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Negative association between chickpea response to competition and crop yield: Phenotypic and genetic analysis

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ABSTRACT

Donald's ideotype and empirical evidence in cereal and oilseed crops indicate high yield is associated with less competitive plants. In this study we grew 20 chickpea lines in six environments to investigate the association between yield and intra-specific competitive ability and its genetic underpinnings using Fst genome scan based on whole genome resequencing data. We measured yield and its components and calculated response to competition (RC) as the ratio between the trait in outer rows (relaxed competition) and the trait in inner rows (higher competition). Crop yield correlated negatively with RC for yield, biomass, harvest index, seed number, and pod number. Fst genome scan revealed 14 genomic regions under selection for response to competition of yield, seed number or biomass, and 6 genomic regions under selection for yield in inner or outer canopy rows. Candidate genes in these regions include members of the nitrate-transporter 1 family, patatin and hormone-related genes. The top genomic regions found to be under selection for yield in inner rows and outer rows did not coincide. This genetic architecture provides a mechanistic basis for the observation that phenotypes that are adequate for relaxed competition often perform poorly in dense stands.

1. Introduction

Plant-plant interactions include interactions between neighbours arising from utilisation of a common resource or through interference that is not mediated by resources, such as light or chemical signals (Aphalo and Ballare, 1995; Gillet, 2008; Schmidt et al., 2009; Karban, 2015). Donald (1968) postulated that a successful crop plant will be a weak competitor and suggested a breeding strategy targeting the 'communal ideotype' which is based on introgressing traits for weak competitive ability that confer adaptation to monocultures. This involves a trade-off between individual plant yield and communal yield, which has been recently reviewed by Asplen et al. (2012) and Denison (2015).

The negative association between competitive ability and yield has been particularly tested in cereals. In rice (Jennings and Aquino, 1968; Jennings and Herrera, 1968; Jennings and Jesus, 1968) and wheat (Khalifa and Qualset, 1975; Thomas and Schaalje, 1997) mixed line populations were sown, and the composition studied over generations. Natural selection favoured the more competitive types, increasing their frequency, with a corresponding decrease in total yield per unit area. Hamblin and Donald (1974) observed that shorter barley plants with a lower single-plant yield in the F_3, corresponded to higher plant stand yields in the F_5. In wheat, barley and sunflower, high yield was associated with a less competitive phenotype (Romani et al., 1993; Reynolds et al., 1994; Sadras et al., 2000; Andrade et al., 2005; Sadras et al., 2012). Nasseer et al. (2016) assessed intraspecific competition, and found that high tillering in wheat showed a yield advantage under relaxed competition, but not in a normal cropping community. Duggan et al. (2005) also observed higher yield in reduced tillering lines under high intraspecific competition.

Sukumaran et al. (2015a) found that wheat genotypes that yielded more in high density stands responded less to reduced competition and used genome-wide association (GWAS) to identify markers for early stage selection in low density breeding trials. Similar to GWAS, Fst genome scan identifies genomic regions under selection using a large amount of molecular markers to scan for regions with extreme genetic differentiation between populations. It has been widely used to detect selection signatures in human and livestock genomes (Weir et al., 2005; Holsinger and Weir, 2009; Qanbari and Simianer, 2014). In crops, Fst scan has been

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used to explore the genetics of powdery mildew resistance in wheat (Jordan et al., 2015) development in sorghum (Mace et al., 2013), and carbon isotope discrimination and nitrogen fixation in chickpea (Sadras et al., 2016). One of the advantages of Fst is that it returns robust information with relatively small number of genotypes. In the study of Sadras et al. (2016) for example, Fst scan identified genomic regions associated with agronomic traits in a collection of 20 chickpea lines.

Donald's hypothesis remains largely untested in pulses where the indeterminate growth habit (Cohen, 1971; Loomis and Connor, 1992) and symbiotic nitrogen fixation (Kiers et al., 2013) might influence plant–plant interactions and their impact in crop-level yield. In this paper, we tested the hypothesis of an inverse relationship between competitive ability and crop yield in chickpea and used Fst genome scan to explore the genetic basis of this relationship. Chickpea is a suitable crop for this study for three reasons: it is widely grown as a source of protein worldwide (Berger et al., 2006; Krishnamurthy et al., 2013; Farooq et al., 2016), its draft genome sequence has been published (Varshney et al., 2013), and it has been tested in Fst genome scan studies (Sadras et al., 2016).

2. Methods

2.1. Plant material, crop husbandry and experimental design

We used 20 chickpea lines that represent a broad range in agronomic adaptation, yield, phenology, and seed type (Table 1). This is the same set used in previous Fst scan studies (Sadras et al., 2016). Lines were compared in six environments in South Australia that were a combination of locations, seasons and sowing dates. The six environments were Turretfield (34°33′S, 138°49′E) at recommended sowing time (TOS 1; 8th June 2013 and 6th June 2014) and late sowing (TOS 2; 9th of July 2013 and 15th of July 2014), and Roseworthy (34°52′S, 138°69′E) at recommended sowing time (TOS 1 on 10th June 2014) and late sowing (TOS 2 on 15th July 2014).

