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Improving water use efficiency and drought tolerance in UK winter wheats

by

Eric S Ober[1], Peter Werner[2], Edward Flatman[3] Bill Angus[4] Peter Jack[3] and Chris Tapsell[2]

[1]Rothamsted Research, Broom's Barn Research Centre, Higham, Bury St Edmunds IP28 6NP

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1. ABSTRACT

Wheat yields in the UK are often limited by water deficit during critical stages of crop development. The aim of this project was to provide information that could help guide the identification and development of varieties with greater drought tolerance (DT). A genetically diverse set of 120 wheat varieties was evaluated under irrigated and managed drought conditions in the field. There was significant variation for DT index (DTI), water use efficiency (WUE), yield potential and yield stability. Although the ranking of varieties differed with each year, several varieties showed consistently better than average DTI, and another set poorer than average. There was significant variation between varieties for anatomical and physiological traits associated with performance under water-limited conditions. Each trait, however, explained only a small proportion of the variance in DT or WUE. The combination of traits that describes a superior water-efficient variety, which blends resilience with yield potential, could aid breeding by focusing selection for secondary (proxy) traits, or via molecular markers linked to these traits.

The project also examined the relative ranking of 64 varieties tested across a range of sites that differed in soil water holding capacity. Unfortunately, insufficient drought developed on enough sites to adequately determine consistent differences in the performance of varieties for dry conditions. However, the approach has merit if data on varieties are accumulated across sites and years.

To help understand the genetic control of DT, WUE and component traits, 135 lines were genotyped using 11 diagnostic markers plus seven markers based on published QTL data. A subset of 94 lines was genotyped using 2499 DArT biallelic dominant markers. These genotypic data, in conjunction with the phenotypic data collected from the field experiments, could be used in future association studies to discover the genetic basis of traits controlling DT and WUE.

These results provide a comprehensive and quantitative description of UK winter wheat lines for DT, WUE and traits associated with improved yields under dry conditions. However, the ranking of varieties depended on which measure of DT was used, and the timing and severity of the water deficit. The data gathered in this study confirms previous findings, suggests possible new avenues for genetic improvement, and provides a foundation for further work.

2. SUMMARY

2.1. Introduction

Globally, drought causes more yield losses than any other single biotic or abiotic factor and remains one of the largest threats to food security. In the UK, it is estimated that approximately 30% of the wheat acreage is grown on drought-prone soils and at least 10% of the wheat yield is lost each year due to insufficient soil moisture, with greater losses in very dry years. Therefore, 'drought' in the UK is not an extreme phenomenon that occurs rarely; rather, crops frequently fail to attain their potential output because water supply cannot keep pace with demand, often during critical stages of yield formation. Development of varieties with increased drought tolerance and water use efficiency is therefore crucial to improving the productivity and sustainability of the wheat crop in the UK. Growers, however, have little guidance on which varieties are best suited for dry conditions, and breeders have little quantitative information on which lines are superior, or which traits would be beneficial when there is a shortage of rainfall. The aim of this work was to enable the identification and development of improved wheat varieties for water-limited conditions in the UK.

Drought tolerance can be defined in different ways. The absolute yield under droughted conditions is of primary importance to the grower, and in general, high yielding varieties do well across a range of conditions. However, some varieties are more sensitive to drought than others, so a highly ranked variety in the absence of stress may yield considerably less than other varieties when water is limiting. Therefore, a second useful measure is an indicator of yield stability, or more appropriately, stability in combination with yield potential (the best yield attainable in the absence of stress). Because climatic conditions in the UK can vary each year, it is not possible to measure yield in every possible environment. Therefore, a third measure of performance is the relative sensitivity of a variety to drought: the drought tolerance index (DTI) quantifies the proportion of yield potential that plants manage to maintain under drought, normalised by the intensity of the drought. Thus, a variety can be described by: 1) its yield potential; 2) actual yield under at least one drought scenario; 3) yield stability; 4) drought tolerance *per se* (the DTI). All these measures are inter-related and quantify different aspects of variety performance. In all cases, because in the UK there are frequently seasons and sites with little or no moisture deficit, yield potential of a variety always must be taken into account.

The concept of water use efficiency (WUE) is important when water is a limited and costly resource. WUE is calculated as the ratio of yield to the quantity of water used by the crop. High WUE can be achieved by increasing yield, decreasing water use, or a combination of both. In most circumstances for a rainfed crop, high WUE at the expense of yield would have little benefit, whereas varieties that make the most effective use of water should be at an advantage under any conditions. With little information on how UK varieties differ in WUE or which traits confer more effective use of water, this project aimed to fill some of this knowledge gap.

