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Variation in light interception traits in European spring barley landraces

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Abstract

Improving the efficiency of photosynthesis is a potential strategy for increasing crop yields in the future, but this is only possible if genetic variation exists for this attribute within crop germplasm resources. A key component of photosynthetic efficiency is the plant's ability to intercept light. This study examined the extent of genetic variation, available within barley landraces from Europe, for parameters affecting light interception. Landraces varied in time spent between emergence and full canopy establishment, with those from Northern latitudes reaching canopy closure between 2 and 8 days faster than those from Southern latitudes. There was significant variation in leaf chlorophyll content between the landraces, but this was unrelated to site of origin. Landraces originating from locations with cooler temperature over the growing season held their leaves in a more planophile manner than those from warmer climates, resulting in a negative relationship between leaf angle and mean temperature at site of origin. We conclude that substantial genetic variation in key parameters affecting light interception have evolved among barley landraces in Europe that could be utilised in future breeding programmes to improve the efficiency of photosynthesis and increase crop yields.

Keywords:

Photosynthesis; Landraces; Light Interception, Canopy Structure, Local Adaptation

1. Introduction

Cereal yield increases over the past century have mainly come about from improved harvest index (HI), fertiliser responsiveness and increased arable land area (Evans, 1997; Fischer and Edmeades, 2010; Reynolds et al., 2011, 2009). Yields are now stagnating in many areas of the world in staple crops such as wheat, maize and rice (Mackay et al., 2011; Ray et al., 2012). With potential arable area reaching a limit due to increasing pressure for land use, new avenues for increasing yield must come from increasing production per unit area of ground (Long et al., 2015; Zhu et al., 2010). Most modern cereal breeding programs are derived from a small number of parent plants. Within these breeding programmes there may not be sufficient genetic variation present to exploit novel traits for increasing yield. Breeders may therefore need to look more widely to identify sources of suitable variation.

This situation is well illustrated by barley (*Hordeum vulgare* L.), one of the founding crops of modern agriculture, with major uses in Europe including malt and animal feed. It is widely grown in Scotland with 1.39million tonnes of spring barley and 268,124 tonnes of winter barley produced in 2018 (The Scottish Government, 2018). Barley landraces represent a possible source of genetic variation that could be used for improving traits related to yield (Rodriguez et al., 2008; Villa et al., 2005). A landrace is defined as a 'heterogeneous (genetically and phenotypically variable) variety that is reproduced by farmers as populations that are subject to both artificial and natural selection' (Bellucci et al., 2013). In some marginal areas landraces have been seen to outperform conventional cultivars (Dwivedi et al., 2016; Yahiaoui et al., 2014) as they can be locally adapted to climatic conditions (Bellucci et al., 2013). Landraces have already been used successfully to introduce traits into maize and rice that have increased yield under drought and submergence conditions respectively (Bailey-Serres et al., 2010; Meseka et al., 2015, 2013; Xu and Mackill, 1996).

Yield formation can be summarised in an equation first proposed by Monteith (Monteith and Moss, 1977):

$$Y = 0.487 \cdot S_t \cdot \varepsilon_i \cdot \varepsilon_c \cdot \varepsilon_p$$

Where Y is yield, S_t is the total amount of incident solar radiation with 0.487 being the fraction which is photosynthetically active, ε_i the efficiency of the plant in intercepting the fraction of photosynthetically active radiation, ε_c the efficiency of the photosynthetic processes converting light to energy and ε_p the proportion of energy produced which is partitioned into harvestable product. Whilst ε_p has largely been optimised there is still potential to improve ε_i and ε_c through optimisation of light interception and photosynthetic reactions (Farquhar et al., 2001; Raines, 2011). Rate of canopy development, amount and arrangement of chlorophyll and the leaf canopy architecture are all characters which can contribute towards ε_i which may be targets for optimisation.

The rate of canopy development is one of the major factors affecting ε_i (Flood et al., 2011; Long et al., 2006; Nunes-Nesi et al., 2016). Early and rapid canopy establishment can allow crops to take advantage of shorter growing seasons in Northern latitudes where the greatest amount of radiation is available in early spring (Murchie et al., 2009; Parry et al., 2011; Richards, 2000; Zhu et al., 2010). Extending the duration of canopy maintenance with slower loss of chlorophyll content during the grain filling phase in 'Stay-green' varieties is associated with an increase in grain weight in barley, maize and wheat and can lead to increased yields (Diaz et al., 2005; Emebiri, 2013; Parry et al., 2011; Zheng et al., 2009).

