Genotype × environment interaction of canola (*Brassica napus* L) in multi-environment trials

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ABSTRACT

In order to investigate genotype × environment (G×E) interaction and to define specific and general adaptation of canola to southwestern Australia wheatbelt, we evaluate the performance of 18 cultivars across 28 locations in 2008 and 2009 using National Varieties Trial data. Finaly-Wilkson, AMMI and GGE Biplot analysis were used to visualize G×E interactions and determine the best performing cultivar for each environment. G×E interaction for seed yield was highly significant (P < 0.001), and accounted for more variance than that attributed to genotypes alone, suggesting that canola genotypes responded differently to variable environments. Three megaenvironments were identified and characterized by different climates. Megaenvironment 1 (ME 1) is characterized by a long growing season and with growing seasonal rainfall > 400 mm, and a cool reproductive phase with twice as much rainfall as in ME 2. ME 2 has 300 to 400 mm growing seasonal rainfall and shorter growing seasons. ME3 represents a extreme dry condition or with hostile soils. Medium-season cultivars such as CB Jardee, CB Argyle and CB Tumby produced higher seed yield in ME 1 while short season cultivars such as ATR Cobbler, CB Tanami, CB Telfer and CB Boomer performed better in ME 2. The results confirm the importance of matching phenology to growing season length, highlighting the need for specifically adapted cultivars even over relatively limited geographic scales, as defined by southwestern Australia.

INTRODUCTION

Canola is the third-largest broadacre crop in Australia and is widely grown across southern Australia. From 1970 to 2000, Australian canola breeders successfully improved yield, adaption, blackleg resistance and seed quality (Cowling, 2007). The availability of better varieties and crop agronomy packages and good prices made canola really attractive to growers and led to its rapid expansion. The area sown to canola in Australia rose from 150,000 ha in 1991 to 1.6 million ha in 1999 (Colton and Potter, 1999). However, the canola industry in 2000 was predominately located in regions with average annual rainfall >450 mm and canola was almost absent from areas averaging less than 325 mm average annual rainfall because of less successful breeding for this region (Cowling, 2007). Canola varieties in Australia were well adapted to medium-high rainfall zone of southern Australia, but not to low rainfall zones (Gunasekera et al., 2006; Cullis et al., 2010). An understanding of the environmental, phenological and physiological factors causing genotype × environment (G×E) interaction helps breeders to exploit specific adaptation (Basford and Cooper, 1998) and optimize yield in different environments. Despite of the importance of canola as a major oilseed crop in Australia, a limited research has been carried out on its adaptation to the Mediterranean-type environments and its G×E interactions compared with wheat. The major objective of this study is to understand the adaptation of canola across southwestern Australia with a Mediterranean-type climate. Using data from the National Variety Trial (NVT), this study employs Finaly-Wilkson, Additive Main effects and Multiplicative Interaction (AMMI) and GGE Biplot analysis to evaluate the significance of the G×E interactions on seed yield, identify megaenvironments, determine the best performing cultivar for each megaenvironment, and discuss the implication of the G×E interactions to canola breeding.

