Variation and Phenotypic Plasticity of Heading Date and Yield Across Multiple U.S. Great Plains Environments

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Introduction:

In wheat, **heading** is a phenological stage that describes the emergence of the inflorescence and indicates a shift from vegetative to reproductive development. Variation in heading date reflects genotypic 'earliness' and is critical for adaptation to specific environments. Poorly timed floral development can expose sensitive reproductive tissues to cold, heat, or water stress and reduce grain yield and/or quality.

The flowering pathway integrates two major genetic systems: **vernalization** in winter wheats requires a threshold level of continuous cold exposure and **photoperiod** in sensitive winter or spring genotypes requires a critical day length to transition from vegetative to reproductive development. Major vernalization and photoperiod genes affect broad adaptation in heading, but less is known about the **earliness per se** (*eps*) genes that contribute quantitative variation and regional adaptability. Most eps genes are detected by QTL mapping and very environment specific, although a few robust QTL have been identified (e.g., Griffiths et al., 2009). Since heading date is highly variable across environments it is useful to consider the range of phenotypic responses.

Phenotypic plasticity is described as the ability of a single genotype to produce a variable phenotype under different environmental conditions (Nicotra, 2010). The extent of plasticity, as well as whether it is beneficial or detrimental varies among traits and when evaluated on different germplasm or environments (Bradshaw, 1965). In many cases, heritability and plasticity are inversely related.

Fine-tuning and optimizing reproductive development in wheat is complex, and involves many quantitative genes that are not well characterized or necessarily stable across environments. A more complete understanding of phenotypic plasticity of heading date could allow deeper understanding of crop adaptation.

Research Objectives:

1. To assess variation in heading date and yield within a panel of hard winter wheat varieties representative of the U.S. Great Plains.
2. To calculate phenotypic plasticity in heading date and yield, and determine whether high plasticity is favorable or unfavorable based on relationships to yield *per se*.
3. To identify whether high heading date plasticity is driven by earliest, average, or latest heading dates; and whether yield plasticity is driven by minimum, maximum, or mean yield across environments.

Materials and Methods:

Germplasm and Field Trials

- Plant materials include 299 varieties in the Triticeae Coordinated Agricultural Project (TCAP) hard winter wheat association mapping panel.
- Germplasm includes elite cultivars, experimental lines, foundational, and historical varieties representative of the U.S. Great Plains (**Figure 1**).
- Trials were grown by TCAP participants at eleven total environments in 2012 and 2013 (**Table 1**).

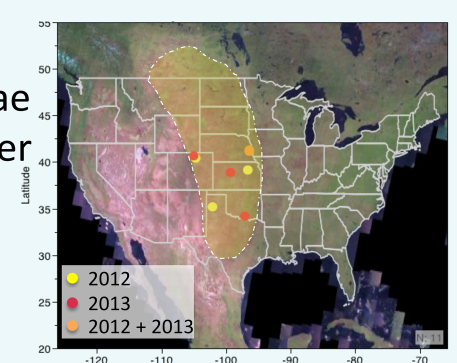

Figure 1: Trial locations in 2012 and 2013. Each environment is a unique year-location-treatment combination. Environments and germplasm are representative of the U.S. Great Plains (highlighted in yellow).

Phenotypic Data:

- Heading was evaluated in each plot using the Zadoks scale at Z59 (**Figure 2**), as the date when the spike was fully emerged from the flag leaf sheath in 50% of the plot.
- Days to heading is the number of days after January 1.
- At sites where anthesis date was collected heading date was back-calculated from pairwise differences between heading and anthesis in other environments.
- Grain yield was collected from each plot at harvest.
- Spatial adjustments were conducted on phenotypic data from each site based on individual field designs.

Figure 2: Wheat spike at heading (Z59).

Data Analyses:

- We evaluated phenotypic plasticity as described by Sadras *et al.* (2009), where the coefficient of plasticity is defined as the slope of the regression line between the trait for a particular entry in a particular environment, and the mean of that trait for all entries in a particular environment.
- A plasticity coefficient (slope) of 1 represents average plasticity, and positive and negative coefficients above- or below-average plasticity.
- Statistical analyses were conducted using R version 3.0.3 and JMP version 10.