2.2. Materials and methods

The relative performance of wheat varieties in response to water availability was assessed by:

- Testing 120 wheat lines (including Recommended List (RL) varieties, elite breeding lines, old varieties and several French varieties) under irrigated and managed drought conditions in the field in 2007 and 2008, and a subset of 66 varieties in 2009. Drought was imposed approximately two weeks prior to flowering by covering plots with large polythene tunnel rainout shelters.
- Testing 64 varieties on eight breeders' sites over three years under natural rainfed conditions.
- Comparing current RL varieties across 13 official test locations comprising contrasting soil types over three years.

In addition, 135 lines were genotyped using 11 diagnostic markers plus seven markers based on published QTL data. A subset of 94 lines was chosen for genotyping using 2499 DArT biallelic dominant markers.

2.3. Results

2.3.1. Varieties

Results showed that significant genotypic diversity for drought tolerance and WUE exists within the wheat germplasm pool used by plant breeders to create new UK varieties. Thus, there is potential to improve the performance of future varieties for dry years and on drought-prone land.

Although the ranking of varieties changed in each trial, several varieties showed consistent contrasts in DTI, determined by measuring yield in test plots grown under fully irrigated conditions and under rainout shelters. For instance, Hobbit and Andalou had significantly better DTI scores than Gatsby and Dover, averaged across three years. The older, tall variety Cappelle Desprez also showed good DTI, but another older, tall variety Maris Widgeon, was poor. Both varieties had low relative yields, but certain characteristics of Cappelle Desprez allowed it to maintain a greater proportion of its yield potential, suggesting some intrinsic capacity to better withstand drought.

Relative comparison of varieties across a range of RL test locations that differed in soil water holding capacity showed only small differences between varieties in 2009. In 2007 and 2008 there was little stress due to sufficient rainfall. In 2006 there was enough water deficit on some sites such that Sahara showed a significant positive slope (by regressing relative yield against site drought stress index), indicating relatively better performance as conditions become drier. In breeders' trials (seven in the UK, one in France) in 2009, varieties showed significant yield responses to the range of water availabilities represented in these trials. For instance, Hobbit had a positive slope, while Exotic showed a negative slope.

2.3.2. Morphological and physiological traits

There was highly significant variation between lines for nearly all measured traits. A number of traits showed significant correlation with various measures of variety performance, such as irrigated yield potential, yield under droughted conditions, DTI and water use efficiency. However, as expected for complex traits, each single character explained only a small proportion of the variance in yield or drought tolerance. Traits that positively correlated with DTI were: maintenance of green canopy, stem dry mass at anthesis, soluble stem carbohydrates, leaf thickness, stem height and water use from deep soil layers (Table 1). Carbon isotope discrimination ratio (Delta) in leaf and grain was negatively associated with DTI but positively associated with yield. Leaf rolling and waxy bloom were positively correlated with droughted yields. Many varieties expressed combinations of both positive and negative traits, making it difficult to assess the value of one trait independently of others. A composite trait score that combined the effects of several key traits was devised as a quantitative description of a drought tolerant or water efficient type that could aid breeding for improved varieties.

Table 1. Relationships between traits and yield or drought tolerance. Positive signs and minuses indicate positive and negative phenotypic correlations, respectively; blanks indicate a neutral effect.

	Drought tolerance index[7]	Irrigated yield	Droughted yield
Maintenance of green canopy[1]	**+**	**+**	
Stem dry mass at anthesis[2]	**+**	**-**	
Stem carbohydrate concentration[3]	**+**	**+**	
Carbon isotope discrimination ratio[4]	**-**	**+**	**+**
Water extraction from deep soil layers	**+**	**-**	
Stem height	**+**	**-**	
Flag leaf thickness	**+**	**+**	
Flag leaf area		**-**	
Flag Leaf rolling			**+**
Flag leaf photosynthetic efficiency[5]		**+**	
Waxiness[6]			**+**

[1] Maintenance of green canopy cover is the proportion of canopy cover at anthesis under irrigated conditions that was maintained under droughted conditions)

[2] Stem dry mass (or also the ratio of ear:stem dry matter) measured at anthesis

[3] Concentration of water-soluble carbohydrates (WSC) in stems sampled at anthesis

[4] Measured in flag leaves at anthesis or grain at maturity

[5] Measured using chlorophyll fluorescence techniques

[6] Appearance of waxy bloom on leaves and stems

[7] The proportion of unstressed yield potential maintained under droughted conditions

There was good correlation between droughted and irrigated yields, indicating that yield potential was important in ensuring good yields when water was limiting. However, some high-yielding varieties were also unstable, losing rank position under droughted conditions. In breeding programmes, selection against traits that increase susceptibility to yield losses under dry conditions while simultaneously selecting for good yield potential may increase both yields and yield stability.

