Variation and Stability in Agronomic Traits Among Geographic Groups of Traditional Landraces Grown Under High Yielding Conditions

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Research Article

Keywords: barley, landraces, agronomic traits, stability, yield

Posted Date: June 18th, 2021

DOI: https://doi.org/10.21203/rs.3.rs-568936/v1

Abstract

Future crop production needs to deliver increased yields with less agronomic inputs in the face of increasingly variable climate, which is predicted to result in greater seasonal variation in production. To support more sustainable production, new crop varieties need to have increased resilience in their agronomic traits to cope with fluctuation in growing conditions. We investigated the breadth of phenotypic expression in yield related agronomic traits among groups of European barley landrace from different geographic origin and Harlan composite cross populations grown under a common high yield test protocol. Stability of agronomic traits and yield were assessed for each group across environments and years. There were significant differences in thousand grain weight (TGW), seeds per ear and shoot production (tillering) among landrace groups and between 2 or 6 rowed ear habit. Modern cultivars and, to a lesser extent, Harlan populations had significantly more stable TGW than other groups. Traits most strongly associated with yield stability in 2 rowed landraces were TGW and tillering, whilst in 6 rowed landraces tillering, ear length and plant height were associated with stable yield. Absence of significant difference in agronomic trait stability among landrace groups was attributed to high phenotypic variation within groups. We conclude that phenotypic variation and stability in agronomic traits among barley landraces could be exploited for enhancing resilience in future crop breeding.

1 Introduction

Increasing the stability of crop production is one of the most important challenges in this century (Powell et al., 2012). Yield stability in agriculture is defined as consistency in crop performance when grown at different locations with varying biotic or abiotic stresses over time (Döring et al., 2018). Most arable crop production is dominated by monocultures of modern elite cultivars that have been bred and subsequently grown under high inputs of artificial fertilizers and pesticides. In barley (*Hordeum vulgare*), which is the fourth most planted crop in the world by area grown (FAO, 2004), the most common genetic structure is the pedigree-bred pure line (elite cultivar). However, barley is also grown in different parts of Europe and world-wide as landraces and other traditional material. Genetically diverse lines, such as traditional landraces and composite cross populations (CCPs) have wider variation in agronomic traits compared to elite cultivars (Nandety et al., 2014). Furthermore, some traditional barley material have increased yield complementation and compensation under varying growing conditions (Ceccarelli, 1994). Most traditional or diverse barley landraces have been locally adapted, often under low input farming, and with high consistency in yield.

In high input systems, the expectation is that yield of elite cultivars will outperform traditional landraces. Although landraces and CCPs may have inferior yield under high agronomic inputs, they demonstrate increased resilience under reduced inputs, or more stressful conditions (Ceccarelli, 1994). However, some traditional landraces and CCPs confer increased yield stability compared to elite cultivars, when grown under challenging environmental or climatic conditions, including high disease burden, extremes in precipitation and variation in soil nitrogen (N) supply (Dwivedi et al., 2017). Explanations for this enhanced stability in crop performance has been attributed to improved resource capture in relation to niche variation (Zuppinger-Dingley et al., 2014), specific genetic variation underlying stability (Mickelbart et al., 2015) or local adaptation (Dwivedi et al., 2017) in the more diverse barley lines.

An approach to exploiting wider genetic resources, including landraces, is to quantify variation and stability in agronomic traits under a common field protocol. Such approaches can be used to compare landraces from different geographic and climatic backgrounds for agronomic and pre-breeding value. This would include a practical guide to phenotypic variance in agronomic traits such as leaf morphology, shoot production (tillering), grain number per ear and mean grain weight (thousand grain weight) that are being associated with improved yield performance. Theoretical studies (Zhai et al, 2014) suggest a trade-off (or yield penalty) between phenotypic plasticity (robustness) and other traits (yield); however, such a practical approach has rarely been tested in agricultural field crop systems (but see Sadras et al., 2016; Fletcher at al., 2015).

Traditional landraces tend to originate from low input conditions under local environmental conditions where genetic by environmental (GxE) effects are best exploited under local conditions (Gage et al, 2019). This contrasts with high inputs systems, or elite cultivars, in which high GxE is controlled using high agronomic inputs. There are very few studies that have compared genetically diverse landraces from different geographic backgrounds in relation to phenotypic expression and stability against elite cultivars when grown under common protocol for achieving high yield. Using pre-adapted genetic resources such as landraces and CCPs provides an opportunity to discover untapped agronomic value, as a large proportion of traditional barley material has remained stored in gene banks with very little information on its agronomic performance.