The trials were sown after canola (2013) and barley (2014), into Calcic Luvisol at Turretfield and after barley, into Calcic Luvisol at Roseworthy. The seed was pre-treated with P – Pickel T fungicide to minimise the risk of *Aschochyta* blight and inoculated with Group N rhizobia immediately before sowing. To account for differences in plant vigour, the target plant density was 55 plants m^{-2} for Desi and 30 plants m^{-2} for Kabuli types. Crops were fertilised with 80 kg ha^{-1} mono ammonium phosphate at sowing. Before sowing weeds were controlled with an initial spray of Paraquat (135 g/L) and Diquat (115 g/L) mix, with follow up grass sprays (mixture of Butroxydim (250 g/kg) and Clethodim (240 g/L) and complementary hand weeding. We monitored crops for fungal symptoms on a weekly basis and applied preventative sprays (Chlorothalonil, 720 g/L) around flowering and podding or whenever symptoms were seen. Crops were treated with insecticide (Omethoate, 290 g/L) to prevent damage from *Helicoverpa spp*. around early podding.

The experiment was set in a randomised design with three replicates. Plot size was 7.25 m^2, comprised of standard six rows (spaced 24 cm in accordance with the design of the seeding machine) of five meters length. Plots were spaced 55 cm apart from each other for decreased competition in outer rows (Rebetzke et al., 2014).

2.2. Crop traits

Phenology was scored weekly to establish the time to 50% of plants in each plot reaching flowering, pod emergence (developing pods of 2–4 mm in length), end of flowering and maturity (yellowing pods) (Berger et al., 2004; Lake and Sadras, 2014). Phenology was expressed on a thermal time scale, calculated from daily mean temperature and base temperature of 0 °C (Berger et al., 2006).

Yield and components were measured in two 50-cm samples taken from outer and inner rows (Bustos et al., 2013; Wang et al., 2013; Rotundo et al., 2014; Assefa et al., 2015). We determined shoot biomass, seed weight, seed number, pod number, seed size, seeds per pod and the derived traits harvest index (seed yield/shoot biomass) and pod wall ratio (pod wall weight/whole pod weight) (Lagunes-Espinoza et al., 1999; Clements et al., 2005; Lake and Sadras, 2014). Response to competition (RC, unitless) was calculated using the ratio of the trait in the outer row and the trait in the inner row, as in previous studies (Reynolds et al., 1994; Sadras et al., 2000; Sadras and Lawson, 2011; Sukumaran et al., 2015b).

2.3. DNA sequencing and F_{st} genome scan

DNA of each of the 20 lines was extracted from young leaf tissue from a single plant using Qiagen DNeasy Plant Mini Kit. Using TruSeq library kit, pair-end sequencing libraries were constructed for each cultivar with insert sizes of ~500 base pairs (bp) according to the Illumina manufacturer's instruction. About 40 million 100 bp pair-end reads for each cultivar were generated using Illumina HiSeq 2000 platform.

Pair-end reads for each cultivar were trimmed, filtered and mapped to the Kabuli reference genome 2.6.2 using SOAP2 (Li et al., 2009). The BAM files containing sequence alignment information of each cultivar were separated into two contrasting groups (10 cultivars in each group) according to adjusted entry means of phenotypes. Fst was estimated in 100 kilobase pair (kb) non-overlapping windows based on the BAM files of two contrasting phenotypic groups using software ngsPopGen (Fumagalli et al., 2013). The Wright's Fst is a descriptive statistic that measures genetic variance among populations in population genetics (Fumagalli et al., 2013). Large Fst means the allele frequencies within each population are different; small Fst means the allele frequencies within each population are similar. he whole genome was scanned to identify regions with extreme population genetic differentiation (large Fst value compared to the surrounding region) which could serve as an indicator of selection signature; the Fst method has been used previously on the same 20 chickpea lines to explore the genetic basis of yield and traits related to nitrogen assimilation and water use efficiency (Sadras et al., 2016). The rationale is that genetic differentiation between groups at a given neutral locus (not under selection pressure) is determined by stochastic random factors such as random genetic drift. If a locus is under natural or artificial selection, the pattern of genetic differentiation may change. For example, regions showing uncommonly large amounts of genetic differentiation (different alleles are fixed in different groups) may have undergone diversifying selection. To avoid high error rate of next-generation sequencing data resulting in biased estimate of allele frequency, site frequency spectrum (SFS), the distribution of sample allele frequencies jointly for all sites (single nucleotide polymorphism in this case) and all cultivars, is incorporated into estimation of Fst (Fumagalli et al., 2013). This is a Bayesian framework where Fst is estimated from posterior probabilities of sample allele frequencies at each locus without genotype calling. To minimise the effect of sampling error, the Fst value for each single nucleotide polymorphism (SNP) within a window of 100 kb was averaged. We define regions with the top 0.1% Fst as genomic regions under selection. We do not intend to seek statistical significance, however, this serves to pinpoint regions where Fst values are extremely different from those in the rest of the genome. Different traits have different thresholds due to different Fst distribution (Supplementary Fig. 1).The adjacent genomic regions under selection are binned together and treated as one region.

Table 1
Selected features of 20 chickpea lines used in the study of competition. Yield response to competition (RC) is unitless; beginning of flowering and maturity are thermal time from sowing. Data are averages across all six environments, with range in parenthesis.

