



Comparison of three types of $G \times E$ performance plot for showing and interpreting genotypes' stability and adaptability

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Abstract

A $G \times E$ performance (interaction, profile) plot for showing genotype-by-environment data is discussed. Three versions of such a plot are compared: the regular performance plot; the performance plot based on coded data (environment-centered performance plot), in which the environment means of a trait are subtracted from data; and the performance plot based on data standardized in environments (environment-standardized performance plot). The plots are compared for six soybean genotypes studied in eight environments. The regular performance plot best conveys information about genotype stability in a static sense, and provides more information about the environments than the two other plots. The environment-centered performance plot better presents genotype stability in a dynamic sense and adaptability. The environment-standardized performance plot poorly represents stability in both senses and adaptability.

Keywords: Genotype-by-environment interaction; Genotype selection; Interaction plot; Profile plot; Soybean; Visualization.

Introduction

Plotting genotype-by-environment data may offer much useful information about genotype stability and adaptability; DeLacy et al. (1996) even state that "the major interpretative aids are the graphics and no pattern analysis [to analyze data from multi-environment trials] is complete until these are produced and examined". Various displays exist for such plotting. Some of them are rather simple in construction and reading for example a performance (interaction or profile) plot, plots used by Basford and Tukey (1999), and a dot plot of Cleveland (1994), which was recently proved efficient in the present context by Laffont et al. (2007). A common extension of the performance plot is the plot with environment means on the horizontal axis; in this way the environments are not treated as a categorical but quantitative variable. This plot is quite common in analyzing stability with regression methods (e.g., by the method of Eberhart and Russell, 1966). Other

plots are more complex and usually based on some decompositions of the genotype-by-environment matrix—for example those from AMMI (e.g., Gauch, 1992) or GGE biplots (e.g., Yan and Kang, 2003); Yang et al. (2009) has recently showed that these methods, which are becoming more and more popular these days, should be applied with caution to interpret genotype-by-environment interaction. Those simple and complex displays can offer different kinds of interpretations (Laffont et al., 2007).

This paper focuses on the simplest type of plot among these, the plot of performance of the genotypes across a range of environments (so on genotypes' response to environments) (DeLacy et al., 1996). Its advantage is simplicity and easy interpretation; in fact, it is used as a standard display to show interaction between two factors, so should be easily understood even by non-experts. Its disadvantage is that only a small number of genotypes can be presented on it (DeLacy et al., 1996). Note that performance plots can include all genotypes or just one (or several) of them, which would enhance comparisons. In addition, quite often instead of genotypes their groups (obtained for example by clustering, e.g. Haussmann et al., 2000) are presented on the profile plots, which certainly overcomes the problem of too many profiles within one plot.

But a performance plot is not limited to its most common layout. Following the concepts of Fox and Rosielle (1982), we can adjust the regular performance plot, which is based on original data, to account for the influence of environments. In this paper two variations of the regular performance plot are discussed. One is based on the so-called coded data (in which the genotype data are environment-centered), while the other on the standardized data in environments. In fact, performance plots for standardized data can be found in literature (e.g., Alagarwamy and Chandra, 1998; Haussmann et al., 2000; Haussmann et al., 2001; Babić et al., 2008), which to the best of the author's knowledge cannot be said about the performance plot for coded data.

This paper aims to compare these three performance plots for showing genotype stability in both static and dynamic concepts and adaptability. Hereafter, stability in a static sense will be represented by the variance of a genotype across environments (Lin et al., 1986), and describes how stable a genotype yields across environments, not accounting for other genotypes. Stability in a dynamic sense means the extent to which a genotype's performance is similar to the mean performance of all genotypes in the environments, and will be represented by the ecovalence (Wricke, 1962). Adaptation of genotypes describes performance in terms of a trait with respect to a given environment or given conditions: wide adaptation means that a genotype performs well in most environments, while specific adaptation means that a genotype performs well in a subset of environments (Annicchiarico, 2002; Van Eeuwijk et al., 2005). As we are discussing methods for visual exploration of data, we have to keep in mind that the aim of these plots is to help one to picture and interpret the data, in that way supporting statistical inference of them.