The chlorophyll arrangement throughout the canopy will also affect the ε_i as canopy with a more even distribution of chlorophyll throughout the leaf layers along with a greater total volume of chlorophyll may increase total light captured by reducing the number of leaves becoming saturated in the upper layers of the canopy (Ort et al., 2011; Yin and Struik, 2015). Saturation of upper leaf layers is a limiting factor in light interception as the electron transport systems fall at relatively low light levels (Björkman and Demmig, 1987). A horizontal leaf arrangement leads to saturation of the upper canopy whereas a canopy with an upper leaf angle of 75^0 from the horizontal can have double the efficiency of energy capture of a horizontal canopy at midday (Long et al., 2006). Leaf size also affects light interception and there is a trade-off between leaf size and self-shading (Amanullah et al., 2007; Long et al., 2006).

The primary aim of this study was to assess a collection of European spring barley landraces for variation in traits associated with light interception efficiency including the timing of canopy development, chlorophyll content and arrangement, leaf canopy architecture and HI. The secondary aim of the study was to relate any variation found in light interception traits to environmental conditions from the locations which the landraces originated in order to understand the factors that may have led to their local adaptation. From these tests, results are put into context of how trait variation can be considered for improvements in plant breeding and resilience to climate change.

2. Methods

2.1 Seed source and Experimental Design

The field experiment was carried out at Scotland's Rural College's Boghall farm in Midlothian, Scotland, UK (55°52'26"N 3°12'26"W) in spring and summer of 2014 and 2015. The soil type at these sites is a sandy loam (Macmerry Series). The farm is situated on the south-east slope of the Pentland hills at an elevation of 190m and the previous crop in the fields on both years was spring barley.

The barley landrace material was collected from gene banks (Table 1) prior to the start of this project and the landraces were specifically chosen to represent a wide latitudinal range across Europe which encompasses a spread of different climatic conditions and season lengths. The latitude and longitude of their original collection was used for collection of climatic data (Table 2). The landraces were a mixture of 2 and 6 row types dependent on the number of rows of seeds present on each ear. The modern cultivar Concerto was included to represent modern pedigree bred germplasm as a comparison to the landraces and was included as it was the main variety in Scotland during the experimental years.

The experimental design was a fully randomised, blocked design with three blocks in 2014 and four in 2015 and twelve plots per block(Plots measured $0.5m^2$). Four replicate plants per plot were used as technical replicates. Plots were sown on 09/04/14 and 23/04/15 and each plot was treated with 120kg/hectare of nitrogen by hand with 60kg applied on 26/04/14 and 25/04/15 for respective years and an additional 60kg two weeks after the first application. An herbicide treatment was applied when the plants reached GS23 (Harmony 70g/ha + Oxytril 0.5L/ha + High load micra.m 1.0L/ha).

2.2 Climate

The climate in the location of original collection for each of the landraces was included as a possible factor influencing the canopy structure. Climate data were obtained from the national meteorological offices in each country of origin (Table 2). The area over which the weather data was collected varies between countries from local weather data to regional data depending on the scale of reporting. It was always taken as the closest reported point to the latitude and longitude of origin of the landraces. The climatic variables reported are the total rainfall (mm) for spring/summer, the total number of sunlight hours for spring/summer and the average daily temperature (°C) for spring/summer. The data are long-term averages with FRA1, FIN1, BRI1 and SPN1 (Table 2) being from 1981-2010. GER2, NOR1, NOR2, CZE1 and GER3 and from 1961-1991 and ITA1 (Table 2) is from 1971-2000.