In order to exploit the potential benefits of wider genetic variation for future crop breeding, we tested the hypothesis that traditional landraces a CCP (Harlan & Martini, 1929), express wider phenotypic variation in agronomic traits, but with greater yield stability than modern elite cultivars. We tested this hypothesis by comparing five geo-climatic landrace groups comprised of two or six rowed ear habit along with a group of Harlan CCPs and a group of elite cultivars grown under a common high-yielding field evaluation protocol over several years and sites. We used European geographic region of origin (North, East, South and West; Metzger, 2005; Peel et al., 2007) based on gene bank information. Agronomic traits of interest were plant height, shoot production (tillering), final ear number (population), number of seeds per ear, ear length thousand grain weight (TGW), and flag leaf dimensions. Breadth of phenotypic expression and stability across sites were examined among the nine groups, with main comparisons being between landraces, CCPs and cultivars, and between the and 2 or 6 rowed ear habit.

2 Materials & Methods

2.1 Plant material

Seed of landraces (also referred to as ‘traditional lines’ or ‘old varieties’) were obtained from IPK Gatersleben, Nordic Gene Bank, CGN Wageningen, GRC-INRA, NGBA and cultivars from several UK breeding companies. Bulked CCP material from the original composite-cross Harlan populations was sourced from Prof. Quelset at UC Davis, California via Michigan State University and represented several generations of composite cross populations differing in their crossing designs (Harlan & Martini, 1929; Supplementary material).

Landraces were divided in four geographical groups; north, west, east and south Europe (Metzger et al., 2005; Olesen et al., 2011). The north (N) group included lines from Norway, Sweden, Finland and Denmark; west (W) included Ireland, UK, the Netherlands, Belgium, France, Switzerland and Germany; east (E) was Poland, Lithuania, Estonia, Czech, Slovakia, Austria, Romania, Serbia, whilst south (S) was Spain, Italy, Greece and Malta. Apart from S, each geographical group was divided into two (2) and six (6) rowed ear habit. The South group consisted of only the 6-rowed type. The number of lines in each group were: E2 29, E6 15, N2 11, N6 9, W6 13, W2 51 and S6 8. There were 10 two-rowed elite cultivars commercially grown in the UK and 40 CCP lines, developed in the USA.

All seed stocks were stored at 4°C for two weeks prior to sowing. The experimental design was a fully randomised. Each line was hand sown as a mini plot (0.5 m^2) in 2012 and drilled as a mini plot (1 m^2) in 2013 at three SRUC trials centres: (i) Humbie in East Lothian (55°50'45"N 2°52'29"W), (ii) Bush Estate, Mid-Lothian (55°52'26"N 3°12'10"W) and (iii) Drumalbin, Lanarkshire (55°37'41"N 3°45'07"W) which represented a range of soil and climatic conditions (Figure S1) that where associated with high crop productivity. The mini plots were drilled with a Wintersteiger Rowseed S drill (Trials Equipment UK Ltd). All plots were treated with standard 120 kg N ha^{-1} ammonium nitrate fertilizer applied in a 50:50 split to the seed bed and at leaf 3, and a comprehensive fungicide treatment to keep all foliar diseases to a minimum during the growing season.

2.2 Measurement of plant traits and yield components

Seven agronomic traits and yield were measured. Three replicate plants per plot were used as

technical replicates. Plant height was measured after flowering, from base of the main to the base of the ear in three plants per plot. In the same plants, the length and width of the flag (final) leaf were measured as a proxy of leaf area. At harvest ripe, the population of fertile ears per plot (Ears) was counted, and ears hand harvested. Mean grain number per ear and ear length and were measured in each ear, in the laboratory. Ears were threshed in a Wintersteiger Grain Thresher and grain collected to measure TGW. Yield was estimated as grain weight from the whole plot at harvest ripeness, adjusted to 15% moisture content. After ear counts, grain number was counted in each ear.

2.3 Data analysis

Each of the nine barley groups were treated as experimental units for statistical analysis of differences and variation in yield and agronomic traits. REML (Genstat 19, (VSN International, 2018) was used to test for differences between combined geographic region and ear type for the traits, and differences were considered significant for $P < 0.05$. Individual lines e.g. landraces were nested within the year-site combination and used as a random factor, whilst geographic region (N, S E and W) and ear habit (2 or 6) combinations were the fixed effect. Significant differences were tested at the 5% level. Correlation between plant and yield traits was calculated using the Pearson method.