MATERIALS AND METHODS

The study zone comprises the cereal growing region of southwestern Australia, covering low-, medium-, and high rainfall zones. The average annual rainfall ranges from less 300 mm in the low rainfall zone to greater 550 mm in the high rainfall zone. The standard sowing dates are from the beginning of May to the end of June after the break of the season following a major rainfall event. The multiple environment trials (MET) dataset included a total of 18 cultivars across 28 locations in 2008 and 2009, which were extracted from the National Variety Trial (NVT) database. They consisted of 11 sites with 16 varieties in 2008 and 20 sites with 13 varieties. These sites include Kojonup, Williams, Mt Barker, Tunney, Gibson, south Stirlings in the high rainfall zone (annual rainfall of 500-700 mm), Cunderdin, Buntine, Mingenew, Katanning, Wickepin, Wagin, Mt Madden, Scaddan Northampton, Calingiri, Nabawa, and Munlinup in the low and medium rainfall zone (annual rainfall of 300 to 500 mm). All trials were arranged as a rectangular (row × column) array with six columns with the number of rows depending on the number of entries (Cullis et al., 2006). This study focuses on commercial varieties only. All varieties were replicated three times (Row 1 and 2 were treated as the first replicate, Row 3 and 4 as the second replicates, and Row 5 and 6 as the third replicate). The varieties included CB Argyle, CB Jardee HT, CB Tumby HT, CB Scaddan, CB Tanami, CB Telfer, Flinders TTC, Hurricane TT, Tawriffic TT, Thunder TT, Tornado TT, Rottnest TTC, Bravo TT, ATR Cobbler, ATR Barra, and ATR 409. Seed yield was determined by a machine harvesting of 13.2 m^2. Time to flowering (days after sowing), defined as the time at which 50% of plant population reached full flowering, was recorded in 2009. Finlay-Wilkinson analysis (F-W) (Finlay and Wilkinson, 1963), AMMI analysis (Gauch and Zobel, 1997), and GGE Biplot (Yan et al., 2000) were used to model G × E interactions.

RESULTS

Principal component analysis of trial site environments and site productivity represented by the site mean yield showed that there were considerable differences between the environments (Fig. 1). The first two principal components accounted for 73% of the variation. The analysis indicates three contrasting environments. The first is the high rainfall zone (≥400mm) with cooler growing condition indicated in solid dots (Fig.1); the second is the low rainfall zone (≤300 mm) with slightly warmer growing condition indicated in grey dots; the third has medium rainfall (300-400 mm) but much warmer growing conditions indicated in open circles. This group also includes four locations close to the biplot origin.

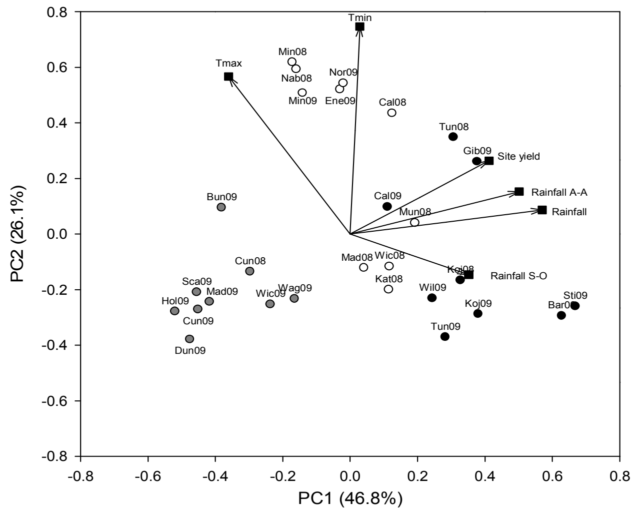

Fig. 1 Principal component analysis of trial site environments and site mean yield of genotypes. The solid circles represent sites with growing season rainfall of ≥ 400 mm, the grey circles ≤ 300 mm, and open circles 300-400 mm. The locations are denoted by the first 3 letters of the town names followed by the year (08: 2008 and 09: 2009). The loadings of the environmental variables are showed as vectors. Rainfall – Growing season rainfall; Rainfall A-A - rainfall from April to August representing rainfall during pre-anthesis rainfall; Rainfall S-O-Rainfall from September to October representing the rainfall during seed filling; Tmax and Tmin - the maximum and minimum temperatures during the growing season, respectively.

