



Do interactions with neighbours modify the above-ground productivity response to drought? A test with two grassland species



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ABSTRACT

Natural systems are predicted to be exposed to more frequent and more intense drought events in the near future. Plant–plant interactions form an important part of the whole of mechanisms that govern the responses of plant species and communities to drought. The accuracy of predictions on ecosystem functioning would therefore be improved by determining when plant interactions need to be considered and how these interactions can drive species responses. In this study, we assessed the effect of neighbour plants on the drought response of a target plant. Two grassland species (*Plantago lanceolata* and *Lolium perenne*) were grown in the presence of either six conspecific or three conspecific and three heterospecific neighbours in sunlit growth chambers. They were subjected to drought by withholding water for 20 days. Regardless of the identity of the target plant, having *P. lanceolata* as a neighbour increased the susceptibility to negative drought effects on biomass production while *L. perenne* neighbours buffered the target's drought response. Our results therefore suggest that drought responses depended largely on the identity and the traits of the neighbours. Such findings demonstrate that current models to predict ecosystem functioning may be misleading by not sufficiently taking plant–plant interactions into account.

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1. Introduction

Natural systems are increasingly subjected to environmental change. Low soil water availability caused by drought is one of the major limitations for plant growth (Chaves and Oliveira, 2004; Schulze et al., 1987), while the probability and severity of drought episodes is projected to further increase (IPCC, 2013). Drought studies have therefore been carried out in considerable numbers, typically focusing on the morphological, physiological and biochemical changes of individual plants (e.g. Chaves et al., 2002; Flexas et al., 2004; Lawlor and Tezara, 2009). Decreased water availability limits plant productivity mainly by stomatal closure, down-regulation of photosynthesis, slower cell expansion and/or by carbon allocation to the roots and to protective molecules (Benjamin and Nielsen, 2006; Chaves et al., 2002; Praba et al., 2009). However, how individual plants in a community respond to water deprivation is not only determined by species-specific characteristics but also by the nature of interactions with neighbouring plants.

Differences between species in the ability to sequester resources and to produce biomass lead to diverse plant–plant interactions involving competition and partitioning of resources in varying degrees (Hooper, 1998; Hooper et al., 2005; Verheyen et al., 2008). These interactions are obviously critical in determining the outcome of the response to resource depletion. For instance, if competition between species for water is low, a species will likely respond less to water deprivation when surrounded by neighbours from the other species (=heterospecific) than when surrounded by neighbours from the same species (=conspecific) (if the water content before the onset the drought is similar, see Van Peer et al., 2004). Spatial complementarity in water use occurs when species differ in root distribution, so that heterospecific neighbours at least partially extract water from different soil zones (Nippert and Knapp, 2007; Verheyen et al., 2008). On the other hand, differences in water use between species can cause an altered timing and intensity of soil drying, which can favour or disadvantage the target's susceptibility to water deprivation. If a species is surrounded by neighbours with a high water consumption, it will likely suffer from water deprivation earlier than if it were surrounded by water saving species, irrespective of whether its neighbours are con- or heterospecific.

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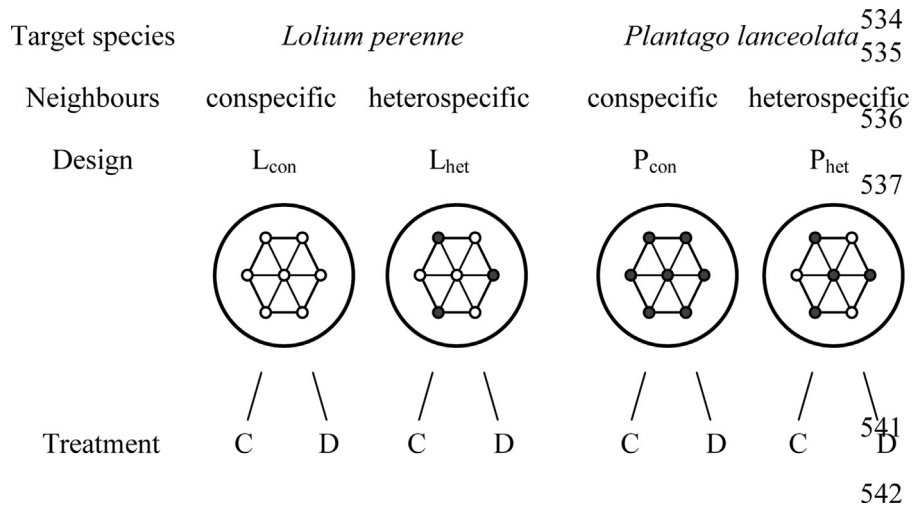


Fig. 1. Schematic presentation of the target-neighbour designs with control (C) and drought (D) treatments. The drought treatment was obtained by withholding water for 20 days (day of year (DOY) 197–217), whereas in the control treatment the watering regime was not interrupted. White circles represent *Lolium perenne* individuals, grey circles represent *Plantago lanceolata* individuals. The inner diameter of the containers is 19 cm and plants are positioned at 5 cm interspace.

