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Does the presence of neighbouring weeds alter the expression of adaptive plasticity to subsequent drought stress in soybean?

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ABSTRACT

Phenotypic plasticity in response to stress may limit plastic responses to subsequent stresses. This may result in a maladapted phenotype, thereby limiting further expression of plasticity to subsequent stress. It was hypothesised that exposure of soybean (*Glycine max* (L.) Merr.) to far-red-enriched (FRE) light reflected from neighbouring weeds would reduce plasticity to subsequent drought stress. Soybean seedlings were grown in a field fertigation system and exposed to a simulated delay in early-season weed control followed by one or two drought stresses. In contrast to control plants, stem elongation induced by FRE light was maintained under drought stress. Stem elongation, however, did not result in a cost to fitness. In addition, no further interactions were found between FRE light and drought. Total biomass plant^{-1} was reduced by drought stress, which also altered biomass allocation between shoots and roots. Vegetative plasticity in response to drought, however, did not recover total biomass and resulted in a rapid, linear decline in seeds plant^{-1}. Reproductive plasticity in response to drought maintained seed weight despite losses in seeds plant^{-1}. These results demonstrate that the frequency, type and severity of stress influences the ability of soybean to express adaptive vegetative and reproductive plasticity such that delays in early-season weed control may not result in a maladapted phenotype to subsequent drought stress.

1. Introduction

Plants respond to the presence and proximity of neighbouring plants by developing shade avoidance characteristics such as stem elongation and changes to biomass allocation between above and below-ground biomass (Frankland and Letendre, 1978; Smith, 1982; Schmitt and Wulff, 1993; Smith and Whitelam, 1997). This plastic response can occur prior to direct shading through reduced light quality, specifically the red to far-red ratio (R/FR) of light, reflected or transmitted from neighbouring vegetation (Smith, 1982; Ballaré et al., 1987, 1990). As chlorophyll selectively absorbs light in the red region of the spectrum, light that is reflected or transmitted from neighbouring vegetation is far-red-enriched (FRE), resulting in a decrease in the R/FR ratio (Kasperbauer, 1971). Under high plant densities where light may become limiting, plants displaying the shade avoidance phenotype, accumulate more biomass and have greater fitness than plants which have a reduced shade avoidance response (Dudley and Schmitt, 1996; Weinig, 2000a). The growth stage at which FRE light induced shade avoidance responses occur, may limit phenotypic plasticity expression to subsequent environmental cues such as abiotic and biotic stresses (Weinig and Delph, 2001).

Phenotypic plasticity is generally considered an adaptive response, enabling plants to match their phenotype to a wide range of environmental conditions (Bradshaw, 1965; Lloyd, 1984; Schlichting, 1986). Plasticity in various morphological and physiological traits has been observed in response to environmental stresses such as drought (Pedrol et al., 2000; Baquedano et al., 2008), flooding (Pigliucci and Kolodynska, 2002), salinity (Huang et al., 2015), UV light (Weinig et al., 2004) and shade (Dorn et al., 2000). The limitation to these adaptive responses, however, occurs when the selection pressure changes and is no longer influencing plant development. As a result, the initial expression of plasticity may result in a phenotype that is no longer adapted to the current environmental selection pressures (van Kleunen and Fischer, 2005; Valladares et al., 2005, 2007; Sanchez-Gomez et al., 2006; Ghalambor et al., 2007). For example, stem elonga-

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Abbreviations: FRD, far-red-depleted; FRE, far-red-enriched; DS, drought stress; TDS, two drought stresses.

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tion induced by FRE light reflected from neighbouring vegetation has been suggested to limit subsequent phenotypic responses to additional environmental stress through reduced plant structural stability (Schmitt et al., 1995; Weinig and Delph, 2001) and a reduction in resource-harvesting organs such as leaves and roots (Morgan and Smith, 1978; Cipollini and Schultz, 1999; Maliakal et al., 1999). Optimal plastic responses to multiple environmental stresses occurring throughout the life cycle of a plant may not be possible and as a result, fitness will be reduced (Dudley and Schmitt, 1996; Weinig 2000a, 2000b; Weinig and Delph, 2001).

Reduced fitness has been observed in soybean (*Glycine max* (L.) Merr.) as a result of FRE light reflected from early emerging weeds increasing plant-to-plant variability (Green-Tracewicz et al., 2011). Soybeans are well known to express vegetative and reproductive plasticity (Carpenter and Board, 1997; Vega et al., 2000) which has been attributed to its determinate and indeterminate growth pattern, variability in branching and plant architecture and the strength of the source-sink potential (Kasperbauer, 1987; Borrás et al., 2004). Expression of phenotypic plasticity in soybean has been observed in response to a variety of stresses including drought (Desclaux et al., 2000), nitrogen (Rufty et al., 1984), elevated CO_2 (Kumagai et al., 2015) and reduced light quality (Green-Tracewicz et al., 2011). The growth stage at which these stresses occurred has been shown to directly influence fitness (Andriani et al., 1991; Desclaux et al., 2000; Conley et al., 2008). None of these studies, however, explored the potential for an interaction between multiple stresses.