The ANOVA showed that seed yield was significantly affected by E and G, which explained 86% and 4% of the sum of squares of treatment effect (G+E+GE) (SS) in 2008 and 78% and 6% of the treatment SS in 2009. The G × E interaction explained 10% ($P < 0.0001$) of the treatment SS in 2008 and 16% ($P < 0.0001$) for the treatment SS in 2009. The G × E interaction effect was two and a half times as large as the genotype SS in both years. After division by its large degree of freedom, the interaction mean square (MS) was still significant by an *F*-test in both years. This indicates that the G × E interaction was significant and real. The Finlay-Wilkinson analysis showed that the regression of seed yield of individual genotypes against the site means was significant ($P < 0.01$), indicating significant cross-over interaction between G and E. The F-W analysis accounted for 81.1% and 74.2% of the variance of seed yield in 2008 and 2009, respectively. However, the F-W analysis explained only 6.7% of the G×E interactions in 2008 and 27% of the G×E interactions in 2009.

The partitioning of GE interaction through AMMI analysis showed that IPCA1 and IPCA2 were significant factors. IPCA1 and IPCA2 explained 53% and 21% of GE sum of squares in 2008 and 45.6% and 28.9% of GE sum of squares in 2009. Fig. 2 shows both main and interaction effects for both genotypes and environments. The biplot captures the genotypes SS of 9.72 and the environment SS of 193.43, and IPCA 1 captures 11.99 of the interaction SS of 22.63 in 2008 and the genotypes SS of 5.51 and environment SS of 71.09, and IPCA 1 captures 6.85 of the interaction SS of 15.01 in 2009. The biplot revealed 95.3% of the treatment SS in 2008 and 91.1% in 2009. More variation in seed yield is caused by the interaction pattern captured in IPCA 1 than the genotype main effects. Despite the large contribution of E to the variation of seed yields, it is irrelevant to cultivar evaluation. Breeders are more interested in the contribution of G+GE to yield. The combined SS of G (9.72) and IPCA1 (12.0) accounted for 67% of the G + GE SS (32.35) in 2008. The combined SS of G (5.51) and IPCA1 (6.85) contributed 60% of the G + GE SS (20.52) in 2009. The IPCA1 was positively ($P < 0.05$) related to the growing season rainfall in 2008 and 2009, and negatively ($P < 0.05$) related to the maximum temperature in 2009.

The genotypes at the right of Fig. 2a and near the top and right of Fig. 2b are the medium season varieties performing better in the high rainfall environment. The genotypes at the left of Fig. 2a and at the bottom of Fig. 2b are the short season varieties yielding better in the poor yielding environment. CB Jardee HT was the highest yielding cultivar in the Kojonup and Tunney in 2008. CB Tumby HT and CB Jardee HT were two high yielding cultivars at Kojonup, Stirlings, Williams and Calingiri and CB Telfer, CB Tanami, ATR Cobbler did better at drier sites in 2009. Despite of is early maturity, ATR Cobbler appears to have a broad adaptability because it produced relatively high yield in both years.