2.3.3. Water use efficiency

Water use efficiency (WUE) in a subset of 21 varieties was calculated on the basis of grain or total biomass yields and estimated water use, derived from calculations of crop evapotranspiration and measurements of soil water extraction in droughted plots.

- Significant genotypic variation was observed for WUE, which was affected largely by differences in yield.
- There were small but significant genotypic differences in water use and patterns of soil water extraction: some varieties such as Xi19 removed more water from deep soil layers (80-110 cm from the soil surface) than others such as Spark. Xi19 also showed greater drought tolerance than Spark.
- There was a slight negative correlation between yield potential and water extracted from deep soil layers, indicating a potential cost to greater root activity at depth. However, within a high-yielding group of varieties, a difference of 10 mm extra water extracted can translate to 0.2 t grain/ha at a typical WUE of 0.2 t/ha/mm.
- There was good correlation between WUE, droughted yields and drought tolerance *per se*, indicating that improvements in one trait will benefit the others.

2.4. Discussion

Improvements in wheat yields under water-limited conditions are a global challenge and pressing need. In arid areas, development of varieties that yield well when water is limiting is done empirically by direct selection for yield under these conditions. However, this is not practical in the UK or other regions that have periods of dry weather that are unpredictable in timing and severity. There has been considerable interest in secondary traits associated with drought tolerance and WUE as criteria for indirect selection for these targets. Findings from this project reveal that a drought-tolerant UK wheat phenotype (ideotype) is comprised of several characters, each of which individually makes a partial contribution to success under soil water deficit. The challenge is to quantify this ideotype to enable phenotypic selection on a large scale in breeding nurseries, or to pyramid a sufficient number of molecular markers.

Results also showed that one ideotype is not sufficient for the UK environment: varieties that are most successful during a water deficit prior to flowering, but with recovery of stress during grain filling, are different than those that yield relatively better when deficits develop only after flowering.

It is impossible for breeders to know which kind of drought predominates, so focus on traits such as maintenance of green canopy, which is important regardless of the timing of deficits, could be more fruitful than attempting to match the timing of sensitive developmental phases with potentially stress-free periods. Measurement of WUE in a range of varieties under dry field conditions revealed that the effective use of water can be improved mostly by increasing grain yields.

Evaluation of multi-location variety trial data to gain much-needed information on suitability of current varieties for drought-prone areas adds value to data already gathered in these trials. The approach used in this project could be applied to each new set of RL results, accumulating data on varieties during their lifetime on the List.

Novel contributions and outcomes from this project that can benefit the UK and international wheat community include:

- A comprehensive and quantitative description of a large set of UK winter wheat lines for DT, WUE and traits associated with improved yields under dry conditions. These lines can be used in selective crosses to create new varieties, and can be crossed to make bi-parental mapping populations in order to study the genetic control of traits more closely. Phenotypic datasets can be used for mining further information about trait x variety x environment interactions.
- Sets of varieties that show consistent contrasts in stem carbohydrates, carbon isotope discrimination ratio (extreme lines identified here already have been crossed in a WGIN-sponsored project), leaf morphology, etc.
- Methods that have been adapted to measure morpho-physiological traits rapidly and inexpensively on large numbers of varieties grown under field conditions.
- A cost-effective protocol to evaluate current RL varieties for drought tolerance and yield stability using multi-location RL trial data, including a database of soil, weather and variety data that can be augmented each year to increase the ability to differentiate between varieties according to water availability.
- A database of genotypic and phenotypic data that can be analysed for marker-trait associations.

Data sharing and collaboration agreements have been established with ADAS (ERYCC LINK project [LK0992]), Nottingham University (WGIN2 Drought work package), Triticarte Pty, Ltd (association studies) to make further use of the phenotype and marker data collected in this project.