Multiple stresses are the norm in nature. It is therefore important to understand how the interaction between stresses may influence fitness. Throughout the life cycle of a soybean plant, subsequent stresses occur as a result of timing and efficacy of weed control, nutrient availability, pest populations and weather conditions. In this study, we asked the question “if early season weed control was delayed, would the presence of weeds growing with soybean seedlings result in a maladapted phenotype to subsequent drought stress?” In studies conducted by Page et al. (2011), it was found that the shade avoidance response induced by FRE light reflected from neighbouring weeds reduced the tolerance of maize (*Zea mays* L.) to subsequent drought stress. Similar studies have not been conducted with soybeans. For this study, we hypothesised that if soybean seedlings were exposed to FRE light reflected from neighbouring weeds due to a simulated delay in weed control, then these seedlings would have reduced adaptive plasticity to subsequent drought stress.

2. Materials and methods

2.1. Experimental design

Field experiments were conducted in 2012 and 2013 at the Arkell Research Station (43°53′N, 80°18′W; 325 m above sea level) in Guelph, ON, Canada. A University of Guelph soybean (*Glycine max* (L.) Merr.) *cv.* OAC Wallace was selected for the experiment and a commercial turfgrass mix of *Lolium pereene* L. and *Poa pratensis* L. were used as the surrogate weed species and maintained at a height of 5 cm by manual clipping. Experimental units consisted of a 28 cm diameter, 22 L white plastic pail filled with a baked clay medium called Turface® MVP® (Turface Athletics, Buffalo Grove, IL, USA). The soil surface of each pail was covered with a clear plastic sheet. A 15 × 10 cm hole was cut in the centre of each plastic sheet to facilitate soybean seedling emergence. To establish two light quality treatments, either Turface® (weed-free treatment, henceforth referred to as far-red-depleted FRD, R/FR = 1) or turfgrass (weedy treatment, henceforth referred to as far-red-enriched FRE, R/FR = 0.3) was laid directly on top of the plastic to ensure

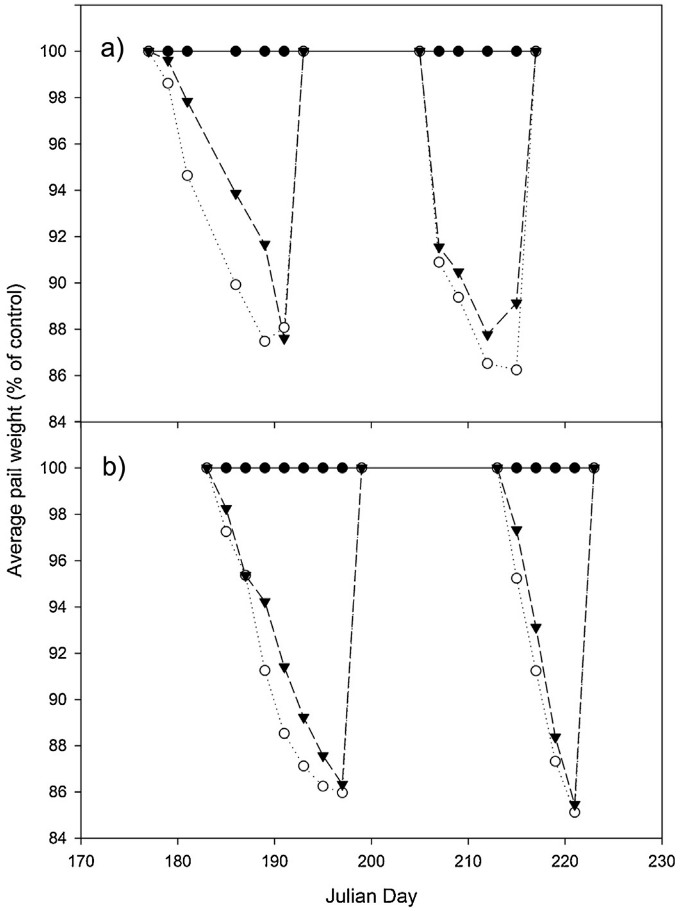

Fig. 1. Mean pail weight differential of two pails per treatment per replication expressed as% of control in (a) 2012 and (b) 2013. Control (●), FRD-DS (○) and FRE-DS (▼).

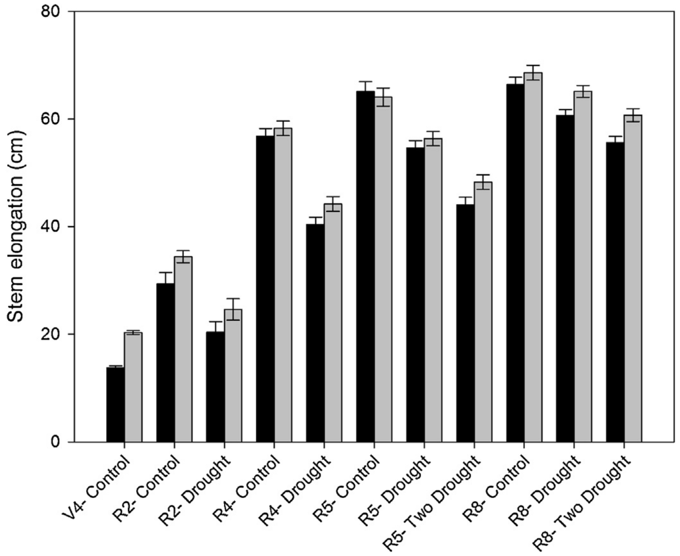

Fig. 2. Stem elongation (cm) as determined through analysis of covariance of height (cm) with shoot biomass (g) as a cofactor the following growth stages, V4, R2, R4, R5 and R8. FRD treatments are in black, FRE treatments are in grey. Data are expressed as least square means ± SE.