Line	Type	Yield ($g\,m^{-2}$)	Yield RC	Flowering (Cd°)	Maturity (Cd°)
Sonali	Desi	285 (168–399)	1.55 (0.68–2.10)	947 (782–1087)	1695 (1542–1885)
CICA1229	Desi	302 (216–420)	1.58 (0.95–2.50)	992 (822–1201)	1651 (1438–1851)
PBA Striker	Desi	354 (213–500)	1.48 (0.90–2.23)	995 (782–228)	1656 (1438–1851)
Genesis079	Kabuli	380 (236–520)	1.48 (0.91–2.95)	1021 (811–1171)	1757 (1607–1885)
Genesis836	Desi	300 (170–465)	1.34 (1.00–1.84)	1028 (844–1201)	1724 (1571–1916)
Howzat	Desi	330 (243–479)	1.59 (1.11–2.32)	1033 (834–1216)	1716 (1557–1885)
PBA Slasher	Desi	342 (216–428)	1.55 (1.12–2.12)	1034 (834–1216)	1726 (1557–1902)
Genesis509	Desi	333 (168–463)	1.31 (0.82–1.74)	1035 (799–1228)	1672 (1504–1851)
PBA Boundary	Desi	305 (138–430)	1.66 (0.79–4.28)	1042 (834–1228)	1705 (1542–1902)
PBA Monarch	Kabuli	392 (226–627)	1.42 (1.12–1.97)	1045 (844–1239)	1727 (1495–1989)
CICA1016	Desi	302 (174–502)	1.76 (1.13–2.56)	1049 (844–1228)	1700 (1542–1865)
PBA HatTrick	Desi	281 (173–454)	1.55 (0.90–2.15)	1050 (868–1228)	1718 (1542–1902)
CICA1007	Desi	322 (194–398)	1.63 (1.16–2.12)	1054 (899–1228)	1724 (1557–1902)
PBA Pistol	Desi	320 (173–537)	1.68 (1.10–2.95)	1054 (868–1251)	1727 (1542–1902)
CICA0912	Desi	278 (192–392)	1.58 (1.14–2.50)	1056 (868–1282)	1697 (1521–1865)
Jimbour	Desi	323 (221–463)	1.51 (0.76–2.21)	1081 (899–1364)	1716 (1557–1906)
Almaz	Kabuli	321 (182–545)	1.50 (1.00–2.39)	1106 (907–1239)	1916 (1715–2150)
Kyabra	Desi	303 (185–391)	1.53 (1.13–2.32)	1106 (899–1364)	1721 (1557–1902)
Genesis090	Kabuli	336 (164–528)	1.55 (0.75–2.63)	1114 (855–1364)	1841 (1667–2020)
GenesisKalkee	Kabuli	360 (199–562)	1.39 (0.89–2.20)	1224 (999–1426)	1953 (1715–2150)

2.4. Environmental characterisation

Environmental characterisation lags behind phenotyping and genotyping efforts, hence our interest in quantitative, rather than nominal (e.g. location/season), environmental indices (Sadras et al., 2013). Two daily indices were used to quantify the water and photothermal environments, shown to be related to crop yield (Sadras et al., 2015; Lake et al., 2016). They were based on daily rainfall, temperature, radiation, vapour pressure and humidity from the nearest available weather station (https://www.longpaddock.qld.gov.au/silo/).

Daily water stress index was simulated using the chickpea module of Agricultural Production Systems Simulator (APSIM) software and actual weather data (Keating et al., 2003; Holzworth et al., 2014). Water stress index is the ratio between water supply (soil and root characteristics) and demand, driven by radiation, temperature and humidity. The range of the stress index is 1 (no stress) to 0 (maximum stress – growth has ceased). Details are in Lake et al. (2016).

Daily photothermal quotient corrected by vapour pressure deficit (PTQ_{vpd}) relates to non-stressful thermal effects on canopy size and yield (Sadras et al., 2015). It was calculated as PTQ_{vpd} = radiation/(average temperature−vapour pressure deficit); we assumed a base temperature of 0 °C. For both water stress index and photothermal quotient, we divided the season into 200°-day intervals and calculated the average index for each interval centred at the flowering date for each environment across lines.

3. Results

3.1. Environmental conditions

The driest environments were the late-sown 2014 crops where seasonal rainfall was 100 mm for Roseworthy and 146 mm for Turretfield compared to 251 mm in the wettest environment, i.e. Turretfield, normal sowing in 2013. The normal-sown crops experienced an average of 2.1 °C cooler maxima and 0.82 °C cooler minima than the late-sown crops and received 2.8 $MJ\,m^{-2}$ less radiation per day; vapour pressure deficit averaged 1.42 kPa for normal-sown crops and 1.62 kPa for late-sown crops.

Fig. 1 aggregates individual weather factors in physiologically meaningful indices: water stress index (Fig. 1a) and PTQ_{vpd} (Fig. 1c). At pod set (100–200 °Cd after flowering, there was a 19% difference in the water stress index between the least and most stressful environments, and a difference of ~0.6 $MJm^{-2}\,°C^{-1}kPa^{-1}$ for the highest and lowest PTQ_{vpd}.