2.3 Crop Measurements

2.3.1 Canopy establishment

The Growth Stage (GS) of the plants were recorded weekly throughout the growth season and was assessed using the HGCA (AHDB) growth stage guide which is based on the Zadoks 100 point growth scale (HGCA (The Scottish Executive), 2006; Zadoks et al., 1974). The plot was deemed to have reached a specific growth stage when at least 50% of the plants in the plot had reached that growth stage. Additional, in depth, assessment of four replicate plants per block of the canopy structure including leaf angle, length and chlorophyll content (by proxy with SPAD readings) were measured at GS24, GS39 and GS59. At GS24 the plant is made up of the main shoot and four tillers and is in the establishment phase of its lifecycle. By GS39 stem extension is underway and the flag leaf is fully emerged meaning that canopy establishment is complete. At GS59 the ear has fully emerged from the boot and the plant has progressed from vegetative growth to reproductive growth.

2.3.2 Chlorophyll content, Distribution and Leaf Dimensions

The leaf chlorophyll content was assessed by proxy using of a SPAD meter (Minolta Corp, Ramsay, NJ). SPAD readings were taken on the uppermost leaf excluding the flag leaf on a weekly basis midway along the length of the leaf blade. SPAD readings at GS39 and 59 are reported here.

Leaf area was measured by detaching the leaves where they meet the stem and immediately passing them through a leaf area meter (Li-3100 are meter, LiCor Inc., Lincoln, NE) which calculated leaf area in cm^2. Leaves were passed through the meter three times and the readings averaged. The leaves that had been used for leaf area measures were then placed in individual paper bags and dried in an oven (Ecocell, MMM Medcenter, Munich, Germany) at 80^oC for 48 hours. The leaves were then weighed using a precision balance (Kern PLJ, D-72336, Kern & Sohn Gontbl, Balingen, Germany) in grams. The specific leaf area (SLA) was calculated as leaf area divided by leaf dry weight. The leaf area, dry weight and SLA were all measured at GS39 on the uppermost leaf excluding the flag leaf.

2.3.3 Leaf canopy architecture

Leaf angle was measured at GS39 and 59 in relation to the stem directly above it using a Helix Oxford protractor (Maped Helix, West Midlands, UK) to the nearest 5^0. Care was taken to avoid bending the leaf away from the stem by minimising handling prior to this measure being taken.

2.3.4 Allocation of resources

Harvest took place on 12/08/14 and 04/09/15. The ears on the shoots used for the earlier structural measurements were individually hand threshed and the grain number, row count and grain weight recorded and the 1000grain weight calculated. Grain weight was measured using a precision balance

(Kern PLJ, D-72336, Kern & Sohn Gontbl, Balingen, Germany). The ear and the straw were harvested to allow calculation of harvest index. The straw was dried in an oven (Ecocell, MMM Medcenter, Munich, Germany) at 80°C for 48 hours and weighed using a precision balance (Kern PLJ, D-72336, Kern & Sohn Gontbl, Balingen, Germany). Harvest index was then calculated by dividing the grain weight by the combined weight of the grain plus the straw plus the chaff. A total yield in tonnes per hectare was not calculated for the lines as the experimental design limited the amount of material that could be collected for each plot.

2.4 Statistical Analysis

We used an Analysis of Variance (ANOVA) model to determine whether there was a significant amount of variation among the landraces in each trait of interest at a significance level of $p=0.05$. Year was included as a factor to see if differences between the two years of the trial were present and if there was an interaction between the year of the trial and variation between the landraces in the trait of interest. The results of the ANOVA are reported as the test statistic F-value to show the ratio of between to within group variability with the degrees of freedom as a subscript followed by the p-value. Effects of year of the trial are also reported if significant. Regression analysis of climate and latitude with each measure of canopy structure was carried out to see if there was a relationship between traits and local climatic conditions of each landrace line. A multiple regression of leaf angle with latitude and temperature was used to examine if both factors regressed significantly with leaf angle. The linear regression of leaf angle with temperature is reported below as this was the significant factor. Results of the regression are reported as the test statistic t-value to show if the slope of the regression is significantly different from zero with the upper degree of freedom as a subscript followed by the p-value which is taken as significant at a level of $p=0.05$. In the regression analysis year was included in a factor to see if the response differed between years and this is reported where significant. All figures report an average of all data between the years. Correlation analysis was carried out on allocation of resources factors to assess if relationships were present between the variables.