The coefficient of variation (CV) was used as an estimate of stability for each landrace group across the sites (baseline packages R v3) where each line was represented in each combination of year/location. REML was used to assess CV differences between geographic regions and ear type. In this case the random factor was variety (ID). Association between each trait was also tested. The final number of IDs was 192 (81 two rowed and 79 six rowed accessions), which constituted the nine barley groups.

3 Results

3.1 Agronomic traits and yield

Geographic region and ear row habit influenced expression of agronomic traits. Grain yield of E2 landraces was significantly lower than E6; however, there was no significant difference between 2 and 6 rowed habit for N2 vs N6 or W2 vs W6 (Table 1a & b). There was no significant difference in yield among landrace groups N2, E2 and W2. In contrast, E6 had significantly higher yield than S6. With the exception of N2 and W6, E6 landraces significantly outyielded all other groups including elite cultivars. The CCP group had the lowest yield.

Thousand grain weight of elite cultivars was significantly higher than other groups, with the CCPs being significantly higher than landraces E2 and all 6 rowed landrace groups. Thousand grain weight was significantly higher in 2 rowed groups N2 and W2 compared to their 6 rowed counterparts, N6 and W6 (Table 1b). Within the 6 rows, E6 and S6 had significantly higher TGW than N6 and W6.

As expected, grains per ear were significantly higher in 6-rowed (on average 51 grains per ear) than in 2-rowed (27 grains per ear) habit for all geographic groups (Table 1b). Within the 6 rows, both N6 and W6 had significantly more grains per ear (approximately 60 grains per ear) than other groups.

Ear length was significantly shorter in the 6-rowed habit than in the 2-rows. Within the 6 rows, the CCP and S6 were significantly shorter than other groups. (Table 1b).

Flag leaf length was more explained by geography than rowed type with the longest leaves in E2 and E6. On the other hand, flag leaf width was explained by rowed type, where 6 rows, except for CCP, showed significantly wider leaves than 2 rowed groups. N6 had significantly wider leaves than all other groups, whilst the CCPs had significantly shorter and narrower leaves than all other 6-rowed types.

Ear population per plot differed significantly between ear rowed habits within N and W groups (Table 1b). Variation in ear population was mostly explained by rowed habit with two rowed landraces having most. Within the 6 rowed habit, there was further group structure with N6 and CCP having significantly the fewest ears per plot. Landrace groups N2 and W2 had significantly higher ear population that elite cultivars.

Generally, plant height differed between geographic regions where landraces from E, W and N were tallest and S6, CCP and modern cultivars shortest.

3.2 Associations between agronomic traits and yield

For two-rowed barley there were significant correlations between yield components and plot yield. Grain yield was positively correlated with ear population (r = 0.54) and TGW (r = 0.24). TGW was also positively correlated with ear length (r = 0.34) and ear population (r = 0.31). Ear length was also associated with seeds per ear (r = 0.41). There were positive associations between flag leaf width and TGW (r = 0.44) or seeds per ear (0.40). Seeds per ear was also correlated with plant height (r = 0.31). In contrast, flag leaf length was negatively correlated with TGW (r =-0.25) (Table 1c).

Grain yield of six-rowed barley was positively correlated with and ear population (Table 1d; r = 0.54) and seed number per ear (r = 0.32), but not to TGW, as in the two-rows. Ear length was correlated with seeds per ear (r = 0.37). In contrast to the 2 rowed barley, grain yield was positively correlated to plant height (r = 0.39), grain yield and flag leaf width (r = 0.24). Seed number per ear was also positively related to plant height (r = 0.53), flag leaf width (r = 0.49), flag leaf length (r = 0.46), and there was a negative correlation between flag leaf length and TGW (-0.30).

3.3 Stability in agronomic traits and yield

Generally, grain yield, and ear population, was less stable (with high CV) relative to other agronomic traits, though leaf width had high CV, especially in the 6 rows (Table 2a). Elite cultivars and CCPs were significantly more stable (lower CVs) for TGW compared to landraces (Table 2a). In seeds per ear, 2 rowed landraces and elite cultivars were more stable than 6-rowed landraces and CCPs. There were no significant differences in stability among groups for ears per plot, grain yield, flag leaf length or width, plant height or ear length (Table 2b).

3.4 Associations in stability (CV) between agronomic traits and yield stability

For 2 rowed barley there were significant correlations between grain yield CV and ears population CV (r = 0.36) and TGW CV (r = 0.24). Ear length CV and seeds per ear CV were also positively correlated (r = 0.44), Correlations between plant height CV and seeds per ear CV (r = 0.44), ear length CV and plant height CV (r = 0.36), ear length CV and flag leaf width CV (r = 0.28) were positive (Table 2c).