3.2. Phenology

Flowering time across environments ranged from 947 °Cd from sowing for Sonali to 1224 °Cd for Genesis Kalkee (Table 1). Time to pod emergence ranged from 1110 °Cd for Sonali to 1325 °Cd for Genesis Kalkee, and end of flowering ranged from 1356 °Cd for PBA Striker to 1510 °Cd for Genesis Kalkee (Table 1). The earliest maturing variety was CICA 1229 while the latest was Genesis Kalkee. The environment with the shortest average season was Roseworthy late-sown in 2014, with 874 °Cd to flowering, 979 °Cd to pod emergence, 1233 °Cd to end of flowering and 1571 °Cd to maturity. Turretfield normal sowing in 2013 was the longest season with 1235 °Cd to flowering, 1422 °Cd to pod emergence and 1625 °Cd to end of flowering; maturity was not scored for this environment.

3.3. Yield and its association with phenology

Across environments and varieties yield ranged from 138 to 627 $g\,m^{-2}$ (Table 1). Across environments there was a positive relationship between yield and time to maturity ($r = 0.60$, $P < 0.0001$); relationships were also significant but weaker for other phenophases. However, sowing time was the driver of this relationship as normal-sown crops were higher yielding and had longer phenophases. To remove this effect we split the data by time of sowing; this revealed (i) no association of phenology and yield in late-sown crops and (ii) yield associations with time to pod emergence ($r = -0.26$, $P < 0.05$), end of flowering ($r = -0.27$, $P < 0.05$) and maturity ($r = 0.42$, P 0.01) in normal-sown crops.

3.4. Response to competition

Averaged across lines, yield response to competition ranged from 1.40 to 1.87 and was larger in environments with higher water supply/demand ratio and higher PTQ_{vpd} (Fig. 1b,d). The response to competition of yield and its components varied among lines and environments (Table 1, Fig. 2); yield response to competition was associated with low crop yield across all environments. Fig. 2 illustrates the response to competition of yield, and its components

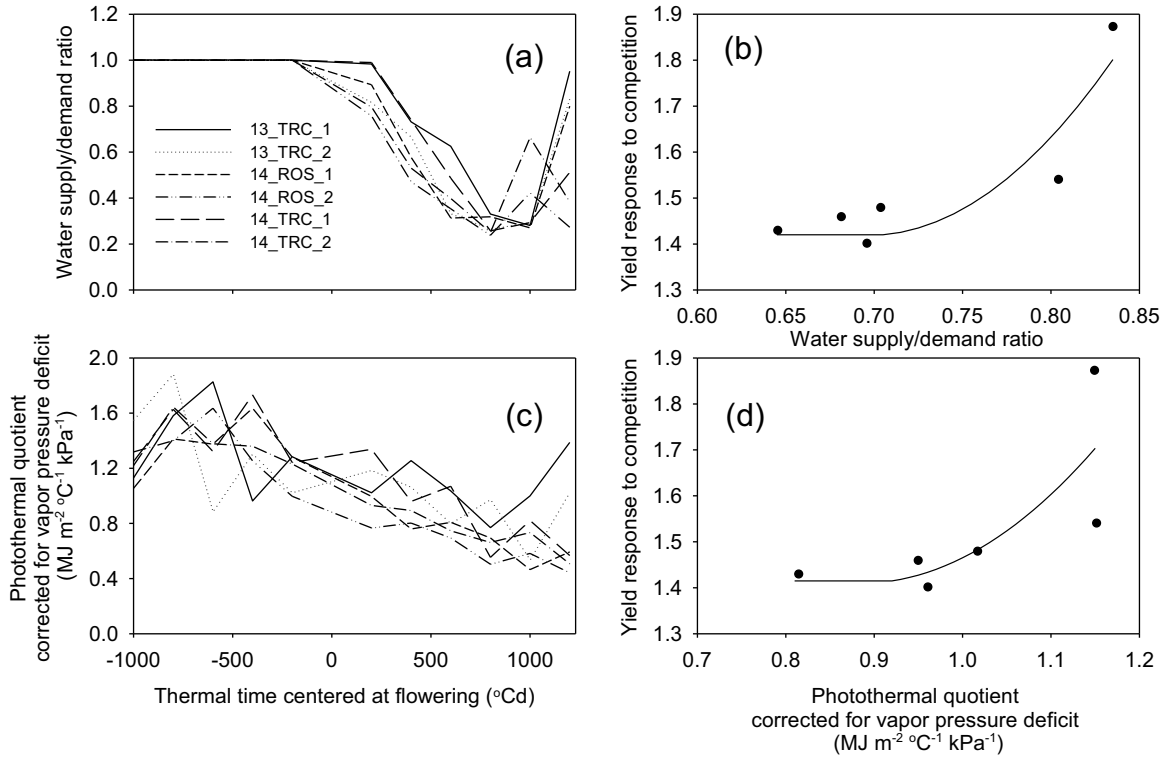

Fig. 1. (a) Patterns of water stress during the growing season (1 indicates no stress while 0 indicates maximum stress). (b) Relationship between the average water stress within the critical period for yield determination and yield response to competition for the six environments. (c) Patterns of photothermal quotient corrected for vapour pressure deficit during the growing season. (d) Relationship between average photothermal quotient corrected for vapour pressure deficit within the critical period for yield determination and yield response to competition for the six environments. The critical period was 200Cd° before flowering to 600Cd° post flowering.

seed number and seed size, using the approach of Sukumaran et al. (2015b). This demonstrates the association of yield (O+I) with a lesser difference between yield in the inner (I) and outer (O) rows. The same applies for grain number, whereas seed size was largely unresponsive to competition.