In this study, two target species were subjected to drought by withholding water for 20 days. To investigate the importance of neighbours on the drought response, the targets were surrounded either by six conspecific or by an equal mix of conspecific and heterospecific neighbours. We hypothesise that, if complementarity is limited, such as is presumably the case for the two species we selected (Weeve, 1975), neighbours can favour or disadvantage target plants, by altering the water availability for the targets, depending on the rate of water use of the neighbours. To detect these effects, we determined above- and below-ground biomass, soil water status, stomatal conductance and photosynthesis.

2. Materials and methods

2.1. Experimental set-up

For this study, two common and co-occurring grassland species with comparable height and rooting depth (Weeve, 1975) (*Lolium perenne* L. and *Plantago lanceolata* L.) were each grown as target plant surrounded by six neighbour plants at equal distances. The six neighbours were either conspecific to the target (further referred to as 'conspecific neighbours') or composed of three conspecific and three heterospecific plants (further referred to as 'heterospecific neighbours') (Fig. 1). This yields four designs with different combinations of targets and neighbours: *L. perenne* or *P. lanceolata* with conspecific or heterospecific neighbours (further referred to as L_{con}, L_{het}, P_{con} and P_{het}, respectively) (Fig. 1).

The species were sown end of March 2010, with a time lag to prevent differences in size at the start of the experiment (Cotrufo and Gorissen, 1997) due to differences in germination rate (*P. lanceolata* day of year (DOY) 76, *L. perenne* DOY 88). The seedlings were transplanted end of April (DOY 116–118) in PVC containers (19 cm inner diameter, 40 cm height, 11.33 L), filled with sandy soil (93.2% sand, 4.6% silt, 2.2% clay; field capacity 0.13 m³ m⁻³; pH 7.6; total Kjeldahl-N 0.42 g kg⁻¹; 1% C in humus). The seven plants were placed in a hexagonal grid at 5 cm interspace with the target species positioned at the centre of the grid. All communities were fertilised with 10 g m⁻² NH₄NO₃, 5 g m⁻² P₂O₅, 10 g m⁻² K₂O and micro-elements (Fe, Mn, Zn, Cu, B, Mo). The fertiliser was given dissolved in water in two equal amounts at DOY 140 and 180.

Three replicates per design (yielding 12 containers) were randomly placed in each of eight sunlit, climate-controlled chambers facing south. The study was conducted in climate controlled

greenhouses so that water deprivation was the only environmental variable. The chambers followed fluctuating air temperatures mimicking an average daily air temperature course, calculated over the period 1996–2005. The distances between the chambers were maximised to avoid mutual shading. The interior surface area was 1.5 m × 1.5 m, the height at the north side 1.5 m and at the south side 1.2 m. The top of the chambers consisted of a colourless polycarbonate plate (4 mm thick), whereas the sides were made of polyethylene film (200 μm thick), both UV transparent. The experimental set-up is located at the Drie Eiken Campus, University of Antwerp, Wilrijk, Belgium (51°09' N, 04°24' E), where average annual precipitation is 776 mm (evenly distributed throughout the year) and average annual air temperature 10.6 °C. Every half hour, the air temperature was monitored with a temperature sensor (Siemens, type QFA66, Erlangen, Germany). During the experiment (28 April–5 August 2010, DOY 118–217), monthly average air temperature was 12.7, 18.4 and 20.9 °C in May, June and July, respectively.

Irrigation was calculated from the monthly rainfall over the period 1995–2005 and corrected for differences in evapotranspiration (ET) inside and outside the chambers. To this end, De Boeck et al. (2006) calculated ET inside the chambers from changes in soil water content (SWC) and the amount of administered water, and the outside ET with Hamon's equation (Haith and Shoemaker, 1987) based on day length, vapour pressure and air temperature. The containers were watered every two days according to the 10 year average of 14–15 raining days per month during the growing season. Total monthly irrigation matched 61.5, 64.4 and 85.1 mm in May, June and July, respectively. Water could freely drain from the containers while capillary rise of ground water towards the containers was prevented by a drainage system placed below the chambers.

2.2. Imposed drought

Each design was subjected to two treatments: a drought treatment and a control treatment (Fig. 1). The treatments were given at chamber level. Four of the eight chambers were subjected to a period of water deprivation by withholding water for 20 days (DOY 197–217) (referred to as 'imposed drought' or 'drought'). In the other four chambers, the watering regime was not interrupted (control treatment). The length of the imposed drought was chosen to be severe but not extreme, based on a previous experiment in the

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