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Screening field pea for adaptation to water and heat stress: Associations between yield, crop growth rate and seed abortion

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ABSTRACT

We compared 29 pea (*Pisum sativum* L.) accessions including advanced breeding lines and commercial varieties in environments spanning a 3-fold range in yield. Environmental variation in yield was primarily accounted for by modelled water availability and maximum temperature in a window from 400 °Cd before to 200 °Cd after flowering. Our aims were to investigate (i) the trade-off between yield under stress and yield under favourable conditions, and (ii) the associations between yield and two traits: growth rate in a critical developmental window, and pod wall ratio (pod wall weight/whole pod weight).

Trade-offs between yield in favourable and stressful conditions were not apparent but differences among accessions in their response to favourable environments were larger than differences in yield under stress. High plasticity of yield is therefore a desirable attribute for our combination of accessions and environments.

Crop growth rate, calculated from calibrated NDVI (normalised vegetative difference index), accounted for 50% of the variation in seed number and for 44% of the variation in yield; both relationships fitted a ligand-binding function. The non-linearity of the relationship between seed number per m^2 and crop growth rate suggests a decoupling between growth and reproduction that may constrain yield potential. Accessions with smaller seed set more seeds per unit crop growth rate.

In a sample of 4550 pods (approx. 157 pods per accession), variation in pod wall ratio was dominated by the variation in seed weight per pod, rather than pod wall weight. Seed abortion accounted for 47% of the variation in seed weight per pod and 37% of the variation in pod wall ratio. Yield was negatively correlated with pod wall ratio, which ranged from 11 to 26% across accessions. We estimated a genotype-dependent increase in yield of 73 kg ha^{-1} per 1% reduction in pod wall ratio.

In combination with selection for both yield in favourable environments and yield plasticity, maintenance of crop growth rate and low pod wall ratio could contribute to adaptation to heat and water stress.

1. Introduction

Crop adaptation to stress can be improved by breeding and selection for yield potential or for yield in target environments, selecting for secondary phenotypic traits, using genomic approaches or with some combination of these methods (Richards, 1995; Ceccarelli et al., 2007; Cattivelli et al., 2008; Fleury et al., 2010). In field pea growing regions of Australia, water deficit and elevated temperature at critical developmental stages constrain crop yield (Sadras et al., 2012a). With the aim of improving the yield of pea in these environments, here we explore the associations between yield and two traits: growth rate in a critical developmental window and seed abortion. We emphasise the physiological bases of these traits, potential tradeoffs between stress adaptation and yield under favourable conditions, and rapid and inexpensive screening methods required for breeding (Araus et al., 2008; Passioura, 2012).

Physiological principles justify the focus on growth rate in a critical developmental window as a major driver of yield (Andrade et al., 2005). In common to most grain crops, pea yield is a primary function of seed number (Poggio et al., 2005; Jeuffroy et al., 2010). Seed number is, in turn, proportional to the crop growth rate in a species-specific critical window and inversely related to the maternally driven potential seed size (Sadras, 2007; Sadras and Denison, 2009; Gambín and Borrás, 2010). Intra-specific variation

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in the boundaries of the critical window cannot be excluded, but a common window was found for a set of French pea varieties (Guilioni et al., 2003).

Shading experiments showed that the critical window was between 10 days before and 40 days after flowering for semi-leafless pea "Nitouche" under high-yielding conditions in southern Chile (Sandaña and Calderini, 2012). Water and heat stress experiments in France identified a critical window between the beginning of flowering and the beginning of seed fill of the last seed-bearing phytomer that applied to several pea cultivars (Guilioni et al., 2003; Jeuffroy et al., 2010; Lecoeur and Guilioni, 2010). For practical purposes, the growth rate calculated for a shorter period (flowering to 400 °Cd post-flowering) returned sound predictions of seed number (Jeuffroy et al., 2010). This simplification circumvented the uncertainty associated with the determination of the beginning of seed fill for the last seed-bearing phytomer which marks the end of the critical window. Under Australian conditions, correlations between yield and water deficit for pea "Kaspa" indicated a region-dependent critical window of approximately 400 °Cd bracketing flowering (base temperature = 0 °C) (Sadras et al., 2012a); this represents a shift of ~200 °Cd before flowering in the beginning of the critical window in relation to the French studies.