A principal component analysis visualises the relationships between crop yield ($g\,m^{-2}$, measured in inner rows) and response to competition of different traits for all lines across environments (Fig. 3). Crop yield had a strong, negative correlation with response to competition of yield, seed number, pod number, biomass and harvest index ($P<0.0001$) and was unrelated to response to competition of seeds per pod, seed size and pod wall ratio.

We used a ratio to describe response to competition, with subsequent analysis of the form $Y_{(I)}$ vs $Y_{(O)}/Y_{(I)}$, where Y is yield, I is inner row and O is outer row. The common term $Y_{(I)}$ may give rise to spurious correlations (Brett, 2004). However, the likelihood of spurious correlations is low for two reasons. Firstly, spurious correlations are more likely when the variation in the shared term $Y_{(I)}$ is >1.5 times larger than the non-shared term $Y_{(o)}$ (Brett, 2004) whereas the shared term in our data had a coefficient of variation (0.26) that was almost equal to the non-shared term (0.25). Secondly the coefficient of variation for the sampled population was less than 0.4 which also reduces the chances of spurious correlations (Brett, 2004). Furthermore, response to competition of yield correlated with response of competition of other traits such as biomass, for which there is no common term in the calculations (Fig. 3).

3.5. Genomic regions under selection for yield in inner and outer rows

Fig. 4 compares the selection signature for yield in inner and outer rows. Four genomic regions with exceptionally large Fst values (top 0.1%) have been identified to be under selection for yield in inner rows, whereas only two genomic regions with exceptionally large Fst values have been identified for yield in outer rows. The genomic regions under selection for yield in inner rows and outer rows did not overlap. Genes are listed in Supplementary Table 1.

3.6. Genomic regions under selection for response to competition

The distribution of Fst was highly skewed toward zero with average Fst of 0.0444 for yield (RC), 0.0854 for seed number (RC) and 0.0974 for biomass (RC) (Supplementary Fig. 1). Five genomic regions have been identified with exceptionally large values for yield (RC) and biomass (RC), and four genomic regions for seed number (RC) (Fig. 5). Some genomic regions have been identified to be under selection for different traits. For example, a genomic region in Ca4 (Ca4:2,401,618.Ca4:2,501,618) is identified as under selection for yield (RC), seed number (RC), and biomass (RC). Another genomic region in Ca4 (Ca4:1,901,618.Ca4:2,001,618) is identified as under selection for both yield (RC) and biomass (RC). Supplementary Table 1 shows the complete list of genes present in the regions under selection for yield response to competition.

4. Discussion

4.1. Response to competition, yield components and environment

Previous studies in cereals and sunflower conform with the theory of Donald's ideotype with more competitive lines producing a lower yield in pure stand (Jennings and Aquino, 1968; Jennings and Herrera, 1968; Hamblin and Donald, 1974; Khalifa and Qualset, 1975). This is the first study that investigates grain legumes. Our finding also conforms to theory: lines that are more responsive to competition have a lower yield than their less responsive counterparts.

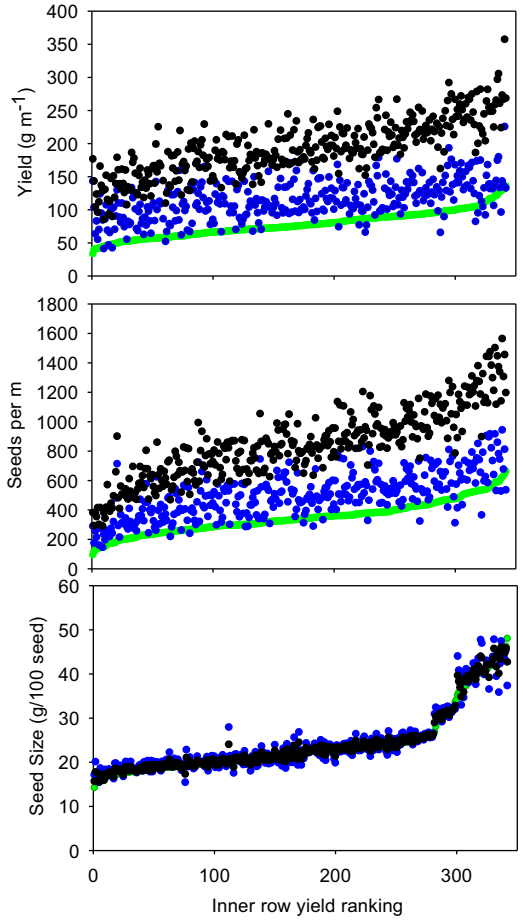

Fig. 2. Comparison of (a) grain yield, (b) seed number and (c) seed size measured in the inner rows (I, green), outer rows (O, blue), and the total (I+O, black). Data is based on all lines from all environments (n = 360). The x-axis was sorted by the inner row value. For seed size, the average of O and I was used. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

