poole et al., 2005). These fossil forests experienced solar conditions of the high latitudes (solar incidence angle, day/night cycles) under otherwise hospitable conditions, a situation unmatched today. Likewise, subtropical and tropical conditions prevailed during the past at latitudes which

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are much cooler at present (Utescher et al., 2009). Apart from combinations of temperature, water availability and latitude which lack a modern analogue, past CO_2 levels were much higher or lower than today. CO_2 – being the substrate of photosynthesis - is a highly important environmental parameter for plants. Good examples in this respect are the results pertaining to so-called "super-elevated" CO_2, meaning levels exceeding 1000 ppm, often related to conditions of space stations where levels of 5000 ppm and more can easily develop (Wheeler et al., 1999). Beyond 1000 ppm, plant responses become, firstly, erratic and, secondly, sometimes deleterious, comprising chlorosis and other damages (see citations in Wheeler et al., 1999). The reason for the high sensitivity of plants to CO_2 is easy to find: CO_2 is the substrate for photosynthesis, and therefore a crucial factor for the regulation of plant gas exchange and numerous other physiological processes.

For photosynthesis to take place, plants have to be permeable to let CO_2 diffuse into the leaf (or any other assimilating organ). Being permeable to atmospheric gases means, however, – since the atmosphere is usually undersaturated with water vapor – losing water by transpiration. The development of the active gas exchange regulation is one of the main drivers of early land plant evolution, leading to the existence of stomata on even the oldest upright plant taxa (Edwards et al., 1998; Raven and Edwards, 2014). Together with the existence of a cuticle preventing largely the uncontrolled loss of water vapor, the ability of the guard cells to regulate the stomatal aperture is crucial to plant function.

Closing the stomatal aperture decreases stomatal conductance, g_s, and therefore transpiration, allowing for enhanced water conservation. Decreasing g_s, however, also means lower CO_2 influx, and thereby a decreasing photosynthesis rate. To reconcile both conflicting processes, water conservation and photosynthesis, complex stomatal control processes evolved, with various triggers coming from the environment and from within the plant (Fig. 1) (Buckley, 2005). Guard cells are, for example, sensitive to air humidity and CO_2. There are a multitude of data of stomatal conductance responses to environment that demonstrate trade-offs between CO_2 gain and water conservation. For example, stomata tend to be wide open during the morning hours because relative air humidity is high during this time (Larcher, 2003). High air humidity means a low humidity gradient between leaf internal and external air, and therefore low potential transpiration, allowing the combination of a high photosynthesis rate and a low transpiration rate. In short, under conditions of high air humidity, a plant has access to "cheap" CO_2, meaning that the amount of water that is lost for gaining a certain amount of CO_2 is low. When the air humidity falls, stomata tend to close in order to avoid excessive water loss. Likewise, high soil humidity promotes high stomatal conductances whereas stomata tend to close when the soil becomes dry.

From these considerations one would expect changing CO_2 to affect water relations and therefore water demand of a plant species. In fact, this was often demonstrated in numerous experiments in which plants were exposed to elevated CO_2. The largest amount of recent data available so far comes from so-called FACE experiments (Free Air Carbon Enhancement) carried out with different durations and plant species at various sites, practically around the world, for about twenty years now (Hendrey and Kimball, 1994; Leakey et al., 2009; Norby and Zak, 2011). With the target of elevated CO_2 being about 550 ppm, stomatal conductance decreased in almost all cases, albeit with significant differences between species and growth forms, and also between sites (Ainsworth and Rogers, 2007). Moreover, a decreasing g_s and plant water savings were also demonstrated for natural vegetation under the current anthropogenic CO_2 increase (De Boer et al., 2011; Lammertsma et al., 2011).

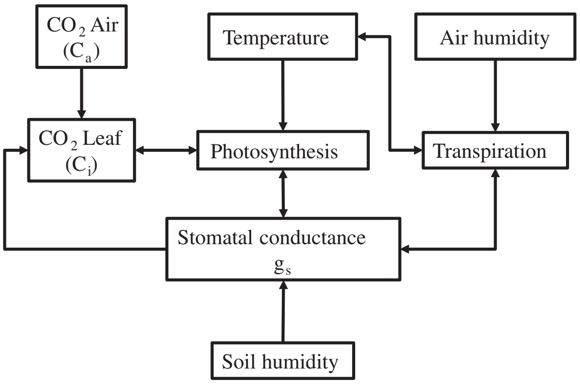

Fig. 1. Basic components of gas exchange and their interaction with environmental parameters. Double-headed arrows indicate mutual dependence between two parameters. Please note that not all factors and interrelationships are included.

It therefore seems that elevated CO_2 could lead to a decrease in species-specific humidity demand. Humidity is an important environmental factor for a plant, and species-specific differences in water requirements dictate habitat suitability to a large degree (Blackman et al., 2012; Engelbrecht et al., 2007). The potential effect of CO_2-modulated shifts in habitat suitability is illustrated by results of process-based vegetation models that include submodels of assimilation and gas exchange for the considered Plant Functional Types or species. For instance, a simulation conducted by Cheaib et al. (2012), demonstrated a drastic effect of CO_2 on future distribution of various tree species. Moreover, temperature affects both photosynthesis and transpiration. Assimilation rate increases with increasing temperature, until an optimum is reached (Bernacchi et al., 2003). A rise in temperature promotes evaporation twofold, firstly via enhancement of diffusion, and secondly via decrease of relative humidity. For palaeoclimate reconstruction based on fossil plant species, these effects pose the question of how reliable are inferences drawn from water and temperature demands of nearest living relatives when these demands may possibly shift under changing CO_2?

In this study, an attempt will be made to, firstly, suggest a rough ecophysiological assessment of the relevance of CO_2 for fossil species distribution, and, secondly, to discuss basic aspects of possible scenarios. At this point it should be mentioned that evolution and performance of C_4 photosynthesis is another important aspect of the interrelationship between plant physiology, plant evolution and atmospheric CO_2 (Edwards et al., 2010; Pagani et al., 1999; Sage, 2004). The case of C_4 will, however, not be further considered here, and we will focus exclusively on C_3 photosynthesis.

2. Methods: conceptual framework to assess potential impact of CO_2 on habitat shifts

2.1. Gas exchange modeling

The question that will be addressed is: to what extent do changes in CO_2 have an impact on assimilation and transpiration under different humidity and temperature regimes? Since CO_2 acts upon water demand via photosynthesis, it appears straightforward to begin with an evaluation of the impact of CO_2 on plant gas exchange and assimilation, considering that sufficient (species-specific) rates of photosynthesis represent a basic necessity for a plant. There are, of course, many factors other than water availability and its interaction with CO_2 that dictate the kind of habitat which can be successfully colonized by a species, such as interactions between taxa (Meier et al., 2011). Harvesting sufficient carbohydrates by photosynthesis is, however, basic to all vital functions of a plant, from primary metabolism tasks to reproduction. In fact, the relevance of carbon starvation is extensively discussed under different aspects, such as the potential threat of carbon starvation caused by stomatal closure under conditions of prolonged drought (Martínez-Vilalta et al., 2012; McDowell, 2011; Sevanto et al., 2014), or low CO_2 during glacials (Bennett and Willis, 2000; Robinson, 1994; Ward et al., 2005).

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