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Phenotypic plasticity of yield and agronomic traits in cereals and rapeseed at high latitudes

P. Peltonen-Sainio[a,*], L. Jauhiainen[a], V.O. Sadras[b]

[a] MTT Agrifood Research Finland, Plant Production, FI-31600 Jokioinen, Finland
[b] South Australian Research & Development Institute, Waite Campus, Australia

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ABSTRACT

In the northernmost European environments of Finland, large variability in the yield and quality of crops is a critical source of uncertainty for growers and end-users of grain. The aims of this study were (i) to quantify and compare the plasticity, i.e., cultivar responsiveness to environment, in yield of spring oat, spring wheat, six-row barley, two-row barley, winter rye, winter wheat, turnip rape and oilseed rape, (ii) to explore the existence of hierarchies or positive correlations in the plasticity of agronomic, yield and quality traits and (iii) to probe for trends in yield plasticity associated with different eras of breeding for yield potential and agronomic traits. Plasticities of yield, agronomic and quality traits were derived as slopes of norms of reaction using MTT Agrifood Research Finland data sets combining long-term (1970–2008 for cereals and 1976–2008 for rapeseed) results from 15 to 26 locations. Plasticity of yield ranged typically between 0.8 and 1.2, was smallest for six-row barley (0.84–1.11) and largest for winter rye (0.72–1.36). We found two types of associations between plasticity of yield and yield under stressful or favourable conditions for cereals but none for rape. In spring wheat, oat and six-row barley, high yield plasticity was associated with crop responsiveness to favourable conditions rather than yield reductions under stressful conditions. Modern spring wheat cultivars had higher maximum grain yields compared to older ones at the same level of plasticity. In winter wheat and rye, high yield plasticity resulted from the combination of high yield in favourable conditions and low yield in stressful environments. Many associations between yield plasticity and other traits were identified in cereals: e.g., high yield plasticity was often associated with higher grain weight, more grains per square meter, later maturity (contrary to turnip rape), shorter plants, less lodging and lower grain protein content and in winter cereals with higher winter damage.

1. Introduction

In the northernmost European conditions, variability in the yield and quality of cereals and rapeseed is critical source of uncertainty for farmers and end-users of grains. In these environments, large seasonal variation in grain yield and quality are associated with (i) extremely short growing season, (ii) highly fluctuating weather, (iii) unfavourable early summer conditions, especially drought, and (iv) environmental and management constraints for yield compensation (Mukula and Rantanen, 1987; Peltonen-Sainio et al., 2009a, 2009b, 2009c, 2011a). Compensation among yield components is common phenomenon in which failure in formation of one yield component is at least partially compensated by enhancement of another yield component at later growth stages. Compensation ability contributes to some degree of yield stability in grain crops (Adams and Grafius, 1971). In northern growing conditions, fast development of grain crops in response to long days underlies a trade-off between enabling harvest in a short season and constraining ability for compensation. Long days inhibit tillering in cereals and restrict tillers' yield potential. Therefore, high seeding rates are used, which again further promotes main shoot dominance at the expense of tillers (Peltonen-Sainio et al., 2009c). On the other hand, low tillering capacity increases costs due to use of roughly double the seeding rate used elsewhere in Europe (Peltonen-Sainio et al., in press). Due to fast development and restricted compensation ability through tillering it can be hypothesised that despite low mean yields typical for high latitudes (Peltonen-Sainio et al., 2007a, 2009d) yields may vary markedly.

Yield stability is often regarded as a desirable feature of cropping systems, but this notion needs to be considered in the context of time scales and yield definitions. In the short term when technological change is minor relative to seasonal environmental variation (Calviño and Sadras, 2002), stability of actual yield (*sensu* Loomis and Connor, 1996) is desirable insofar as it reflects the predictabil-

* Corresponding author. Tel.: +358 341882451; fax: +358 20772040.
E-mail address: pirjo.peltonen-sainio@mtt.fi (P. Peltonen-Sainio).

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ity of the environment and contributes to stable cash flow for the cropping business. In the long term, breeding and selection for yield potential (*sensu* Loomis and Connor, 1996) reduces stability. Using the approach of Finlay and Wilkinson (1963), Calderini and Slafer (1999) showed that modern wheat varieties had lower yield stability than their older counterparts. This decrease in stability was associated with improved capacity of modern varieties to capture the benefit of better growing conditions and no yield reduction under stress (Calderini and Slafer, 1999). More broadly, yield instability was an undesirable trait in a collection of recombinant inbred wheat lines where high instability was associated with poor performance under stress, and a desirable trait in collections of sunflower hybrids and grapevine varieties where high instability was associated with the capacity to capture good environmental conditions (Sadras et al., 2009).

From agronomic and breeding perspectives, yield and quality stability are normally seen in terms of genotype-by-environment interaction. A complementary perspective emphasises the concept of phenotypic plasticity which is well established in ecology and evolutionary biology (Nicotra et al., 2010; DeWitt and Scheiner, 2004; Auld et al., 2010; Snell-Rood et al., 2010) and incipient in agronomic contexts (Reymond et al., 2003; Sadras et al., 2007, 2009; Lacaze et al., 2009; Nicotra and Davidson, 2010; Zhu et al., 2010). Here we use the definition of Bradshaw (1965): phenotypic plasticity is “the amount by which the expressions of individual characteristics of a genotype are changed by different environments”. Quantitatively, phenotypic plasticity can be calculated as the slope of reaction norms, which are mathematical functions relating phenotype and environment (Woltereck, 1909; DeWitt and Scheiner, 2004) or variance ratios (Dingemanse et al., 2009). Studies with a historic collection of South Australian wheat varieties indicated that both methods returned similar indices of plasticity for yield and agronomic traits (Sadras and Lawson, in press).