Results and Discussion: Variation in heading date across environments

Year	Location	Site ID	Moisture Level
2012	Bushland, TX	Bu12	Dryland
2012	Greeley, CO	Gr12D	Limited irrigation
2012	Greeley, CO	Gr12W	Full irrigation
2012	Manhattan, KS	Man12D	Limited irrigation
2012	Manhattan, KS	Man12W	Full irrigation
2012	Mead, NE	Me12	Dryland
2013	Ardmore, OK	Ar13	Dryland
2013	Fort Collins, CO	Fo13D	Dryland
2013	Fort Collins, CO	Fo13W	Full irrigation
2013	Hays, KS	Ha13	Dryland
2013	Mead, NE	Me13	Dryland

Table 1: Environment descriptions and identifiers. Each environment is a unique year-location-treatment combination.

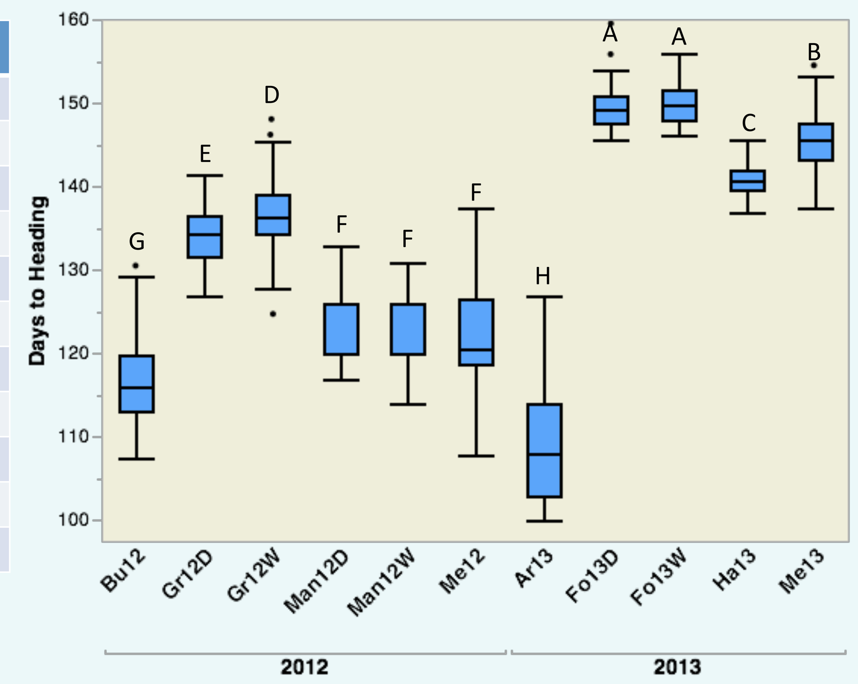

Figure 3: Range of heading dates across environments. Environments not connected by the same letter are significantly different from each other.

- Heading varied significantly among most environments, but results were highly correlated, especially within a single year.
- In general heading occurred earlier in 2012 than 2013. This is likely influenced by the hot, dry spring and widespread drought in 2012.
- Earliness at Ar13 compared with other 2013 environments can be attributed to that site being grown to assess forage quality traits, and its southern latitude.

