Field Crops Research xxx (2016) xxx–xxx

Contents lists available at ScienceDirect

Field Crops Research

journal homepage: www.elsevier.com/locate/fcr

Relationships between $\delta^{13}C$, $\delta^{18}O$ and grain yield in bread wheat genotypes under favourable irrigated and rain-fed conditions

M.J. Foulkes*, J. DeSilva, O. Gaju, P. Carvalho[1]

Division of Plant and Crop Sciences, School of Biosciences, University of Nottingham, Leicestershire, LE12 5RD, UK

A R T I C L E I N F O

Article history:
Received 23 February 2016
Received in revised form 1 July 2016
Accepted 6 July 2016
Available online xxx

Keywords:
Wheat
Carbon and oxygen isotope signatures
Water use efficiency
Drought tolerance
Plant breeding

A B S T R A C T

In previous investigations, carbon isotope composition ($\delta^{13}C$) has been used in C_3 cereals to screen for genotypes with high transpiration efficiency and oxygen isotope composition ($\delta^{18}O$) has been shown to correlate with transpiration rate. We examined associations of $\delta^{13}C$ of the grain and flag leaf and $\delta^{18}O$ of the flag leaf with respect to grain yield in wheat cultivars in UK field conditions. Field experiments were carried out at University of Nottingham in 2009–10 and 2010–11 testing 17 wheat cultivars under fully irrigated and rain-fed conditions. Averaging across years grain yield was reduced by 1.69 t ha^{-1} (16.5%) in the rain-fed treatment ($P < 0.001$). There was a negative linear relationship between grain yield and grain $\delta^{13}C$ amongst cultivars, under both irrigated ($R^2 = 0.47$, $P < 0.01$) and rain-fed ($R^2 = 0.70$, $P < 0.001$) conditions. Grain $\delta^{13}C$ was negatively correlated with flag-leaf stomatal conductance ($r = -0.94$, $P < 0.01$) in a subset of six of the cultivars, indicating that higher transpiration efficiency was associated with lower stomatal conductance. The associations between grain yield and flag-leaf $\delta^{13}C$ and flag-leaf $\delta^{18}O$ amongst cultivars under irrigated and rain-fed conditions were not statistically significant. There was a positive linear relationship between flag-leaf $\delta^{18}O$ and grain $\delta^{13}C$ amongst cultivars under irrigated conditions ($R^2 = 0.38$, $P < 0.01$), indicating a trade-off between transpiration and transpiration efficiency (TE). Genetic variation in grain yield under rain-fed conditions was also associated with delayed onset of flag-leaf senescence ($R^2 = 0.35$, $P < 0.05$). The 17 wheat cultivars ranged in year of release (YoR) from 1964 to 2009 and grain yield increased linearly under irrigated conditions by 60.4 kg ha^{-1} yr^{-1} (0.72% yr^{-1}) and under rain-fed conditions by 47.5 kg ha^{-1} yr^{-1} (0.66% yr^{-1}) over the 45 year period and grain $\delta^{13}C$ composition decreased by 0.0255 and 0.0304‰ yr^{-1}, respectively, indicating genetic gains in wheat yield potential in the UK seem likely to have been achieved through a lower TE, higher water uptake and lesser limitation of stomatal conductance.

1. Introduction

Worldwide, drought limits agricultural productivity more than any other single factor. Wheat (*Triticum aestivum* L.) provides, on average, one-fifth of the total calorific input of the world's population. In the UK, winter wheat is the most widely grown arable crop and contributes c. 16 million tonnes per annum with an average productivity of c. 8.5 t ha^{-1} (DEFRA, 2015). The significantly warmer and more extreme conditions now arising from climate change (IPCC, 2014) mean that new cultivars with greater drought resistance must be developed to maintain food security. In the UK, water deficits can commonly limit wheat yields in some years, where, typically, the onset of drought is post-anthesis, and losses are c. 20–30% (Foulkes et al., 2002).

Plants discriminate against the heavier carbon isotope (^{13}C) during photosynthesis and the extent of this discrimination depends on the ratio of intercellular versus external CO_2 concentration (C_i/C_a) in photosynthetic organs (Farquhar et al., 1982). The carbon isotope composition ($\delta^{13}C$) is negatively related to C_i/C_a (Farquhar et al., 1982), which, in turn, is negatively related to the transpiration efficiency at the stoma (CO_2 assimilation/transpiration). Therefore, carbon isotope composition ($\delta^{13}C$; frequently expressed as discrimination from the source air, $\Delta^{13}C$) is positively associated with TE. When measured in dry matter, $\delta^{13}C$ provides information on the long-term transpiration efficiency of C_3 plants (Farquhar and Richards 1984). Conditions that induce stomatal closure, such as water deficit, restrict the CO_2 supply to carboxylation sites, which then increases the $\delta^{13}C$ (or decreases $\Delta^{13}C$) of plant matter (Farquhar et al., 1989). The carbon isotope signature has been

---

* Corresponding author.
E-mail address: John.Foulkes@nottingham.ac.uk (M.J. Foulkes).