The correlation coefficient of significant relationships is given followed by the p-value. All statistical analysis was carried out using GenStat 16th Edition (VSN International Ltd, Hemel Hempstead, UK).

3. Results

3.1 Growing conditions in experiments

In 2014 the average daily temperature at Boghall ranged from 7°C to 16°C. The average monthly rainfall was 107mm and the average monthly hours of sunlight was 119 hours. In 2015 the average daily temperature ranged from 5.5°C to 14.5°C. The average monthly rainfall was 130mm and the average monthly hours of sunlight was 119 hours.

3.2 Canopy Establishment

Landraces differ significantly in their development rate between GS24 and GS39 ($F_{10,52}$=9.36, $p<0.001$) (Figure 1) ranging from 12-20 days. Year was included as a factor in the analysis and there was a difference between the two years of the trial ($F_{10,52}$=19.78, $p<0.001$) but there was no interaction effect between the landraces and the year. GS24-GS39 is the stage in the plant leading up to full canopy establishment where GS24 consists of a plant with the main shoot and four tillers. It then moves through stem extension until it reached GS39 where the flag leaf is fully emerged. The length of time spent between these growth stages declines significantly in length in landraces from higher latitudes (t_{20}=34.5, $p<0.001$, R^2=0.65) with a significant effect when year was included as a factor ($p<0.001$) in the regression analysis. The modern cultivar Concerto spent longer than the landraces to reach GS24 and a similar amount of time in the canopy establishment stage between GS24 and GS39 to the Southern European landraces.

3.3 Chlorophyll Content, Distribution and Leaf Dimensions

There were significant differences in SPAD readings between the lines at all three growth stages: GS24 ($F_{11,57}$=6.97, $p<0.001$), GS39 ($F_{11,57}$=4.45, $p<0.001$) and GS59 ($F_{11,57}$=2.07, p=0.037) (Figure 2) with SPAD values ranging from 32.5-43.4, 35.2-45.4 and 41.1-48.7 respectively. When year was included as a factor in the ANOVA analysis it was seen that there was a significant difference between the years at GS24 ($F_{1,57}$=35.04, p<0.001) and GS59 ($F_{1,57}$=5.22, p=0.026). There was no relationship between either climate or latitude and leaf chlorophyll content. Concerto had higher SPAD readings than the landraces at all growth stages.

The length of the second leaf showed significant differences between the landraces at both GS39 ($F_{11,57}$=6.38, p<0.001) and GS59 ($F_{11,57}$=8.17, p<0.001) (Table 3) with leaf length between 23.2-30.3 and 20.8-29.7cm respectively. When year of trial was included as a factor in the analysis significant differences were present at both GS39 ($F_{1,57}$=53.32, p<0.001) and GS59 ($F_{1,57}$=34.71, p<0.001). There were no significant differences between the landraces in SLA (Table 3).

3.4 Leaf Canopy Architecture

Landraces differ significantly in their leaf angle at GS39 ($F_{11,57}$=10.48, p<0.001) (Table 3) where the final leaf of the canopy has fully emerged and GS59 ($F_{11,57}$=14.74, p<0.001) (Table 3) where the ear has fully emerged and the plant is switching from the vegetative to reproductive phase of its lifecycle (Table 3). The leaf angles from vertical range from 18-45 degrees and 31-84 degrees respectively. When year of trial was included as a factor in the analysis significant effects were seen at GS39 only ($F_{1,57}$=14.69, p<0.001). Leaf angle increases significantly with average temperature and Fig. 3 shows this relationship at GS59 (which is when the ear is fully emerged and the canopy size is at its maximum) (t_{20}=28.47, p<0.001, R^2=0.56) (Table 3) at the location of origin. The same relationship is present at the earlier GS39 where the flag leaf is fully emerged (t_{20}=12.31, p=0.002, R^2=0.35) (Table 3). Concerto fitted into the pattern of the landraces when temperature of the trial site was used as their origin location.

