Oat phenotypes for drought adaptation and yield potential

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ABSTRACT

We measured yield and its components, phenology, leaf greenness, and concentration of water soluble carbohydrates and concentration of nitrogen in shoots of 29 oat varieties to determine (i) the phenotypic plasticity of these traits as a means to capture genotype-by-environment interactions, (ii) the role of these traits and their plasticity in adaptation to drought, and (iii) putative trade-offs between drought adaptation and yield potential. Varieties spaned grain, hay and grazing types, and ranged from 1301 to 1927 °Cd from sowing to anthesis. Yield was measured in nine environments while other traits were measured in 4–7 out of the 9 environments. Averaged across varieties, yield varied from 0.3 to 4.2 t ha^{-1}. The main environmental drivers of yield were water supply:demand from 500 °Cd before to 500 °Cd after anthesis, and minimum temperature in the same period. Phenotypic plasticity of yield, quantified as variance ratio, ranged from 0.60 to 1.22 for grain types and from 0.28 to 1.06 for their grazing and hay counterparts; high yield plasticity was associated with an asymmetric response to growing conditions: yield increased 3.3 ± 0.28 t ha^{-1} per unit increase in plasticity under favourable conditions, and 0.6 ± 0.16 t ha^{-1} per unit increase in plasticity under stress. For our combination of varieties and environments, genotypes were better discriminated in favourable environments, where selection for high plasticity would improve both yield potential and drought adaptation. After accounting for plasticity, yield residuals revealed consistent phenological thresholds (943 °Cd for GS31, 1470 °Cd for GS60) for adaptation to both favourable and stressful conditions. Yield correlated with leaf greenness (SPAD), particularly during grain fill. As expected from theory, yield was closely related to grains per m^2 and weakly related to grain weight. Grains per m^2 were negatively related to concentration of water soluble carbohydrates in shoots, which were in turn negatively correlated with shoot nitrogen concentration. Under favourable conditions, some varieties maintained a high concentration (> 20%) of water soluble carbohydrates at harvest. Selection against this trait could improve yield potential, but residual labile carbohydrates can also be exploited in dual grain-feed varieties, and can provide flexibility for hay growers when logistics preclude cutting at the common water ripe (GS71) target.

1. Introduction

Oat (*Avena sativa*) shares physiological and agronomic aspects with other cereals, such as a developmental window of responsiveness to stress similar to wheat and barley (Mahadevana et al., 2016), and differences outlined by Murphy and Hoffman (1992) and Marshall et al. (2013). Taxonomically, oat belongs to the tribe *Avenae*, separate from wheat, barley, rye and triticale, which belong to *Triticae*. Ecological and agronomic traits favoured wheat and barley ancestors as candidates for domestication in comparison with their oat counterparts, including local abundance, seed size, and absence of germination inhibitors. Thus, where wheat and barley were already grown as crops in the early Neolithic, oat more likely emerged as a weed in cereal crops, four to five thousand years ago. In current cropping systems, oat competes with wheat and barley for a place in rotations where it features interesting attributes including high competitiveness with weeds and tolerance to major cereal diseases such as take-all (*Gaeumannomyces graminis*).

About 60% of oat is produced in Europe, where average yield between 2000 and 2010 was about 2 t ha^{-1} in Baltic States, 3–5 t ha^{-1} in Scandinavia, close to 6 t ha^{-1} in the UK, and over 7 t ha^{-1} in Ireland (Marshall et al., 2013). In the same period, average yield in Australia was 1.4 t ha^{-1} (http://faostat3.fao.org). This partially reflects differences between European and Australian photothermal and water regimes (Chenu et al., 2013; Peltonen-Sainio et al., 2015; Lake et al., 2016). Breeding effort is smaller in oat than in other cereals; the EU Plant Variety database included 310 oat varieties compared to 1870 wheat varieties in 2012 (Marshall et al., 2013). In Australia, wheat breeding has been supported by sustained investment that has improved yield potential and drought adaptation over a century (Richards et al., 2014). In comparison, the first pre-breeding project funded to

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support oat improvement in Australia was established in 2012 (Zwer et al., 2015).