[1] Present address: Azotic Technologies, BioCity, Nottingham, NG1 1GF, UK.

http://dx.doi.org/10.1016/j.fcr.2016.07.006
0378-4290/

Please cite this article in press as: Foulkes, M.J., et al., Relationships between $\delta^{13}C$, $\delta^{18}O$ and grain yield in bread wheat genotypes under favourable irrigated and rain-fed conditions. Field Crops Res. (2016), http://dx.doi.org/10.1016/j.fcr.2016.07.006

used as a selection indicator for high TE in commercial wheat breeding for water-limited environments (Rebetske et al., 2002; Condon et al., 2002; Condon et al., 2004). Selection for Δ^{13}C was used to develop the Australian spring-wheat cultivars Drysdale and Rees (Richards, 2006). Under severe drought in Australia, Δ^{13}C of grain was negatively correlated with aerial biomass and grain yield for wheat (Rebetske et al., 2002). In other instances of more mild droughts with relatively plentiful water up to anthesis, the relationship between Δ^{13}C and grain yield of wheat has been positive, associated with higher stomatal conductance (g_s) and increased water use (WU; the total water absorbed and further transpired by the plant) and biomass in Mediterranean conditions (Araus et al., 2001, 2003; Condon et al., 2004; Zhou et al., 2015) and in the UK (Aravinda-Kumar et al., 2011). Therefore, except for severe drought conditions, water use appears to be a more important adaptive trait than the water-use efficiency (WUE; ratio of aerial biomass to evapotranspiration) (Slafer and Araus, 2007; Blum, 2009). An important breeding objective is therefore to identify sources of high WU in which any trade-off with WUE is minimized. The δ^{13}C signature provides no definitive information on whether genetic variation in δ^{13}C is being driven by variation in stomatal conductance (g_s) or photosynthetic capacity, although the major role of stomatal conductance has been implied in diverse studies (Araus et al., 2001, 2003; Condon et al., 2004; Aravinda-Kumar et al., 2011; Zhou et al., 2015).

The oxygen isotope signature (δ^{18}O) of vegetative tissues can be used as an indirect measure of transpiration and WU. The oxygen isotope abundance of plant matter (usually expressed as a composition, δ^{18}O of the bulk matter) can also be used to separate the independent effects of assimilation (A) and g_s on δ^{13}C since it is unaffected by photosynthesis (Farquhar et al., 2007). The oxygen isotope signature integrates the evaporative conditions throughout the crop cycle (Barbour et al., 2000) and has been proposed as a proxy method for measuring transpiration and water use in different crop species (Barbour et al., 2000; Sheshshayee et al., 2005; Cabrera-Bosquet et al., 2009a, 2011). δ^{18}O is affected by air humidity and temperature (Barbour et al., 2000; Helliker and Ehleringer, 2002a, 2002b), soil moisture (Saurer et al., 1997; Ferrio et al., 2007) and source water (Williams and Albertson, 2005; Asbjomsen et al., 2008). Nevertheless, when comparing genotypes growing under the same water conditions, δ^{18}O may be used to assess the effect of treatments and genotypic variability on yield in wheat, e.g. in bread wheat (Barbour et al., 2000; Ferrio et al., 2007; Cabrera-Bosquet et al., 2009a; Zhou et al., 2015) and durum wheat (Cabrera-Bosquet et al., 2011; Araus et al., 2013). A negative relationship between δ^{18}O and grain yield was reported in field experiments under fully-irrigated conditions across a set of eight bread wheat cultivars (Barbour et al., 2000) and in nine bread wheat cultivars grown under high-yielding Mediterranean conditions in Spain (Zhou et al., 2015). However, Ferrio et al. (2007) failed to find a phenotypic correlation between δ^{18}O and yield across a set of 24 bread wheat genotypes growing under three different water regimes. Therefore, studies reporting the use of δ^{18}O in water-limited cereals grown under real field conditions are still scarce and the results are contradictory.

The combined measurement of δ^{13}C and δ^{18}O in plant tissues is of interest in breeding due to their relationship to photosynthetic and transpiration performance of the plant during the course of crop growth, i.e. measurement of δ^{13}C and δ^{18}O can be potentially be used to identify genotypes which minimise any trade-off between transpiration efficiency (TE; ratio of aerial biomass to transpiration) and transpiration. This may help plant breeders to select genotypes that are better suited to drought. A positive relationship between genetic variation in grain δ^{18}O and grain δ^{13}C was observed (implying a negative relationship between TE and transpiration) in durum wheat for 10 cultivars under irrigated and unirrigated conditions (Araus et al., 2013) and in bread wheat for nine cultivars under high-yielding conditions (Zhou et al., 2015). Previously studies reporting the effect of water limitation on both the carbon and oxygen signatures amongst genotypes were conducted in pots in maize (Cabrera-Bosquet et al., 2009b), in the field in seedlings of tropical tree species grown in a tropical environment (Cernusak et al., 2009) and in the field in durum wheat (Araus et al., 2013). However, no previous studies have investigated the effects of water limitation on both the carbon and oxygen signatures amongst bread wheat genotypes. Our objectives were firstly to examine associations between δ^{13}C, δ^{18}O and grain yield and associated physiological mechanisms amongst 17 bread wheat cultivars grown under favourable irrigated and rain-fed conditions and secondly to quantify changes in grain yield and the carbon and oxygen signatures with the year of release (YoR) in field experiments at Nottingham, UK in two seasons.