Material and Methods

Plant material

The data come from a two-year plant breeding experiment on soybean, conducted in four locations; first reported by Mungomery et al. (1974), the data are given in Basford and Tukey (1999). Out of 58 genotypes, the six last ones were chosen for the present paper

(genotypes 53-58). This is to make the plots easy to read and compare. Eight environments are given by combinations of years 1970 and 1971 and four Australian locations (Redland Bay [R], Lawes [L], Brookstead [B] and Nambour [N]). Soybean yield (t/ha) was chosen as a trait of interest for the present paper. The yield for a particular genotype in an environment is the mean yield from two blocks. See Mungomery et al. (1974) or Basford and Tukey (1999) for the details of the experiment.

Performance plots

In the regular performance plot, environments are forming the horizontal axis and genotypes (or more often, groups of genotypes) are forming the traces (profiles). It is common to order environments from the worst to the best, which is done based on environment means. In this way information about the genotypes' performance in various conditions is easily accessed; this rule is not always followed (e.g., Ogonnaya et al., 2007; Dehghani et al., 2008). Another useful addition is the mean profile, which represents the mean trait value of genotypes in environments; also this rule is infrequently broken (e.g., Ogonnaya et al., 2007). In addition, it is useful to order genotypes on the legend from the best to the worst in terms of the mean across the environments in that way the reader of the graph can immediately access this important information. Such a performance plot shows at the same time (a) stability of a genotype in a static sense (which can be seen by looking at changes across environments on a profile for the genotype), (b) stability of a genotype in a dynamic sense (which can be seen by looking at changes across environments on a profile for the genotype compared to the mean performance), and (c) adaptability of a genotype (which can be seen by looking at how the genotype outperforms the mean profile across environments).

The environment-centered performance plot is constructed in a very similar way as the regular performance plot, but for the data centered for the mean across the genotypes in a particular environment:

$$(1) \quad Y_{ge}^c = Y_{ge} - \bar{Y}_e$$

where Y_{ge}^c and Y_{ge} are respectively the environment-centered and original trait value for the g th genotype in the e th environment, and \bar{Y}_e is the mean of the trait across all genotypes in the e th environment. Fox and Rosielle (1982) call such transformed data the "coded data" (hence the index c).

The environment-standardized performance plot is based on data standardized by the following formula:

$$(2) \quad Y_{ge}^s = \frac{(Y_{ge} - \bar{Y}_e)}{S_e}$$

where Y_{ge}^s is the standardized trait value for the g th genotype in the e th environment, and S_e is the estimated phenotypic standard deviation of the trait in the e th environment, calculated with the standard formula:

$$(3) \quad S_e = \frac{1}{E-1} \sum_{e=1}^E (Y_{ge} - \bar{Y}_e)^2$$

E being the number of environments.

Note the difference between the coded and standardized data: in the latter the former data are divided by the phenotypic environment-wise standard deviations (Fox and Rosielle, 1982; DeLacy et al., 1996). Through the transformation (1), the environment means are all equal to 0, so the mean performance is equivalent to the horizontal line for $Y=0$; the standard deviations in environments are the same as of the original data, so the information about variability in the environments is kept. Through the standardization (2) the environment means are also zero, but in addition the standard deviations in the environments are all equal to 1, so each environment has now an equal variability (so, equal weight) in the plot. In that way, the information on variability (hetero- or homogeneity of genotypes' performance) in the environments is lost.

The performance plots were drawn with R (R Development Core Team, 2010) function `xypplot()` of the `lattice` package (Sarkar, 2008). The aspect ratio of the plots (the ratio of the height of the data rectangle to its width) was chosen according to the banking to 45° rule, which optimizes the comparison among the lines (Cleveland, 1994); note that the aspect ratios for the three performance plots based on the same data set may differ. In addition, a Cleveland dot plot (Cleveland, 1994) was drawn with the `dotplot()` function of the same package.