A focus on plasticity allows for valuable theoretical frameworks and tools. From an evolutionary perspective, Bradshaw (1965) advanced the notion that there is a hierarchy of plasticities, i.e., stable traits are often associated with plastic, related traits. Auld et al. (2010) updated the theoretical and empirical evidence for a broader range of relationship between trait values and trait plasticities; correlations between plasticities can also be seen in the context of integration studies (Kliebenstein, 2010; Pigliucci, 2003). Positive and negative correlations between plasticity of yield and plasticity of phenological and agronomic traits have been reported for grain crops, grapevine and olive (Sadras et al., 2009; Trentacoste et al., in press). Combining Bradshaw’s concept of hierarchy of plasticities and the model of Smith and Fretwell (1974), new insight was gained into the trade-off between seed number and size in grain crops (Sadras, 2007; Gambín and Borrás, 2009). From an agronomic perspective, here we propose that long-term variety trials of grain crops are a sound model to quantify correlations between plasticities of relevant traits including yield and its components.

The aims of this study were (i) to quantify and compare the plasticity in yield of spring and winter cereals and spring turnip rape and oilseed rape in the northernmost European growing regions, (ii) to explore the existence of correlations in the plasticity of a suit of agronomic, yield and grain quality traits, and (iii) to determine if there have been trends in yield plasticity associated with different eras of breeding for yield potential and agronomic adaptation.

2. Materials and methods

2.1. Data sources

Long-term field experiments of MTT Agrifood Research Finland for cereals were conducted in 1970–2008 and for rapeseed in 1976–2008 at 15–26 different locations in Finland, depending on crop and production area. The experiments were part of the MTT Official Variety Trials and all followed procedures specified for that purpose (Kangas et al., 2010). In addition to MTT Agrifood Research Finland, which has numerous regional research units in Finland, some of the experiments were organised by plant breeding companies and private agricultural research stations.

All experiments were arranged as randomised complete block designs or incomplete block designs. Three to four replicates were used. Each year the tested set of cultivars and breeding lines changed, but long term-check cultivars were used. Annual turnover of cultivars and breeding lines was usually less than 20%, which made it possible to separate effects of environment and genotype. Plots were 7–10 m $\times$ 1.25 m, depending on location and year. Seeding rate depended on crop, conforming to the commonly used seeding rates in Finland. Weeds were chemically controlled with agents commonly used at each time period. Diseases were not routinely controlled with fungicides. This represents a trade-off between the need to account for farmer practices in Finland, which do not include systematic fungicide application, and the estimates of time trends in yield which would include a composite of yield and disease tolerance. Fertiliser use depended on cropping history, soil type and fertility and was comparable with standard practices in Finland.

MTT long-term field experiments included 12,264, 7814, 7453, 5375, 4668, 4058, 3222 and 2060 total records for spring barley, spring wheat, six-row barley, winter rye, two-row barley, turnip rape, winter wheat and oilseed rape, respectively. Only cultivars and advanced breeding lines (hereon together referred to as cultivar) with sufficient number of results were selected from dataset. Utilized number of cultivars were 87 (more than 40 results per cultivar), 81 ($\geq$25 results), 50 ($\geq$30 results), 64 ($\geq$20 results), 50 ($\geq$25 results), 64 ($\geq$20 results), 44 ($\geq$20 results) and 39 ($\geq$15 results) for spring barley, spring wheat, six-row barley, winter rye, two-row barley, turnip rape, winter wheat and oilseed rape, respectively. All species were analyzed separately using SAS-software.

2.2. Quantifying plasticity

The effects of environment and genotype were separated by the following two-way ANOVA model:

$$y_{ijk} = \mu + \alpha_i + \delta_{jk} + \varepsilon_{ijk} \tag{1}$$

where y_{ijk} is observed value for ith cultivar in jth year and kth experimental site, μ, is intercept, α_i is the effect of cultivar, δ_{jk} is the effect of environment and ε_{ijk} residual effect. Estimated values of the environment, $\hat{\delta}_{jk}$, were used to quantify plasticity for ith cultivar:

$$y_{jk} = y + \beta_i\hat{\delta}_{jk} + \varepsilon_{jk} \tag{2}$$

where y_{jk} is observed value, y is intercept, β_i is regression coefficient (=plasticity for ith cultivar), $\hat{\delta}_{jk}$ is environmental parameter estimated in Eq. (1), and ε_{jk} is residual. $\beta = 1$ corresponds to the average plasticity.

Both models were fitted for the following traits depending on crop: yield (kg ha^{-1} at 15% moisture content), growth duration (d) from sowing (BBCH00, Lancashire et al., 1991) to physiological maturity (BBCH92 for cereals and (BBCH87–BBCH89 for rapeseed), single grain weight (mg), grains per square meter (no.), plant height (cm, the average length of the plant stand according to three measurements per plot), lodging (%, the proportion of plot area lodged at maturity), winter damage (%), grain or seed protein content (%, by using the Kjeldahl-method and converting to dry matter), hull content (%), falling number (s), seed oil content (%, by determining with heptanes-alcohol extraction and converting to dry matter) and