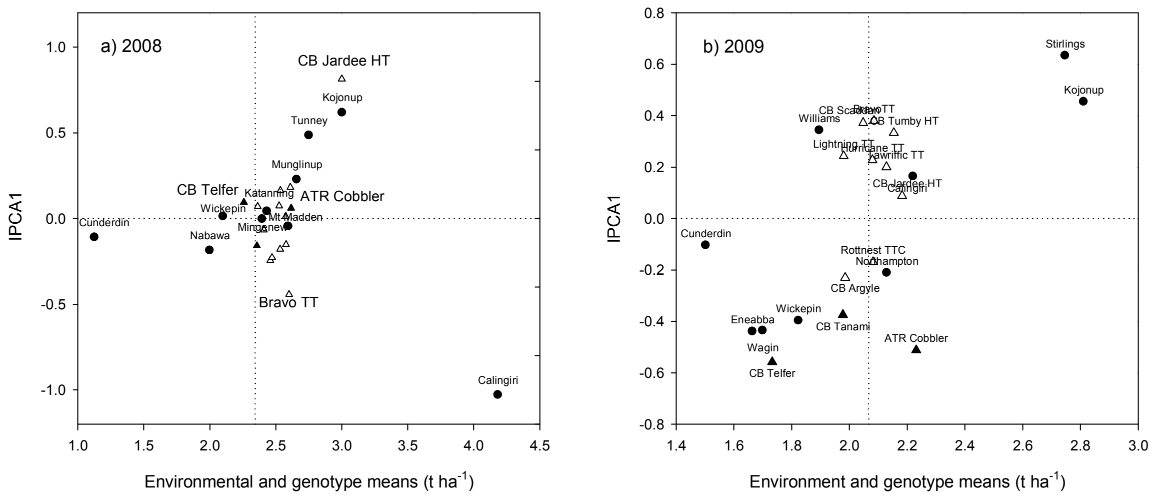

Fig. 2 AMMI-1 biplots showing the main and IPCA1 effects of both genotypes and environments on seed yield in (a) 2008 and (b) 2009. The genotypes are denoted as ∆ (medium maturity) and ▲(early maturity); closed circles denote environments. IPCA-Interaction Principle Components Analysis.

The AMMI-1 nominal yield of genotypes as a function of the environmental IPCA1 score can be used to assess the adaptability of each cultivar and aid to identify cultivar that yielded the highest at specific environmental IPCA1 ranges (Fig. 2). The norminal yield is defined as the yield from the AMMI model equation without the environment deviation (Gauch and Zobel, 1997). In 2009, CB Tumby had the highest nominal yield at the environmental IPCA1 > 0.1045. The environments within this IPCA1 score range include Calingiri, Kojonup, Williams and Stirlings. ATR Cobbler produced the highest nominal yield at the environmental IPCA1 < 0.1045. The environments within this IPCA1 score range include Cunderdin, Eneabba, Wickepin, Wagin and Northampton. CB Jardee produced similar yields to ATR Cobber and CB Tumby at around the environmental IPCA1 of 0.1045. In 2008, CB Jardee was the winning cultivars at the majority of environments (Kojonup, Katanning, Nabawa, Tunney, Mingenew, Mt. Madden, Cunderdin, and Wickepin) while Bravo won at Calingiri.

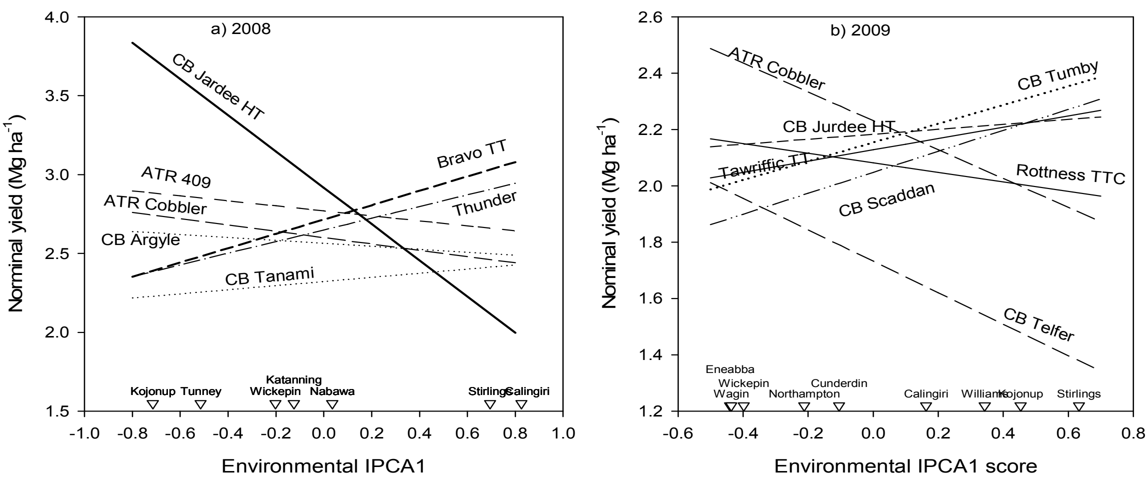

Fig. 3 AMMI nominal yields for different canola cultivars as a function of the environment interaction principle components analysis axis (IPCA) 1 score in a) 2008 and b) 2009. The scores for environment are indicated by open triangles with the location name next to it along the abscissa. The cultivars names are plotted next the lines of each cultivar.