Studies on oat adaptation to water-limited environments are scarce, because most efforts are localised in comparatively favourable environments where breeding targets lodging, diseases, grain quality and winter hardiness (Marshall et al., 2013). Early work on drought was mostly focused on northern European conditions (Larsson and Gorny, 1988; Peltonen-Sainio, 1991; Peltonen-Sainio and Makela, 1995; Makela et al., 1997; Peltonen-Sainio et al., 2015). Studies with naked oat (*Avena nuda* L.) in pots indicated greater osmotic adjustment, higher concentration of abscisic acid in leaves, greater desiccation tolerance and less cell membrane damage in new Chinese varieties (released after 2008) compared with landraces released before 1950 under severe drought (Wang et al., 2017). Recent work on oat metabolomics uses artificial conditions (Sanchez-Martin et al., 2015) overlooking the need to match adaptive traits to specific environments and the scaling of traits up to crop level (Jordan and Miller, 1980; Tardieu, 2012; Sadras and Richards, 2014; Chenu, 2015).

Phenotypic plasticity is "the amount by which the expressions of individual characteristics of a genotype are changed by different environments" (Bradshaw, 1965). Theoretical aspects of plasticity in developmental biology, ecology and evolution (West-Eberhard, 2003; Weiner, 2004; Pigliucci, 2005; Dingemanse et al., 2010) increasingly illuminate the interactions between genotype and environment in crops (Nicotra and Davidson, 2010; Peltonen-Sainio et al., 2011; Trentacoste et al., 2011; Sadras and Rebetzke, 2013; Alvarez Prado et al., 2014; Rogiers and Holzapfel, 2015; Grogan et al., 2016; Sadras et al., 2016).

Long-term profitability of farming business requires simultaneously managing the risk of yield losses in dry seasons, and capturing the benefits of favourable seasons (Anderson, 2010). This can involve trade-offs in crop traits seeking both adaptation to drought and high yield potential. The aim of this study was to screen a collection of oat varieties for both adaptation to yield under dry conditions, and yield potential. Environmental variation was generated by combining locations and seasons, and modelling was used to quantify the actual patterns of water supply and demand. Phenotypic plasticity was quantified to capture genotype-by-environment interactions and elucidate putative trade-offs between adaptation to water deficit and yield under favourable conditions (Sadras and Richards, 2014).

2. Methods

2.1. Plant material, environments, crop husbandry and experimental design

We compared twenty nine cultivars or advanced lines (referred to as "varieties" hereafter), which were selected by the Australian oat breeder to represent a range in agronomic uses (grain, hay, grazing), growth habit, phenology and height (Table 1). Rainfed crops were grown in nine environments resulting from the combination of locations and seasons (Table 2A). Soils were loamy at Pinery, clay loam at Riverton, sandy loam at Waikerie and clay at Turretfield.

Crop husbandry followed the protocol for the Australian National Variety Trials as described in http://www.nvtonline.com.au/trials/protocols/. Varieties were laid out in a randomised design with three replicates. Individual plots were five 3.2 m long rows sown at 165 seeds m^{-2} in all sites except Waikerie, where plots were six 5 m long rows at 180 seeds m^{-2}. In all cases, row spacing was 0.21 m and crops were fertilized with 120 kg ha^{-1} of diammonium phosphate (22 kg of N ha^{-1} and 55 kg of P$_2$O$_5$ ha^{-1}) at sowing.

2.2. Traits

Grain yield was measured in all 9 environments, and other traits were measured in at least four environments (Table 2B). Phenology was monitored weekly using the scale of Zadoks et al. (1974). The time from sowing to stem elongation (GS31), booting (GS45), panicle emergence

Table 1

Grain, hay and grazing oat varieties and advanced lines with contrasting growth habit and phenology. Varieties are ranked for plasticity of yield (unitless), which was derived from measurements in nine environments. Average (± standard error) plant height and thermal time from sowing to flowering (GS60, base temperature = 0 °C) were derived from measurements in four environments.