For 6 rowed barley there were significant correlations ear length CV and seeds per ear CV (r = 0.48), grain yield CV and ear population CV (r = 0.46), ear length CV and grain yield CV (r = 0.29), but a negative correlation between ear length CV and TGW CV (r=-0.27). Other positive correlations were ear length CV and plant height CV (r = 0.38) and grain yield CV and plant height CV (r = 0.36). (Table 2d).

4 Discussion

4.1 Influence of geography and ear row habit on expression and stability in agronomic traits and yield

The hypothesis that groups of locally adapted barley landrace expressed wider phenotypic variation but higher yield stability in traits compared to elite cultivars was only partially supported by our data. Landrace groups had very wide diversity in yield and traits compared to elite cultivars. Apart from specific seed weight (TGW) and seeds per ear (SE), there was no difference for stability (CV) between groups of landraces and modern cultivars. The CVs for particular landrace groups were high compared to those reported in wheat by Doering et al.(2018), which used modern cultivars from a FAO global dataset. Such high variation among individual landraces within the seven geographic groups indicates a breadth of phenotypic expression that could have value in pre-breeding, as well as agronomic value under a high yielding growing environment. Individual landraces, rather than a landrace group, need to be carefully selected, but these results are encouraging for sourcing of pre-breeding material for enhancing production under high yielding growing regions, even outside the geographic region of origin. This approach would be consistent with other studies (Abay & Bjørnstad, 2009; Al-Abdallat et al., 2017) that tested large panels of pre-adapted landraces and old varieties under contrasting low inputs and water stress.

The only agronomic trait to indicate a strong geographic influence was leaf length where N2, N6, W2 and W6 had long leaves. This was confirmed in an earlier study on light interception in European barley landraces, which included a subset of the current study material, although there was no difference between specific leaf areas (Florence et al., 2019).

Traits most strongly associated with yield stability in 2 rowed landraces were TGW and tillering, whilst in 6 rowed landraces tillering, ear length and plant height were associated with stable yield. However, there was no significant difference in yield and yield stability between any of the two rowed landrace groups, or the modern cultivars, despite conventional agronomic inputs. We found there was less variation in yield between 2 rowed groups than for 6 rows, which contradicts former studies (Nurminiemi & Rognli, 1996; Garcia del Moral et al., 2003; Psawari et al., 2008). Nurminiemi & Rognli (1996) found that Nordic barley 6 rowed lines were more stable in terms of yield than 2 rowed barleys which in turn had higher performances, although this was assessed by the Finlay Wilkinson linear regression method rather than correlation of variation. Testing adaptation to Mediterranean environments using a wide amount of material, A. Pswarayi et al. (2008) found that locally adapted landraces were better suited to low yielding environments (< 2 t/ha) where modern material was showing higher yields in high yielding environments. Similarly, the study of Garcia del Moral et al. 2003) found that 6 rowed barley grown under Mediterranean conditions were more stable than their 2 rowed counterparts which was attributed to compensation through seeds per ear rather than tillering. Differentiating from this, our experiment also showed tillering stability strongly correlated to yield stability in six rows. Further research into yield stability variation among specific lines would identify novel combinations of traits underlying yield stability between rowed types.

4.2 The role of genetic variation in agronomic trait stability

The Harlan CCP population is composed of crosses between different parents (Harlan and Martini, 1929) which are more genetically variable than landraces or modern elite cultivars (Harlan & Martini, 1929). In our study we found no differences between CCPs, landraces and elite cultivars for grain yield, although TGW was high and more stable in CCPs and elite cultivars compared to landraces. The latter result is supported by Einfeldt et al. (2005) in a study on barley heterozygosity effects on yield and yield stability under drought stress in which CCPs showed improved stability compared to respective parents albeit with increasing drought stress. In contrast, Mühleisen et al. (2014) found a higher yield stability for hybrid winter wheat varieties than single line cultivars. Although the CCPs had high stability in TGW and height, they were intermediate or low in stability for other traits; this contrasts with a studies on agronomic traits and yield in wheat composite cross populations (Doering et al., 2015) or barley mixtures (Creissen et al., 2016).

Given the genetic background and origin of the different landrace groups and modern cultivars, the stability of the yields under the tested growing environment was expected to vary more than observed. Instead, we found no significant yield stability differences between the different groups which was surprising, given that all groups were tested under a common high-yielding field evaluation protocol.