Fig. 4 is a polygon view of GGE Biplot which is constructed by plotting the first principle component scores of the genotypes and the environments against their respective scores for the second principal component. The GGE biplots accounted for 61.4% of G +GE in 2008 and 67.5% of the total variation of G+GE in 2009. A polygon is formed by connecting the markers of genotypes (CB JArdee, AB Argyle, CB Scaddan and CB Boomer in 2008; ATR Cobbler, CB Telfer, CB Scaddan and CB Tumbyin 2009) that are farthest from the Biplot origin with straight lines such that all other genotypes are contained inside the polygon. By drawing perpendicular lines (dotted line) to each side of the polygon passing through the origin, the locations are divided into sections (Fig. 4). In 2009, the 3 sections contained environments represent 3 mega-environments and each of them has a winning cultivars located at the corner of the polygon. CB Tumby was the highest yielding cultivar in the megaenvironment that consisted of Stirlings, Mt Barker, Tunney, Calingiri, Williams, and Gibson (Megaenvironment 1: ME1). These locations had growing season rainfall > 400 mm and cooler seed filling temperatures in this megaenvironment. Kojonup stands a separate environment with a winning cultivar of CB Scaddan. However, since Kojonup had similar growing conditions to the location listed in ME 1 and the seed yield of CB Scaddan was not significantly different from that of CB Tumby at Kojonup, we put Kojonup under ME1. ATR Cobbler was the highest yielding cultivar at the megaenvironment consisting of Cunderdin, Wagin, Mingenew, Eradu, Wickepin, Northampton, Mt Maden, and Holt Rock (Megaenvironment 2: ME2). The majority of locations in this megaenvironment have growing season rainfall between 280 and 400 mm and higher mean temperatures for seed filling than ME 1. CB Telfer yielded the highest at the megaenvironment formed by Scaddan, Dudinin, and Buntine (Mega environment 3: ME3) in which growing season rainfall was less than 280 mm, short growing season, and possible very hostile soils. Cultivars CB Argyle and Hurricane were located close to the origin, indicating they yielded close to the grand mean yield and made a minimum contribution to GEI. In 2008, only two mega environment were identified probably due to less difference in rainfall between the locations. CB Jardee was the highest yielding cultivars in the majority of locations while CB Argyle was the winning cultivars at Calingiri and Nabawa.