Results

The regular performance plot shows that the environments offered quite diverse conditions for soy bean (Figure 1). Mean yield in the worst environment was slightly above 1.5 t/ha, while in the best was almost 3.5 t/ha. None of the genotypes was stable in a static sense (see also Table 1). The same can be seen for the stability in a dynamic sense, although some genotypes seem to present some extent of dynamic stability for example genotypes 56 and 57. These two genotypes showed also wide adaptability (genotype 57 yielded over the mean in each environment, while 56 slightly below the mean only in one environment); the other genotype with wide adaptability was genotype 53, which yielded over the mean in all environments clearly this genotype was unstable in both dynamic and static senses (see also Table 1). Genotype 58 was the worst genotype, yielding very low in all environments but one. One environment (R71) offered very homogenous conditions for all genotypes, because all of them had almost the same seed yield.

Table 1. Mean yield and stability in dynamic (represented by ecovalence) and static (represented by variance of yield across environments) senses for the soy bean genotypes studied.

Genotype	Mean yield (t/ha)	Variance across environments	Ecovalence
57	2.89	0.44	0.53
53	2.87	0.35	1.02
56	2.82	0.59	0.60
55	2.53	0.43	0.59
54	2.14	0.45	1.46
58	1.54	0.75	1.92

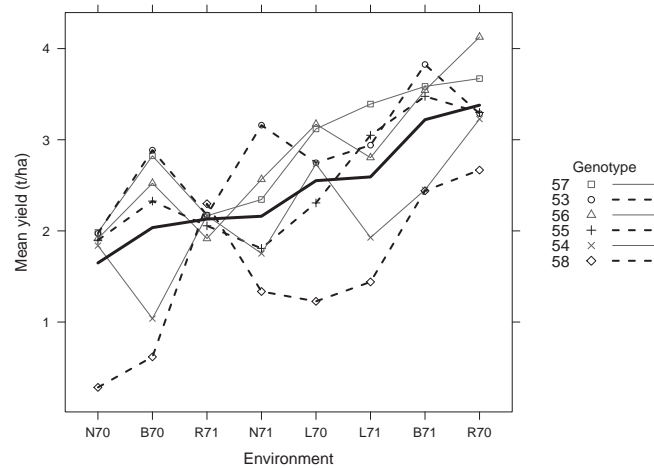


Figure 1. Performance plot for seed yield of six soybean genotypes in eight environments. Data come from Basford and Tukey (1999). Environments on the horizontal axis are ordered by an increasing mean yield and genotypes in the legend by a decreasing mean yield.

Stability in a dynamic sense is much easier to see and interpret on the environment-centered plot (Figure 2). One needs to compare a profile for a genotype with the mean profile; this means comparing the extent to which these two profiles are parallel. Hence it is easier on the environment-centered performance plot, on which the mean profile is a horizontal zero-line, than on the regular performance plot (Figure 1). See for example the lines representing the changes from environment L71 to B71 on both plots and note the difficulty in comparing these changes for various genotypes on the regular plot. We can see that all genotypes yielded higher in B71 than in L71. On the environment-centered performance plot the dynamic stability can be easily seen (Figure 2) here we compare reactions for different genotypes and see that, for example, for these two environments the greatest increase in yielding compared to the mean performance was obtained for the worst genotype, and that for three genotypes a smaller increase than the mean increase (represented by the horizontal line) was observed. In addition, the difference between the trait value for a genotype and the mean in a particular environment is immediately accessed on the environment-centered plot, while for the regular performance plot one needs to subtract the genotype's value from the mean value (so one needs to judge the vertical distances between two points for two genotypes for each environment). Cleveland (1994, p. 21) discusses these issues, showing that human eye does such a work poorly. Thus the regular performance plot in this context is less efficient in terms of visual encoding of the data than the environment-centered performance plot.