4.3 Associations between agronomic traits and yield

We identified several agronomic traits that correlated with yield, and this could be used as indicators of yield or stability. Our findings were supported by Hadjichristodoulou (1990) and Liller (2013), who also found positive correlations of TGW with grain yield for both 2 and 6 rowed barley. Correlation between flag leaf width and seeds per ear, and also TGW, in two rowed barley was consistent with the work of Thirulogachandar et al. (2017) who found a positive relationship between leaf width and grain number. This association may be explained by the fact that the *Vrs1* genes which underlies rowed type in barley is also linked to the development of flag leaf width and longitudinal vein number through rapid growth of leaf primordial cells increasing the size of leaf primordia (Thirulogachandar *et al.*, 2017). Flag leaf length, on the other hand, was negatively correlated with TGW, an indication of leaf elongation and grain development trade-off.

The strong correlation between plant height and grain yield in six rows was unexpected as the opposite would be expected with dwarfing genes increasing yield by optimising the harvest index (Xu et al., 2017). Nevertheless, this correlation may be explained by the underlying genetic interactions between genes involved in ear development (*Vrs1*) and height which seem to interact together with heading time and tillering (Thirulogachandar et al., 2017). We found strong correlations between ear number and yield in both rowed types but for two rows there was an additional strong correlation between ear number and TGW. Environmental responses differ between these two barley types where two rows maintain seed production through variation in tiller number and seeds per ear whereas in six rows the variation is in the seeds per ear and specific grain weight and the tiller number is stable (Arisnabarreta & Miralles, 2008;

Liller et al., 2015). Interestingly there is a small positive correlation between TGW and seeds per ear for two rows where seeds per ear has no significant relationship with yield and tillering.

4.4 Agronomic traits and yield stability associations

Traits most strongly associated with yield stability in 2 rowed landraces were TGW and tillering, whilst in 6 rowed landraces tillering, ear length and plant height were associated with stable yield. Overall, agronomic traits were more stable than yield, though seeds per ear for 2-rowed was an exception. Similarly, a study on the bimodality of trait and yield component stability across different crop species (Fisher et al., 2017) showed a similar pattern of high stability for leaf area but low for yield. Similar to the study by Muehleisen et al. (2014) we found no significant correlation between grain yield and any measured trait other than TGW and ears population for 2 rows. Contradicting the Muehleisen (2014) study however, we found that 6 rowed barley had a significant correlation with plant height, ear length and also ears population. With the CV for ear population being strongly associated with yield CV then it would be a good indicator for yield stability.

Our results had a much lower number (4) of year by location environments than Muehleisen (2016) and Mohammadi et al., (2010), but still agreed with most stability traits. Another reported study (Joernsgaard & Halmoe, 2003) with a low number of environments (3) did not show similar traits for stability.

For six rows there is compensation between traits with negative correlation between the ear number CV and seeds per ear CV which is in contrast to previous work which observed this trade-off only in 2-rowed barley (Hadjichristodoulou, 1990; Gambín & Borás, 2009).

5 Conclusion

Landraces and CCPs housed in genebanks are a rich source of genetic material for crop improvement where useful variation in agronomic traits and yield components can be exploited under high yielding growing conditions (Dwidevi et al., 2016; 2017). However, these resources are largely untapped. Identification of novel variation and the selection of specific landraces (genotypes) for enhanced stability in desirable traits and yield components under appropriate testing systems as described herein is a key next step to support development of more resilient crop cultivars. Large field screenings of genebank material over different locations and years can be used to identify useful variation for pre-breeding applications. Our results indicate that barley resources from different geographic regions may have value in pre-breeding of barley for specific growing conditions. Our findings showed that landraces among different geographic groups had beneficial agronomic traits or yield components even compared to elite cultivars. Beneficial traits include high yielding varieties from eastern Europe, stable TGW in the 6 rowed Harlan CCP population and a positive association between height and yield stability in all 6 rowed groups. A small number of individual lines from different groups showed high yield stability and will be subject of further research.

Declarations

This work was supported by the Scottish Government Strategic Research Programme. The authors declare no conflict of interest. We would like to thank the technical team from SRUCs Crop & Soil Systems group for their help with field work and sample processing during the project.

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Tables

Due to technical limitations, table 1,2 is only available as a download in the Supplemental Files section.

Supplementary Files

This is a list of supplementary files associated with this preprint. Click to download.

- Supplementarymaterialstability2.xlsx
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