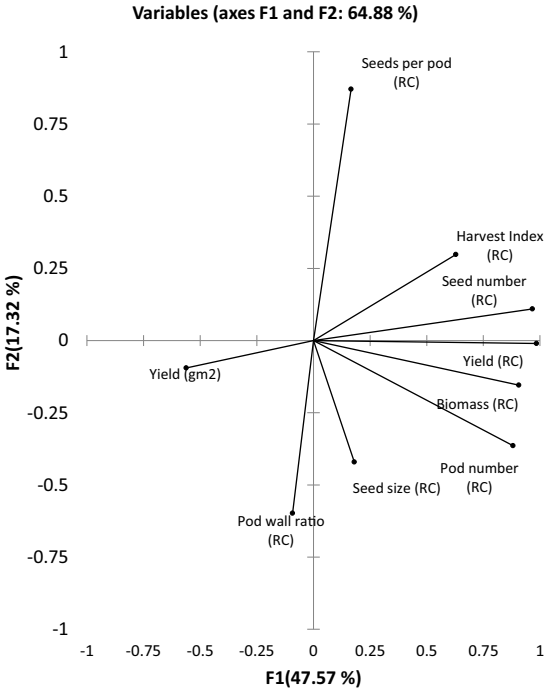

Fig. 3. PCA of crop yield (yield g m^{-2}) and response to competition (RC) of yield and yield components. Data is from all lines and environments.

Yield response to competition has been reported as 5–84% in sunflower Sadras et al. (2000), from 6 to 90% in wheat (Fischer and Laing, 1976; Austin and Blackwell, 1980; Reynolds et al., 1994; Sadras and Lawson, 2011; Sukumaran et al., 2015b) and 41–45% in barley (Romani et al., 1993). This compares with our responses from 31 to 76%. Response to competition of yield was mediated by response of competition of seed number. This is in agreement with both yield response to competition in other species (Khalifa and Qualset, 1975; Reynolds et al., 1994; Sadras and Lawson, 2011; Sukumaran et al., 2015b) and current models of crop yield assuming that crops accommodate environmental variation through seed number, and a conserved seed size (Sadras, 2007; Sadras and Slafer, 2012; Slafer et al., 2014).

The response to competition was larger in favourable environments (lower water stress and higher PTQ_{vpd}), as found in other studies. In wheat, Sadras and Lawson (2011) reported a range of response to competition from 79% in a favourable environment to only 27% under stress. In *Chenopodium acuminatum* and *Abutilon theophrasti* a larger response to competition occurred in the fertilised treatments (Sugiyama and Bazzaz, 1997; Wang et al., 2014). In sunflower, hybrids that were tolerant of disease showed larger response to reduced competition (Sadras et al., 2000), while in wheat, high tillering plants only showed yield gain at low competition or in high resource environments (Nasseer et al., 2016).

For the normal time of sowing, the negative relationship between yield and time to flowering, pod emergence and end of flowering, coupled with the positive relationship between maturity and yield, conforms to physiological principles surrounding indeterminate species; earlier flowering and later maturity mean a longer reproductive window and higher yield in favourable conditions. Normal sowing also means less likely stress during the critical period for yield formation despite the longer flowering duration (Lake and Sadras, 2014).

4.2. Genomic regions under selection for yield and response to competition

Theory (Donald, 1963; Donald, 1968; Donald, 1981; Denison, 2011; Denison, 2015) and empirical evidence (Pedró et al., 2012) show that the phenotype that favours yield under competition (i.e. crop yield) and the phenotype that favours seed production in isolated plants or under relaxed competition are different. Here we show a genetic architecture that accounts for these earlier conclusions based on phenotypes. By using stringent criteria (top 0.1% Fst threshold for each trait) we have identified five genomic regions under selection for yield response to competition, four for yield in inner rows and two for yield in outer rows. The top genomic regions under selection for yield in crop conditions are different from the top genomic regions under selection for yield of plants under relaxed competition. Although each one of these regions could have a contribution in the opposite condition, the magnitude of this contribution is different. Furthermore, the top regions for yield RC are also different from those identified for yield in inner and outer rows. These regions could have minor but opposite effects in inner and outer rows, which would place them beneath the Fst threshold in each case but emerging when RC is calculated. In other words, neither the phenotypes nor the genotypes that favour yield under relaxed competition are necessarily superior in dense stands. This genetic architecture justifies the search for and focus on communal traits as suggested by Donald and highlights the caution needed in extrapolating from individual plants or single rows to normal crop configurations, where plant–plant interference is significant.