The environment-standardized performance plot (Figure 3) fails to convey most of the information discussed above. No information about stability in a static sense is provided. The same can be said about stability in a dynamic sense note how difficult it is to interpret the profiles for the genotypes. Look at genotype 56 and its reaction to changing environment from B70 to R71: even though this change is the same as that of genotypes 57 and 53 (Figure 2), from Figure 3 it seems that this change was huge. This is because this genotype was the

worst in environment R71, which was homogenous in terms of yielding (the difference between the worst and the best yielding genotypes was smaller than 0.5 t/ha). Hence standardized data provide no information about stability. It informs about wide adaptability, showing in which environments a genotype yield is higher than the mean yield, but this cannot be assessed in the original units, but standardized which is rather a disadvantage than advantage: even a small, unimportant difference may appear to be noticeable.

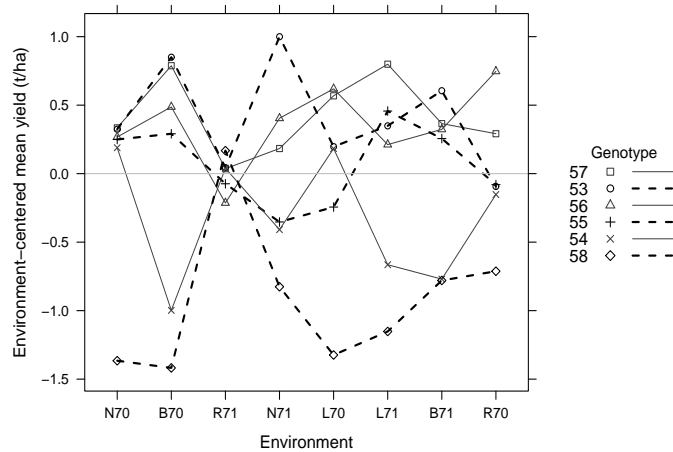


Figure 2. Environment-centered performance plot corresponding to the performance plot from Figure 1. Data come from Basford and Tukey (1999). Environments on the horizontal axis are ordered by an increasing mean yield and genotypes in the legend by a decreasing mean yield.

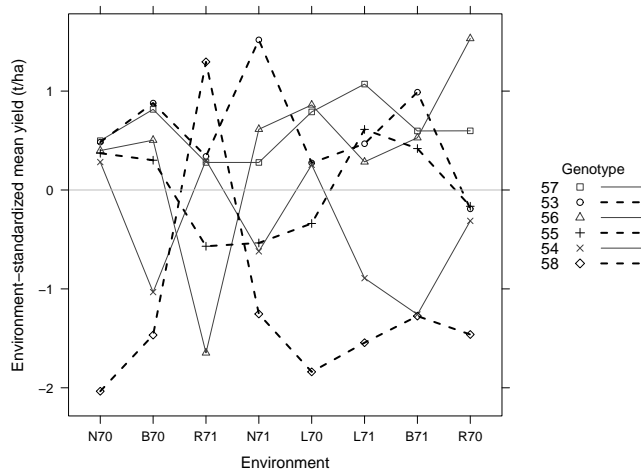


Figure 3. Environment-standardized performance plot corresponding to the performance plot from Figure 1. Data come from Basford and Tukey (1999). Environments on the horizontal axis are ordered by an increasing mean yield and genotypes in the legend by a decreasing mean yield. The grey reference line represents the mean profile.

Discussion

Most promising genotypes of a crop species are those which have high and stable yield. Stability can be considered in various ways, which can be grouped in two main types: stability in static and dynamic concepts. The former refers to stable yielding of a genotype over environments, while the latter refers to stable yielding of a genotype over environments as compared to mean yielding of a particular group of genotypes considered (Lin et al., 1986). It is easy to imagine that stability in these two concepts does not have to be related, and that the dynamic stability of a genotype strongly depends on other genotypes being considered in the particular study. A genotype that is very stable statically does not react to changing environmental conditions, while that which is very stable dynamically reacts to changing environmental conditions similarly to the mean reaction within the pool of genotypes. Hence we see that great stability does not have to be a great advantage: for example, a genotype does not have to be stable in a static sense to be the best yielder in every environment, and a genotype that reacts extremely well on one type of environmental conditions (e.g., drought stress), but reacts normally on other conditions, will not be stable in dynamic sense. Hence when studying stability one should look at stability measures as well as genotype performance among environments. Such performance is difficult to see in any type of biplot, but it can be seen on performance plots.