Results and Discussion: Variation in yield across environments

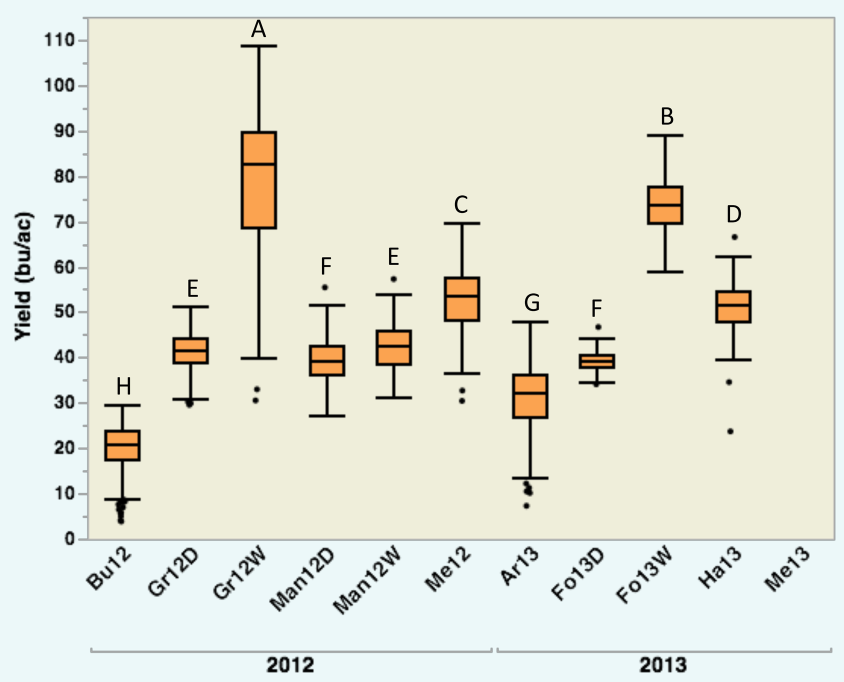

Figure 3: Range of yield across environments. Environments not connected by the same letter are significantly different from each other.

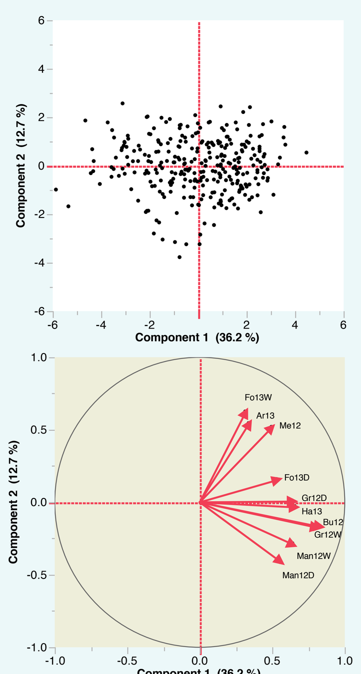

Figure 4: PCA of yield from each entry, in every environment. **A** Score plot **B** Loading plot.

- Yield varied significantly among environments (**Figure 3**).
- In general, arid southern environments had lower yields than irrigated environments or those grown at more northern latitudes.
- The wide range at Gr12W might reflect yield potential of such diverse entries.
- PCA is useful to characterize similarities among environments (**Figure 4**):
  - The PCA score plot displays entries as a loose cloud of dots, which indicates entry performance varied across environments. There are a few possible outliers ('Kharkof' and 'Bronze').
  - The PCA loading plot displays environments as vectors, with more similar environments projected near each other.
  - Fo13W, Ar13, and Me12 were very similar to each other and were most different from Man12D and Man13D.
  - The dry treatments in Colorado (Fo13D and Gr12D) were more similar to each other than their neighboring wet treatments (Fo13W and Gr12W).
  - Entries performed very similarly in Gr12W and Bu12 (r=0.69), even though moisture levels were very different at these environments.

Results and Discussion: Phenotypic plasticity

- There were significant correlations between heading date and yield (r=-0.50, p<0.0001). Earlier development was favorable.
- Heading date plasticity had a strong negative correlation with minimum heading date (**Figure 5**, r=-0.89, p<0.0001). This suggests heading date plasticity was driven by the earliest heading date.
- Yield plasticity had a strong positive correlation with maximum yield (**Figure 6**, r=0.82, p<0.0001). This suggests yield plasticity was a favorable trait in these materials and environments.

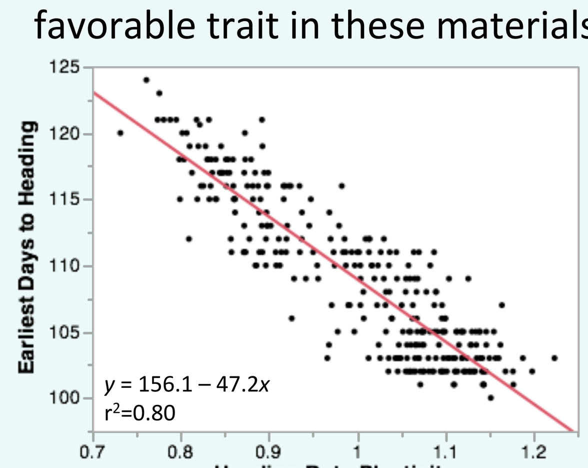

Figure 5: Regression of heading date plasticity coefficient on earliest days to heading.