Variety	Type	Growth habit	Height (m)	Thermal time to flowering (°Cd)	Plasticity of yield
Forester	hay	semi-erect	0.74 ± 0.09	1927 ± 29.5	0.28
Wintaroo	hay	semi-erect	0.83 ± 0.07	1536 ± 7.0	0.58
Riel	hay	semi-erect	0.87 ± 0.07	1708 ± 46.0	0.58
05104-19	grain	erect	0.85 ± 0.07	1312 ± 8.4	0.60
Bettong	hay	semi-erect	0.75 ± 0.07	1474 ± 17.1	0.65
MA6875	grazing	prostrate	0.44 ± 0.05	1619 ± 7.1	0.66
Tammar	hay	semi-erect	0.74 ± 0.07	1603 ± 7.9	0.67
Mulgara	hay	semi-erect	0.85 ± 0.07	1422 ± 5.3	0.67
MA9345	grazing	prostrate	0.53 ± 0.06	1574 ± 10.0	0.74
05097-17	grain	erect	0.81 ± 0.07	1309 ± 9.7	0.77
Tungoo	hay	erect	0.80 ± 0.07	1549 ± 17.7	0.78
Carrolup	grain	semi-erect	0.75 ± 0.06	1425 ± 18.0	0.83
Wallaroo	hay	semi-erect	0.78 ± 0.06	1390 ± 11.0	0.85
Potoroo	grain	semi-erect	0.64 ± 0.05	1433 ± 14.5	0.87
05089-31	grain	semi-erect	0.68 ± 0.06	1371 ± 8.1	0.90
05014-22	grain	semi-erect	0.84 ± 0.07	1312 ± 10.6	0.90
Brusher	hay	semi-erect	0.83 ± 0.06	1404 ± 9.6	0.94
05089-37	grain	semi-erect	0.60 ± 0.05	1416 ± 6.5	0.97
Eurabbie	grazing	semi-erect	0.51 ± 0.06	1541 ± 21.2	0.99
Echidna	grain	semi-erect	0.54 ± 0.06	1502 ± 22.1	1.01
Williams	grain	semi-erect	0.68 ± 0.06	1482 ± 19.8	1.01
05140-3	grain	erect	0.76 ± 0.06	1301 ± 7.7	1.03
Mitika	grain	semi-erect	0.55 ± 0.06	1414 ± 5.1	1.04
MA7930	grazing	prostrate	0.51 ± 0.06	1548 ± 21.9	1.06
Yallara	grain	erect	0.76 ± 0.07	1389 ± 6.1	1.09
05302-19	grain	erect	0.70 ± 0.07	1312 ± 10.6	1.12
Bannister	grain	semi-erect	0.64 ± 0.05	1446 ± 11.1	1.13
Wombat	grain	semi-erect	0.56 ± 0.05	1458 ± 10.5	1.18
Dunnart	grain	semi-erect	0.66 ± 0.07	1453 ± 19.9	1.22

(GS55), beginning (GS60) and mid anthesis (GS65), water ripe as a target for hay harvest (GSS71) and milk ripe (GS75) were estimated and expressed as thermal time (°Cd) calculated with a base temperature of 0 °C.

Shoots were cut from the central rows in 0.50 × 0.50 m samples at GS71 and maturity; fresh weight of the whole sample was determined and moisture to derive dry weight was measured in 0.250 kg fresh-weight subsamples after drying for 48 h at 60 °C. Maturity samples were used to determine grain yield and its components: panicles per m^2, grains per panicle and individual grain weight. The dried samples were milled twice, first with Thomas Wiley® Mill Model 4 to pass a 4 mm sieve; and next with Retsch Cyclone Mill Twister to pass a 1 mm sieve. The ground samples were fed into the NIR sample cell of approximately 80 ml (approximately 22–25 g) and scanned by NIR reflectance spectroscopy (NIR FOSS DS 2500 for GS71 and NIR FOSS XDS rapid content analyser for maturity samples) to estimate crude protein and water soluble carbohydrates (AFIA, 2014). For these determinations, whole samples were used at GS71, and grain was separated from rest of shoot at maturity. Nitrogen was estimated by dividing crude protein by 6.25 (Wu et al., 1977).

Plant height was measured with a ruler at physiological maturity. Flag leaf greenness was measured with SPAD502 Plus (Spectrum Technologies, Inc., USA) at four phenological stages: GS45, GS55, GS65 and GS75. For each replicate, a measure of SPAD was taken as the average of three readings per plot from three plants and three leaf positions, top, middle and lower.

2.3. Environmental characterisation

We translated the nominal "location-season" environment into quantitative patterns of water supply:demand ratio. This approach for