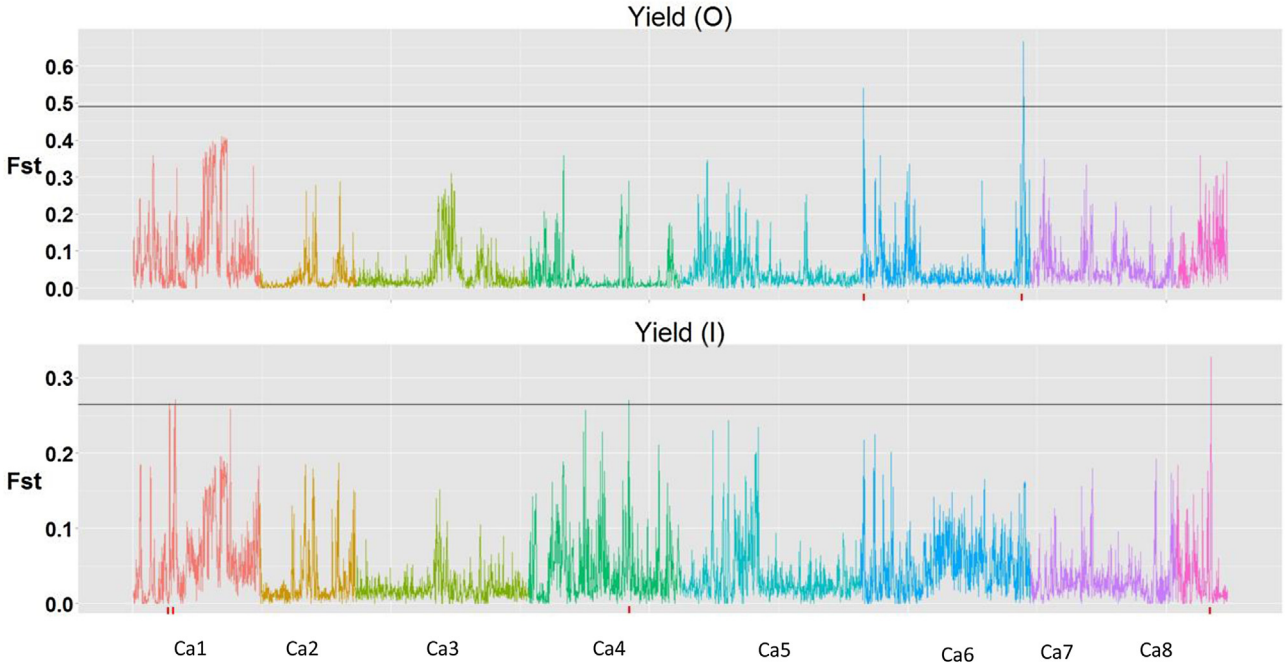

Fig. 4. Fst genome scan of yield of inner (I) and outer (O) rows. Fst value (see method) above the black lines (top 0.1% of Fst) indicate genomic regions with extreme population genetic differentiation (regions under selection). Ca1-8 represent chromosome1-8.

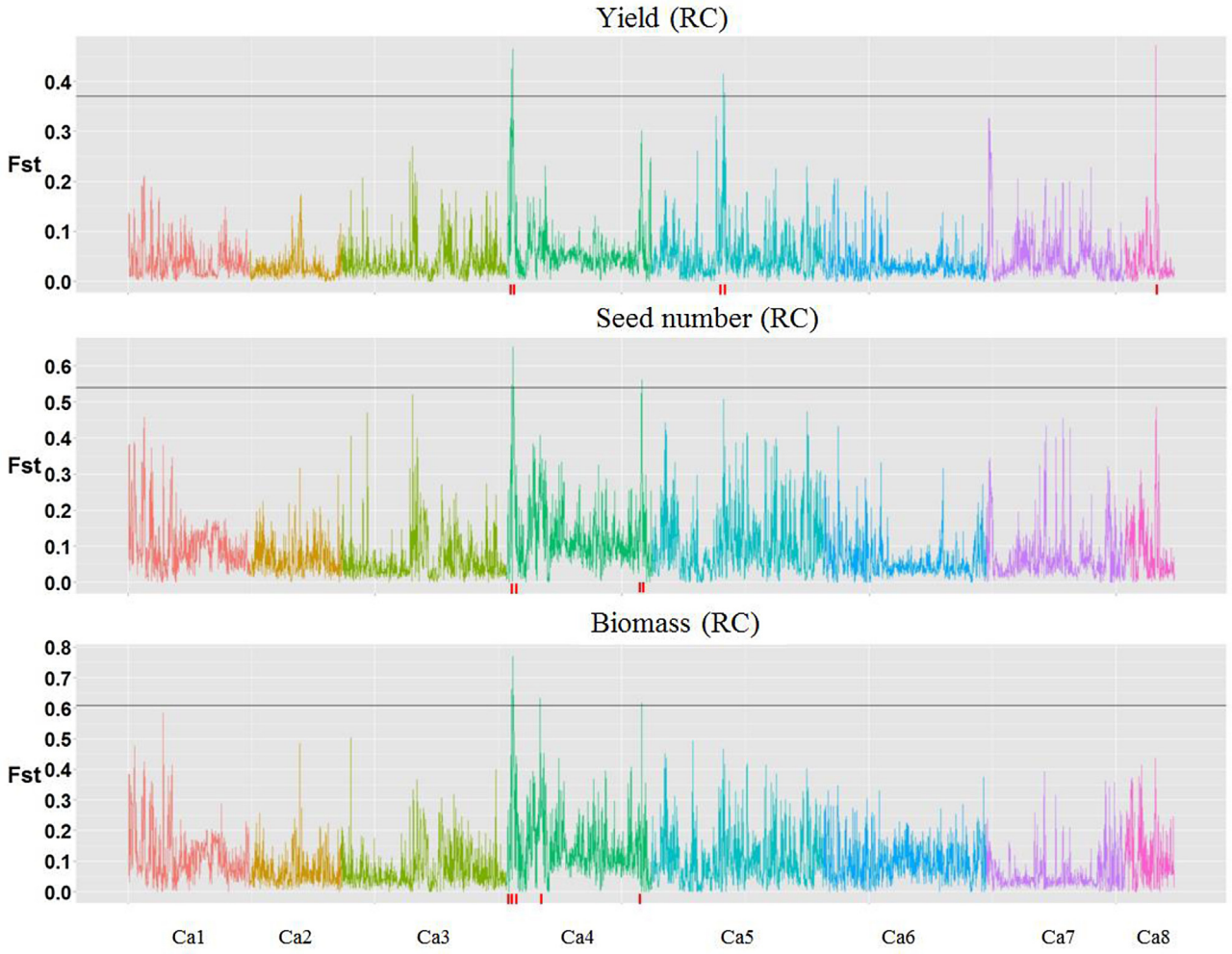

Fig. 5. Fst genome scan of yield (RC), seed number (RC), and biomass (RC). Fst value (see method) above the black lines (top 0.1% of Fst) indicate genomic regions with extreme population genetic differentiation (regions under selection). Ca1-8 represent chromosome1-8.