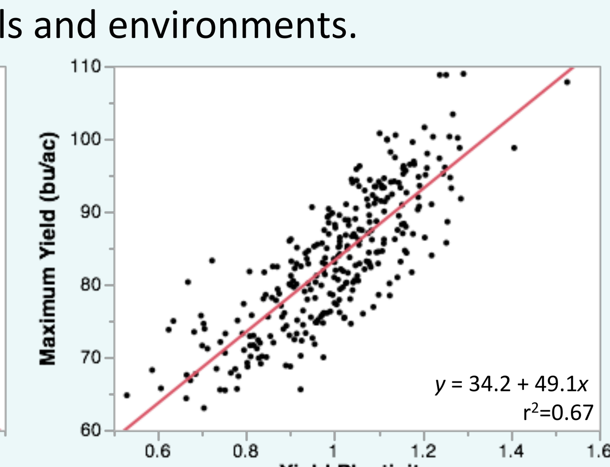

Figure 6: Regression of yield plasticity coefficient on maximum yield.

- Heading date plasticity was positively correlated with minimum (**Figure 7**, r=0.53, p<0.0001), maximum (r=0.46, p<0.0001), and mean (r=0.45, p<0.0001) yields.
- Heading date plasticity explained 28.4% of variation in minimum yield, 21.4% of maximum yield, and 20.1% of average yield.
- Heading date plasticity had a weak positive correlation with yield plasticity (**Figure 8**, r=0.38, p<0.0001).

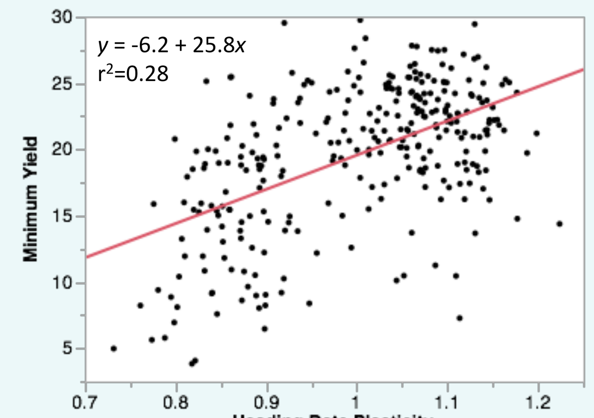

Figure 7: Regression of heading date plasticity coefficient on minimum yield.

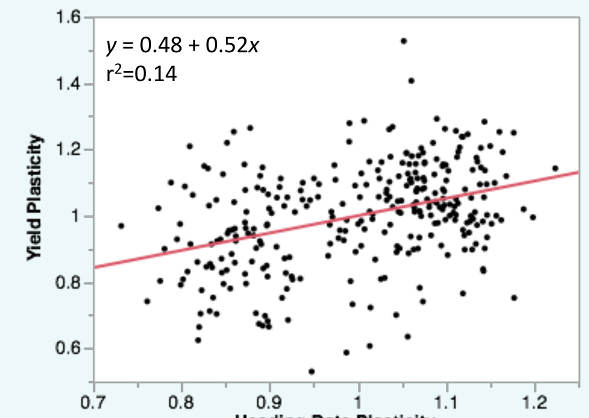

Figure 8: Regression of yield plasticity coefficient on yield plasticity coefficient.

Conclusions and Future Directions:

- Average heading date and yield varied significantly among environments:
  - Days to heading ranged from 109 days at Ar13 to 145 at Me13.
  - Average yield ranged from 20.0 bu ac^{-1} at Bu12 to 78.7 bu ac^{-1} at Gr12W.
- Heading date plasticity was strongly associated with earliest heading date, and yield plasticity with maximum yield. This suggests the most plastic germplasm were able to develop earlier or increase yield in response environmental variation.
- Phenotypic plasticity for both heading date and yield were favorable traits in the germplasm and environments evaluated.
- There were significant correlations between heading date plasticity and yield plasticity, and between heading date and yield *per se*. Future work might involve investigating the genetic basis of trait plasticity through GWAS, and identifying plasticity QTL that co-localize with or are independent of the trait p*er se*.

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