The interactive effects of elevated CO₂, temperature and initial size on growth and competition between a native C₃ and an invasive C₃ grass

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Abstract

A controlled environment experiment was conducted to determine the impact of enhanced carbon dioxide and temperature on competition between the C₃ grasses Austrodanthonia eriantha and Vulpia myuros. Plants were grown in mixtures and monocultures to compare the responses both with and without an interspecific competitor. Temperature and CO₂ were set at current levels (350 ppm CO₂; 20 °C day and 10 °C night temperature), in factorial combination with enhanced levels (700 ppm CO₂; 23 °C day and 13 °C night temperature). To examine the potential impact of initial seedling size on competition under elevated CO₂ and temperature, the two species were combined in mixtures of differing initial sizes. Above-ground growth of all plants was enhanced by increased CO₂ and temperature alone, however the combined temperature and CO₂ treatment showed a sub-additive effect, where growth was less than expected based on the responses to each factor independently. Austrodanthonia in mixture with Vulpia plants of the same initial size experienced a 27% reduction in growth. Austrodanthonia grown in the presence of an initially larger Vulpia plant experienced a 58% reduction in growth. When the Vulpia plant was initially smaller than Austrodanthonia, growth of the Austrodanthonia was reduced by 16%. The growth of Vulpia appeared to be largely unaffected by the presence of Austrodanthonia. Variation in the CO₂ and temperature environment did not affect the pattern of these interspecific interactions, although there was some evidence to suggest that the degree of suppression of Austrodanthonia by Vulpia was less under elevated CO₂. These results do not support the initial advantage hypothesis, as Vulpia was always able to suppress Austrodanthonia, regardless of the initial relative sizes of the competitors. Furthermore, the lack of an effect of changing the CO₂ or temperature environment on the direction of interspecific competition suggests that the competitiveness of the invasive Vulpia will be minimally affected by changes in atmospheric CO₂ concentration or temperature.

Introduction

Over the next 100 years anthropogenic emissions of greenhouse gases are expected to result in at least a doubling of current atmospheric CO₂ concentration, from approximately 350 to 700 ppm, leading to further human-induced perturbations to the global climate system. For temperate Australia, predicted changes include decreased summer precipitation, with up to a 4 °C increase in temperature (IPCC 2001). Because many physiological processes in plants are sensitive to these changing factors, and these sensitivities are likely to differ between species, we can therefore expect associated changes in plant commu-
nity structure and function (Ackerley et al. 1992; Coleman and Bazzaz 1992; Mooney et al. 1999; Moore 2004). Individual species might respond to such changes in their pattern of growth and photosynthetic allocation, changes in phenology, or changes in reproductive output. At a community level there is the potential for these responses to be modified due to both inter and intraspecific interactions (Wayne et al. 1999). Further community-level effects include the possibility of climate change induced shifts in disturbance regimes (Williams et al. 2001), which have the potential to alter successional processes, and to provide opportunity for the introduction and establishment of new species in the community.

Predicting community-level responses is a formidable task, so it is understandable that many early studies targeted single species, often with independently manipulated levels of e.g., CO₂ and temperature (Davis et al. 1998; Mooney et al. 1999; Wand et al. 1999). Focusing on one species and one factor atler atn, however, precludes the detection of the interactive effects among the factors, and the potential for the responses to these factors to influence the competitive balances within plant communities (Morse and Bazzaz 1994; Tueghels et al. 1995).

**Individual plant responses to CO₂ and temperature**

The potential importance of the interaction between CO₂ and temperature on plant growth and development is well recognised (Long 1991; Gifford 1992). An analysis of the biochemistry of photosynthesis predicts that plants utilising the C₃ photosynthetic pathway are expected to *a priori* show a strong CO₂ × temperature interaction, such that the positive growth response to increasing CO₂ concentration is expected to be enhanced at higher temperatures. In contrast, C₄ plants are expected to show little or no response to changing CO₂ concentration, regardless of temperature, due to the CO₂ concentrating mechanism in C₄ photosynthesis (Morison and Lawlor 1999).

The many studies that have sought to simultaneously manipulate both CO₂ and temperature have been the subject of at least two major reviews (Rawson 1992; Morison and Lawlor 1999). Despite the clear theoretical predictions outlined above, both Rawson (1992) and Morison and Lawlor (1999) conclude that observed responses are varied, and that generalisations are difficult to make. For example, although plant growth and development is generally accelerated by increased temperature, manipulating CO₂ was found to variously promote, retard or have a neutral effect. Also, a number of C₄ plants have shown strong and significant responses to experimental manipulation of CO₂ (Morison and Lawlor 1999; Wand et al. 1999). Morrison and Lawlor (1999) discuss these trends in detail, concluding that the variation in the observed results is likely due to the interactions between temperature and CO₂ with many other factors that are not controlled for across experiments, such as differences between edaphic and climatic conditions, differences in plant development patterns, and nutrient status.

**Plant competition, CO₂ and temperature**

Despite significant research on the responses of individual plants or species to simultaneously manipulating both temperature and CO₂, potential impacts on the competitive balance in multi-species mixtures in response to simultaneous manipulation of these two variables has received very little attention. Experimentally quantifying interspecific competition requires the comparison of plants grown in multi-species mixtures with their performance in corresponding monoculture (Harper 1977). In a recent review, Poorter and Navas (2003) listed 33 studies which had investigated the impact of increasing CO₂ on plant competition. Of these 33 studies, 7 considered only intraspecific competition, with the remaining 26 including designs with more than one species. Of these 26, 14 included both the monoculture and multi-species mixtures necessary to quantify the strength of interspecific competition. Of these 14, only one had additionally manipulated both CO₂ and temperature (Tueghels et al. 1995). Outside of this review, we are aware of only one other study which has simultaneously manipulated both CO₂ and temperature, and also investigated interspecific competition via comparison of monocultures and species mixtures (Lilley et al. 2001a).

Although specific studies simultaneously investigating the interactions between CO₂, temperature and plant competition are rare, a number of studies have investigated competition × CO₂ interactions (e.g., Polley et al. 1994; Stewart and Potvin 1996), or have combined CO₂ treatments with other factors such as nutrient levels, soil water or light (see review by Poorter and Navas 2003). There also exist a number of studies in which multi-species mixtures have been subject to CO₂ manipulation, with the response of the