3.5 Allocation of resources

The HI showed significant differences among the landraces in the 2 row lines ($F_{7,37}$=23.72, p<0.001). The 1000 grain weight showed a significant difference between the landraces in both the 2 ($F_{7,37}$=8.12, p<0.001) and 6 row lines ($F_{3,17}$=7.57, p=0.002). When year was included as a factor in the analysis there was a significant difference in 1000 grain weight between the years of the trial ($F_{1,37}$=4.99, p=0.032). The number of grains per ear showed a significant difference between the landraces in the 2 row lines ($F_{7,37}$=5.88, p<0.001) (Table 4). When year was included as a factor in the analysis there was a significant difference in number of grains per ear between the years of the trial ($F_{1,37}$=48.57, p<0.001). There was a significant positive correlation of number of grains per ear with 1000 grain weight with a correlation coefficient of r=0.934, p=0.001 (Figure 4).

4. Discussion

The data collected in this study will allow a picture of the variation present in traits associated with photosynthetic efficiency in spring barley landraces to be assessed. It will also allow the variation seen to be examined for local adaptation to environmental conditions and how this variation can be subsequently used in pre-breeding programs. It was found that differences in rate of canopy development, chlorophyll content and canopy leaf angle all varied significantly between the landraces. Canopy development rate and leaf angle both varied with climatic conditions at the location of origin with shorter duration at higher latitudes and more planophile leaves at lower temperatures, suggesting adaptation to local condition. The traits looked at in this study were assessed out with the local climatic conditions where they originated which suggests that the variation found is under strong genetic control and this could be very beneficial to breeding programs.

4.1 Canopy Establishment

The Scandinavian landraces progressed quickly through stem extension to canopy closure (Figure 1) which would be advantageous for light interception, biomass production and grain development during the early phase of a shorter growing season. There were differences in the time spent in this phase of development between the years of the trial showing that the environment has an effect on development rate but there were also differences between the landraces which showed genetic variation is present between the lines. This has been seen in barley and other cereals including wheat and oats (Goyne et al., 1993; Kemanian et al., 2004; Muurinen and Peltonen-Sainio, 2006; Peltonen-

Sainio, 1997). Landraces from Northern latitudes will likely contain the photoperiod non-responsive polymorphism in the *Ppd-H1* gene (Jones et al., 2011; Turner et al., 2005) allowing them to move into flowering irrespective of day-length. This polymorphism has been linked to leaf size caused by changes in duration of leaf growth (Digel et al., 2016). Reaching full canopy establishment quicker may also be an advantage in out-competing weeds, shading out possible (weed) competitors in organic systems or allowing reduced herbicide application under conventional management (Sim et al. 2007; Kruk et al. 2006). The modern cultivar Concerto spent more time reaching GS24 than the landraces but progressed from GS24-GS39 at the same rate as the landraces from Southern European latitudes reaching full canopy closure later than the landraces. The early development of the Scandinavian landraces may be a trait of interest in developing new varieties which are able to take advantage of early light in a short growing season.

4.2 Chlorophyll Content, Distribution and Leaf Dimensions

During leaf emergence and through canopy closure there were differences in chlorophyll content between the landraces (Figure 2). Variation has been observed in modern varieties in a study of Sardinian wheat, barley and triticale (Giunta et al., 2002) with the varieties showing high levels of variation in chlorophyll content caused by a strong genetic and weak environmental and G*E components suggesting that chlorophyll content has not been driven in a particular direction as a side effect of breeding for other traits such as plant height. An environmental effect was seen in this study as differences in chlorophyll content were seen at some growth stages between the years of the trial. The modern cultivar Concerto was included in this study and had higher SPAD readings than the landraces present. Sufficient variation may already exist for altering the volume of chlorophyll in barley in the current pool of parents but having landraces as an alternative allows options for wider genetic material to be introduced to the breeding programs. Maintaining chlorophyll content for longer may be of benefit, as in rice it was seen that for each extra day of canopy maintenance there was an increase of 0.2 tonnes per hectare in yield (Akita, 1989). Compared to modern cultivars, wheat landraces have been seen to begin to senesce quicker once they have reached grain filling which suggests a potential negative side effect in using landraces in breeding (Gaju et al., 2016). This was visually observed in this study although senescence was not measured directly. This is something pre-breeding programs would need to be taken into account when using landraces.