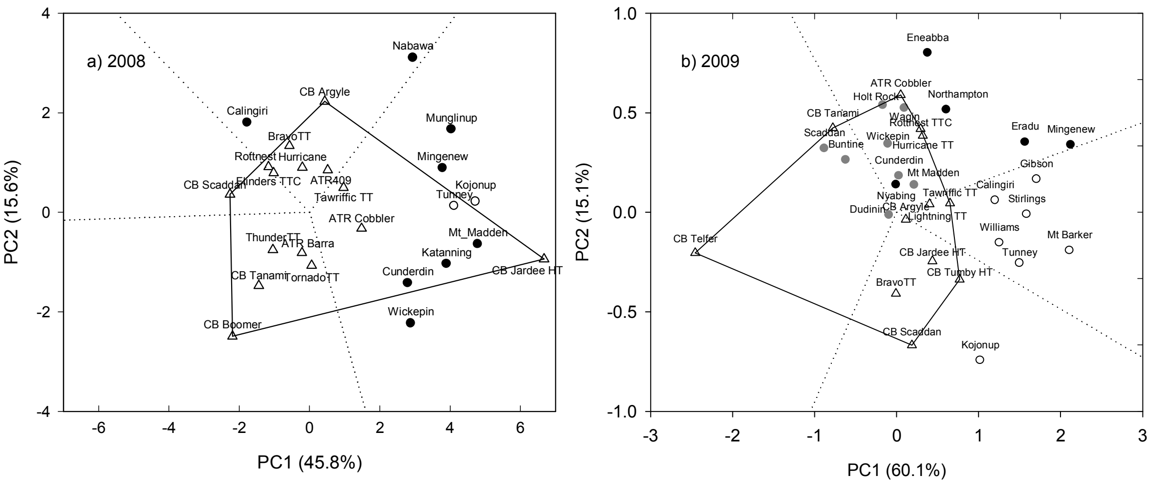

Fig. 4 Genotype plus genotype × environment (GGE) biplot showing the megaenvironments and their respective highest yielding cultivars in a) 2008 and b) 2009. The environments are showed as open circles (growing season rainfall ≥400 mm), black solid circles (growing season rainfall 300-400 mm), and gray solid circles (growing seasonal rainfall ≤ 300 mm). The cultivars are showed as open triangles circles. The names next the dots and circles are the name of locations and name of cultivars, respectively.

DISCUSSION

Analysis of MET dataset of canola in south-western Australia indicates that there were significant G×E interaction effects, namely canola genotypes responded differently to the change of the environment. The interaction patterns revealed by the F-W regression, AMMI plots and GGE Biplots indicate that canola genotypes are narrowly adapted and no genotype has superior performance in all environments (broad adaptability). This study confirms that medium-season cultivars such as CB Jardee, CB Argyle and CB Tumby produce higher seed yield in the favourable high rainfall zone while short season cultivars such as ATR Cobbler, CB Tanami, CB Telfer and CB Boomer performed better in the low and medium rainfall zone. This is consistent with Cullis *et al.* (2010) who found that the mid and late maturing genotypes are better suited to the medium to high rainfall area and the early maturity ones to low rainfall areas. The key outcome of this G×E interaction study has showed that importance of phenology to the adaptation of canola in southwestern Australia. On average, ATR Cobbler, CB Tanami, and CB Telfer were flowered 8 days earlier than CB Tumby over 13 locations. Early flowering has been proven to be critical under terminal drought for canola in south-western Australia (Burton et al., 2008). The higher seed yield of canola with early flowering in the low and medium rainfall region is probably related to its ability to allow seed development to be completed in a timely manner before moisture and high temperature stresses significantly impede seed filling and oil accumulation. A combination of an early date of sowing with an early flowering cultivar would be essential for the production of high yield and high oil canola in the lower rainfall areas of south-western Australia (Si and Walton, 2004). However, these cultivars did not perform well in the favourable high rainfall region because they could not produce enough dry matter or a large number of pods, both of them are crucial to high seed yield (Mendham et al., 1981). In contrast, the medium-season canola such as CB Jardee, CB Argyle and CB Tumby has a longer vegetative growth stage which allows it to accumulate higher dry matter at anthesis and set up more pods and seeds per unit area which are prerequisite for high yielding in canola (Mendham et al., 1984). The medium season canola also utilizes the available water and longer-growing season more efficiently than the short-season ones in the high rainfall region. Our ongoing research also shows that longer-season canola produces significantly higher yield than the short- and medium-season ones in average and above average years in the high rainfall region of southern Australia (Zhang, unpublished data).

Phenological variability is probably a most important trait that is related to the G×E interaction observed in this study. Winter type European *B. napus* was not adapted to Australian conditions and therefore, canola genotypes grown in Australia are normally spring type without vernalization requirement and reduced photoperiod requirement for flowering (Cowling, 2007). This achievement is probably related to the lesson learned from wheat breeding for drought resistance. While canola is grown in the more favorable high rainfall zone of southern Australia, it has gradually extended to low and medium rainfall zone of the cereal growing region as a break crop in rotation with wheat. As the short season cultivars become available, it may play a significant role in the wheat rotation system in southwestern Australia.

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