From the results presented in the paper it follows that the regular performance plot, as the only one of the three plots compared, pictures stability in a static sense. Also as the only one it enables one to read an original value of the trait in the environments. It is also the most efficient in conveying information about the environments, although one needs to keep in mind that this information is not rich simply because performance plots are not focused on environments. Its disadvantages are lower (compared to the environment-centered performance plot) efficiency in visualizing stability in a dynamic sense as well as narrow and wide adaptabilities this is due to less efficient visual encoding of the data in this plot.

The environment-centered performance plot is the most efficient among the three in picturing stability in a dynamic sense as well as narrow and wide adaptability. The adaptability is best shown because one can easily subtract the difference between a particular genotype's value and the environment, so not only can one see whether the trait's value is above the mean, but also how far it is from the mean. This plot is not free of disadvantages, although rather minor ones. Stability in a static sense cannot be seen. Information on environments is poor, although the important information about the diversity of the environments in terms of the trait is kept. Note that this problem is to some extent overcome by ordering environments on the horizontal axis from the worst to the best.

The environment-standardized performance plot fails in almost each category among those considered above. It only pictures narrow and wide adaptability, but worse than environment-centered performance plot. This is because the information about the actual difference about the environment diversity is lost, so one does not know how much the genotype outperforms the mean performance.

One additional thing, not mentioned before, is that on a regular performance plot the mean performance is usually represented by a thick black line in order to make it easily distinguishable from the genotype-wise performances. Since on the environment-centered

and environment-standardized performance plots the mean performance is equal to the horizontal zero line, the corresponding line does not need to be thick; in fact, a thin grey line will suffice, accounting for better readability of the graph (compare Figure 1 with Figures 2 and 3).

Note that the considerations in this paper refer to exploratory graphs that aim to facilitate understanding genotype's performance in terms of stability and adaptability across environments. So these conclusions must not be generalized to other situations, for example statistical analysis as Fox and Rosielle (1982) show, in various situations standardized data will work better than coded data (on which the environment-centered performance plot is based). However, in addition to rigorous statistical analysis to infer about the genotype-by-environment data, plant breeders do also need to look into their data, find patterns in them and understand them. The plots described in this paper are simple to understand by plant breeders, still being powerful in conveying important information about some aspects of the data (except for the environment-standardized performance plot). All discussions in this paper equally refer to the version of the performance plot in which the horizontal axis is formed by environment means instead of environments treated as levels of a qualitative variable. This all does not mean that any stability or adaptability analysis should be based solely on the performance plots. They aim to visualize stability and adaptability of genotypes, showing at the same time the performance of the genotypes in the environments, thereby supporting further detailed analysis based on various methods of analyzing genotype-by-environment interaction (see DeLacy et al., 1996 for a long list of various such methods). Laffont et al. (2007) conclude that dot plots and the same can be said about performance plots provide a clearer visualization of genotype performance than biplots, so these types of plots should not be considered competing or alternative but rather complementary; therefore, these different types of plots should be applied together, in that way providing a more comprehensive picture of data. It is also desirable to support interpretation of performance plots with stability measures, so that the plots support understanding the sources of stability or its lack for example, it can be a different performance in just one environment that is a reason of lack of stability, which can be quickly seen from a performance plot. In addition, all that should be accompanied by formal statistical inference to draw final conclusions.

Future research should focus on optimizing performance plots in terms of number of genotypes and/or environments that can be graphed. Interactive visualization might be an idea for that.

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