Table 1
Reduced height *Rht-B1a*/*Rht-B1b* and *Rht-D1a*/*Rht-D1b*, photoperiod insensitivity *Ppd-D1a*/*Ppd-D1b* and spring/winter classes and year of release (YoR) for 17 wheat cultivars grown in experiments in 2009–10 and 2010–11. The *Rht-B1b* and *Rht-D1b* alleles confer semi-dwarf stature and the *Ppd-D1a* allele confers photoperiod insensitivity.

Cultivar	*Rht-D1*/*Rht-B1*	Spring/winter	YoR	*Ppd-D1*
Maris Widgeon	*Rht-B1a*/*Rht-D1a*	Winter	1964	*Ppd-D1b*
Hobbit	*Rht-B1a*/*Rht-D1b*	Winter	1977	*Ppd-D1b*
Avalon	*Rht-B1a*/*Rht-D1b*	Winter	1980	*Ppd-D1b*
Beaver	*Rht-B1a*/*Rht-D1b*	Winter	1990	*Ppd-D1b*
Hereward	*Rht-B1a*/*Rht-D1b*	Winter	1991	*Ppd-D1b*
Cadenza	*Rht-B1a*/*Rht-D1a*	Spring	1994	*Ppd-D1b*
Rialto	*Rht-B1a*/*Rht-D1b*	Winter	1995	*Ppd-D1b*
Soissons	*Rht-B1a*/*Rht-D1b*	Winter	1995	*Ppd-D1a*
Savannah	*Rht-B1a*/*Rht-D1b*	Winter	1998	*Ppd-D1b*
Paragon	*Rht-B1a*/*Rht-D1a*	Spring	1999	*Ppd-D1b*
Xi19	*Rht-B1a*/*Rht-D1b*	Spring	2002	*Ppd-D1b*
Cordiale	*Rht-B1a*/*Rht-D1b*	Winter	2004	*Ppd-D1b*
Istabraq	*Rht-B1a*/*Rht-D1b*	Winter	2004	*Ppd-D1b*
Glasgow	*Rht-B1a*/*Rht-D1b*	Winter	2005	*Ppd-D1b*
Zebedee	*Rht-B1a*/*Rht-D1b*	Winter	2007	*Ppd-D1b*
Oakley	*Rht-B1b*/*Rht-D1a*	Winter	2007	*Ppd-D1b*
Panorama	*Rht-B1a*/*Rht-D1b*	Winter	2009	*Ppd-D1b*

2. Materials and methods

2.1. Experimental design and plot management

Seventeen wheat cultivars (Table 1) were grown under irrigated and rain-fed conditions in field experiments in 2009–10 and 2010–11 on a sandy loam soil type (Dunnington Heath Series) at University of Nottingham farm, Leicestershire UK (52.834N, −1.243W). Cultivars ranged in YoR (taken as their year first included on the UK Recommended List) from 1964 to 2009, and were chosen because they were representative of the most widely grown cultivars over the 45-year period (Table 1). The cultivars were known to contrast for possession of major genes including the semi-dwarf *Rht-B1* and *Rht-D1* genes and the photoperiod sensitivity *Ppd-D1* gene (Table 1). Fourteen of the cultivars were semi-dwarfs, and three were tall cultivars (Maris Widgeon, Cadenza and Paragon); fourteen were winter wheat cultivars, and three were spring wheat cultivars (Cadenza, Paragon and Xi19); and all were photoperiod sensitive cultivars apart from Soissons which was photoperiod insensitive. Eight of the cultivars were bread-making cultivars (M. Widgeon, Hereward, Cadenza, Rialto, Soissons, Paragon, Xi19, Cordiale and Panorama) and nine were feed or biscuit-making cultivars. The experimental design was a split-plot randomised block with three replicates. Irrigation treatments were randomised on main-plots and cultivars on sub-plots. In the irrigated treatment, a trickle irrigation system was used to

Please cite this article in press as: Foulkes, M.J., et al., Relationships between δ^{13}C, δ^{18}O and grain yield in bread wheat genotypes under favourable irrigated and rain-fed conditions. Field Crops Res. (2016), http://dx.doi.org/10.1016/j.fcr.2016.07.006