Within the regions identified here there are many candidate genes that could theoretically contribute to yield. However, it is interesting to focus on some of them for which there is direct evidence for associations with yield. For instance, the region Yield-Outer-1 in chromosome 6 includes a gene (Ca6:1267008, Ca6:1283051, Ca6:1282482) that bears similarity to the AT2G02040 locus in *Arabidopsis thaliana* (Table S1), which encodes the *PEPTIDE TRANSPORTER 2 (PTR2)* gene belonging to the *NITRATE TRANSPORTER 1 (NRT1)*. Anti-sense expression of *PTR2* causes reduced seed number due to impaired seed formation in Arabidopsis (Song et al., 1997). The *OsPTR9* gene of *Oryza sativa* (LOC_06g49250) is also closely related to the *PTR2* gene of Arabidopsis. Elevated expression of *OsPTR9* in transgenic rice plants enhances ammonium uptake, lateral root formation and grain yield, whereas the loss-of function mutation causes the opposite effects (Fang et al., 2013). Of interest, grain yield was related to uptake of mineral nitrogen and unrelated to nitrogen fixation in field experiments including the same collection of lines in similar environments (Sadras et al., 2016).

There are other examples of members of the NRT1 family affecting embryo development and controlling abortion (Almagro et al., 2008). Noteworthy, another region in chromosome 6, the Yield-outer-2 region, contains a gene (Ca6:62849772) with high similarity to the AT1G69850 gene of Arabidopsis, which encodes another member of the NRT1family.

The Yield-RC-1 region in chromosome four contains a gene (Ca4:1996068) with similarity to the Arabidopsis AT3G63200 locus that encodes the *PATATIN-LIKE PROTEIN 9* gene involved in lipid metabolic processes. Overexpression of a patatin-like protein in *Camelina sativa* (Li et al., 2015) or in Arabidopsis (Li et al., 2013) reduced growth and overall seed production but increased seed oil content. There are also two WRKY transcriptional factors in these genomic regions: WRKY13 and WRKY51. The former is a transcriptional factor that responds to drought stress via suppressing transcriptional factor SNAC1, which mediates drought tolerance by promoting stomatal closure (Xiao et al., 2013). The latter is involved in regulating gene expression involved in phytohormone ABA and GA signalling crosstalk in rice (Xie et al., 2006). In addition, a predicted gene encoding ovate family protein OFPs, is also under selection in Yield (RC). This gene family functions as transcriptional repressors and regulate multiple aspects of plant growth and development in Arabidopsis such as cell elongation and secondary cell wall formation (Wang et al., 2011).

Two seed number (SN)-RC regions, contained genes related to the metabolism of the plant hormone cytokinin which plays an important role in various phases of plant growth and grain development in maize and barley (Powell et al., 2013). The SN-RC-2 region in chromosome 4 contains a gene (Ca4:2446117) with similarity to AT3G63110, which encodes a cytokinin biosynthetic enzyme called *ISOPENTENIL TRANSFERASE 3 (IPT3)* in Arabidopsis. Another region in chromosome 4, SN-RC-3 contains a gene (Ca4:54666172) with similarity to AT5G21482, which encodes the *CYTOKININ OXIDASE 7 (CKX7)* gene. The rice Gn1a gene encoding cytokinin oxidase/dehydrogenase (*OsCKX2*) has been found to increase grain number (Ashikari et al., 2005). Additionally, two Arabidopsis mutants of cytokinin oxidase/dehydrogenase were found to increase total number of seed by 55% compared with the wild type (Bartrina et al., 2011). The SN-RC-2 region in chromosome 4 also contains a gene (Ca4:2560130) with similarity to AT3G23150, which encodes one of the ethylene receptors in Arabidopsis (*ETR2*). ETR2 has been found to be associated with a reduction in effective panicles and seed-setting rate, and delayed flowering in rice (Wuriyanghan et al., 2009).

Evidence from other species suggests that genes within these regions under selection are likely to be involved in different phenotypic responses to competition (Djakovic-Petrovic et al., 2007; Schmidt et al., 2009; Wang et al., 2011; Xiao et al., 2013); however, further research is needed to validate the functions of these candidate genes/SNPs on response to competition in chickpea.

5. Conclusion

This research has demonstrated that a less competitive chickpea phenotype is associated with higher yield and conforms to the idea of the 'communal ideotype'. A corollary of this finding is the caution needed to extrapolate yield-related traits from single plants or single rows to crops. Early generation selection for yield will favour traits that are conducive to individual rather than communal performance. We have identified genetic regions under selection for response to competition and associated candidate genes that offer insight into these processes. Further research on communal traits in pulses is warranted. Molecular markers associated with less competitive types might be useful in breeding, provided they return higher rates of yield improvement than direct selection for yield, or similar rates at lower cost.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.fcr.2016.07.021.

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