Studies with lupins reported negative correlations between grain yield and the pod wall ratio, defined as the ratio between pod wall weight and whole pod weight (pod + seed) (Lagunes-Espinoza et al., 1999; Clements et al., 2002, 2005). This correlation has a number of components including higher harvest index, thinner pod walls, and low rate of seed abortion associated with low pod wall ratio. Clements et al. (2005) explicitly tested and found a positive association between pod wall ratio and aborted seeds per pod in a historical collection of lupins. The pod wall ratio can be screened rapidly and inexpensively, and can therefore be used as a surrogate for seed abortion, a trait of particular importance under water deficit and heat stress. Reported intra-specific variation of pod wall ratio in pea, however, is smaller than in lupins (Lagunes-Espinoza et al., 2000; Clements et al., 2005; Mera et al., 2005).

In this paper, we compared 29 pea accessions comprising a broad range of phenological and morphological traits. The comparisons were carried out in environments with a threefold range in mean yield which was primarily accounted for by water availability and maximum temperature at critical developmental stages. Our aims were to investigate (i) the trade-off between yield under stress and yield under favourable conditions, and (ii) the associations between yield and two traits: growth rate in a critical window, and pod wall ratio.

2. Methods

2.1. Plant material, environments and experimental design

Field pea accessions were chosen for their variation in morphology, phenology and yield reliability as assessed by Plant Breeding Australia (Table 1). Accessions were compared in a range of environments resulting from the combination of seasons, locations and sowing dates (Table 2). Crops were sown in a randomised complete block design with three replicates. Plot size was 7.25 m^2 in 2010 and 14.5 m^2 in 2011 and 2012. In all environments, plots were 6 rows (5 m long in 2010 and 10 m long thereafter) with a targeted plant population density of 55 plants m^{-2}. Agronomic practices for seed treatment, fertiliser, fungicide, herbicide and insecticide applications were carried out in accordance with the specific requirements of each environment as established for the network of Australian field pea National Variety Trials (http://www.nvtonline.com.au/).

2.2. Traits

Table 2 summarises the traits measured in each environment. Phenological stage was monitored weekly and expressed on a

Table 1

Morphological and phenological traits of pea accessions. Leaf type is conventional (C) or semi-leafless (S) where tendrils replace leaflets. Sugar pod is a trait associated with reduced shattering. Phenological traits are the mean from measurements in 10 environments, including first flower (FF), 50% first flower (50%FF), 50% end of flowering (50%EOF), and duration calculated as the difference between 50%EOF and 50%FF.

Accession	Leaf type	Sugar pod	Phenology (°Cd from sowing)			Duration (oCd)
			FF	50%FF	50%EOF	
PSL4 Early	S	✓	580	625	949	323
97-724-5	C		640	675	943	268
03H347P-04HO2003	C	✓	681	727	942	215
Bacara	S		691	728	936	208
Excell	S		702	742	951	209
PBA Twilight	S	✓	700	745	957	212
02-084-6	S	✓	707	745	940	196
04H084P-05HO2008	S		714	746	1012	268
02-084-5	S	✓	708	749	977	228
Laura	C		676	754	1048	294
PBA Oura	S		717	755	962	207
Sturt	C		707	755	1021	265
Helena	C		724	760	983	223
PBA Gunyah	S	✓	688	763	966	203
Moonlight	S		730	765	986	221
02-376-2	S		738	773	1004	231
Parafield	C		749	788	1043	255
03H267-04HO2006	S	✓	766	804	972	168
04H090P-05HO2003	S		769	806	1048	242
03H107P-04HO2026	S		777	824	968	144
97-031-6-6	S	✓	788	825	967	142
02H118P-03HO2009-06TGVP002	S	✓	786	829	963	134
03H536P-04HO2007	S	✓	797	833	1004	171
Yarrum	S		798	835	956	121
03H160-04HO2001	S	✓	808	842	1008	167
02-557-3	S	✓	745	843	1009	166
Morgan	S		815	850	1070	220
Kaspa	S	✓	811	854	995	141
01H280P-02HO2012-04HO5001	C	✓	819	855	979	126