The distribution of chlorophyll will be affected by the size and shape of the leaves and there were differences between the landraces in regard to leaf length at both GS39 and 59 but not in SLA suggesting that lines with a larger leaf surface area are thinner and *vice versa* (Table 3). This is supported by research in barley which showed no differences in SLA between cultivars (Giunta et al., 2002) in contrast to their findings in wheat and triticale which showed variation in SLA. Unfortunately due to experimental constraints caused by the small size of the trial plots it was not possible to measure the leaf area index or light interception. This would have completed the picture of how leaf size and shape is affecting the light capture of the landraces throughout different phases of growth and is something to be explored in future work. Selection for seedling leaves with a larger surface area has occurred in wheat and it was accompanied by an increased early plant biomass and vigour (Zhang et al., 2015). If a similar approach could be applied in barley then light interception efficiency could be increased early in the growth cycle especially in Northern latitudes where the growth season is short (Mukula and Rantanen, 1837).

4.3 Leaf Canopy Architecture

Leaf angle had been associated with cereal yields and our study showed significant variation in leaf angle among barley landraces (Table 3). Early studies in Maize showed a yield increase of 40% with a 10^{o} leaf inclination from vertical (Pendleton et al., 1968). High yielding rice varieties such as 'Takanari' have been reported to have higher photosynthetic rates per leaf than other varieties (Taylaran et al., 2011) and an erect leaf posture (Nan Su San et al., 2018) along with decreased levels of photo-inhibition (Horton et al., 1999; Kumagai et al., 2014). The optimal crop ideotype has previously been that of an overall erect canopy (Donald, 1968) but it is now suggested that decreasing leaf angle from the bottom leaf layer of the canopy to the top would be more efficient in maximising light interception

(Ku et al., 2010; Long et al., 2006; Zhu et al., 2010). Rice hybrids are being developed with 5^0, 10^0 and 20^o flag, 1st and 2nd leaves respectively (Peng et al., 2008). Canopies could be developed not only with variation in leaf angle but also with differential volumes of chlorophyll through leaf layers tailored to local environmental conditions (Ort et al., 2015).

The landraces from Southern latitudes were characterised by an erectophile leaf angle which has a negative relationship with latitude and temperature (Table 3, Figure 3). As latitude and temperature may be related a multiple linear regression was used to try to untangle if leaf angle was responding to one or both of the factors and this showed that leaf angle was responding to temperature. In other work an erectophile canopy structure has been seen to be beneficial in coping with heat stress and increasing water-use- and photosynthetic-efficiency through reduction in heat loads (Ryel et al., 1993; Valladares and Pugnaire, 1999; Werner et al., 2001) reducing excess light levels causing photosynthetic saturation at midday (Falster and Westoby, 2003). This suggests a degree of local adaptation to climatic temperature and light levels in canopy structure although more work would be needed to confirm this. The modern cultivar Concerto which has been developed for a climate midway in the range seen for the landraces fitted well with the regression seen in the landraces with temperature possibly indicating that this pattern has been retained in new breeding material.

4.4 Allocation of resources

Variation among landraces in yield components and resource partitioning was observed (Table 4) and studies have found relationships between numbers of grain and grain weight (Acreche and Slafer, 2006; Calderini and Reynolds, 2000) with wheat showing a reduction in average grain weight with increasing numbers of grain (Acreche and Slafer, 2006). There is uncertainty over whether competition between grains for resources reduces weight when there are more grains present (Borrás et al., 2004). In the barley landraces, an increase in grain weight with grain number in the 2-row lines (Figure 4) may be a consequence of lower tiller numbers and more resources allocated per ear. Landrace total yields were not obtained on an area basis due to constraints created by the small plot size. This would have been informative in understanding how canopy structure traits affects final yield. However, as landraces would need to enter a pre-breeding program to introduce traits of interest into new varieties high yields could be maintained through careful trait selection. Source-sink limitations will need to be considered when improving traits associated with photosynthetic efficiency as yields have been shown to be sink limited with the number of grain per m^2 being the major contributor to yield as opposed to grain weight (Burnett et al., 2016; Lynch et al., 2017; Madani et al., 2010; Serrago et al., 2013). In order for greater photosynthetic efficiency to enhance yields sink strength must be increased with higher number of floret production, higher numbers of productive tillers and the capacity for larger grains (Reynolds et al., 2009).

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