Biplot Analysis of Host-by-Pathogen Data

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ABSTRACT

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Effective breeding for disease resistance relies on a thorough understanding of host-by-pathogen relations. Achieving such understanding can be difficult and challenging, particularly for large data sets with complex host genotype-by-pathogen strain interactions. This paper presents a biplot approach that facilitates visual analysis of host-by-pathogen data. A biplot displays both host genotypes and pathogen isolates in a single scatter plot; each genotype or isolate is displayed as a point defined by its scores on the first two principal components derived from subjecting genotype- or strain-centered data to singular value decomposition. From a biplot, clusters of host genotypes and clusters of pathogen strains can be simultaneously visualized. Moreover, the basis for genotype and strain classifications, i.e., interactions between individual genotypes and strains, can be visualized at the same time. A biplot based on genotype-centered data and that based on strain-centered data are appropriate for visual evaluation of susceptibility/resistance of genotypes and virulence/avirulence of strains, respectively. Biplot analysis of genotype-by-strain is illustrated with published response scores of 13 barley line groups to 8 net blotch isolate groups.

Additional keywords: genotype-by-environment interaction, genotype-by-strain interaction, GGE biplot, host-by-pathogen interaction

Agricultural, biological, and ecological studies are often characterized by the presence of complex genotype-by-environment interactions. As a special form of genotype-by-environment interaction, host genotype-by-pathogen strain (used synonymously with host-by-pathogen or genotype-by-strain in this paper) interaction is the center of pathology research. This is especially true for host-pathogen systems in which there are clear race differentiations such that a host genotype can be described as resistant or susceptible only to specific races. Since large variability can exist both within the host and within the pathogen, understanding the host-by-pathogen interaction patterns for a particular host-pathogen system can be difficult and challenging. Graphical methods are desirable, if not necessary, to fully understand a large data set with complex host-by-pathogen interactions.

Gabriel (4) developed a biplot method for graphical visualization of a "rank-two" matrix. A rank-two matrix with m rows and n columns is a matrix resulting from mul-

tiplying a matrix with m rows and two columns (referred to as "the row matrix") by a matrix with two rows and n columns ("the column matrix"). The row matrix can be presented as m points (markers) in a two-dimensional plot. Likewise, the column matrix can also be displayed as n points in a two-dimensional plot. Superimposing the two plots results in a biplot (4). One advantage of such a biplot is that the value of each element in the rank-two matrix can be graphically visualized based on simple geometric relations between the corresponding row and column markers. Gabriel (4) further proposed that, if a two-way table from actual research can be sufficiently approximated by a rank-two matrix via principal component analysis, it could be graphically analyzed using a two-dimensional biplot. Since then, biplots have been frequently used in visual analysis of genotype-by-environment data (1-3,5,7-9).

Recently, biplot analysis of genotype-by-environment data has been advanced such that many important questions can be graphically addressed using a "GGE biplot" (10,11,13). These questions include the which-won-where pattern, mega-environment investigation, mean performance and stability of genotypes, discriminating ability and representativeness of environments, etc. A GGE biplot displays GGE, which is short for genotype main effect (G) plus genotype-by-environment

interaction (GE); it is the part of variation that is relevant to cultivar evaluation. The environment main effect (E) is removed, as it is irrelevant to cultivar evaluation. The GGE biplot methodology has been extended to visual analysis of genotype-by-trait data (14), diallel cross data (12), and used for quantitative trait loci mapping (W. Yan and D. E. Falk, *unpublished*). Using a recently published data set on barley net blotch (*Pyrenophora teres* Drechs) (6), this paper describes the GGE biplot methodology for graphical analysis of host genotype-by-pathogen strain data.

MATERIALS AND METHODS

Data source. Barley net blotch is an important barley disease throughout the world. Gupta and Loughman (6) reported a survey of current virulence of this disease on barley in Western Australia. They collected 79 net blotch isolates from infected leaf samples across barley growing regions in Western Australia, nine historical isolates collected and lyophilized during 1975 to 1985 from the same regions, and one isolate from eastern Australia. They tested these isolates on 47 barley differential lines and cultivars. Based on cluster analysis and using seedling response data, they classified the pathogen isolates into 8 isolate groups (IG) and the barley genotypes into 13 line groups (LG). They summarized the average response of each LG to IG in a table and verbally explained the LG by IG interactions. Their summary table is adopted here as Table 1, which will be used to illustrate biplot analysis of genotype-by-strain interaction. Among the isolate groups, IG48 consists of isolates collected from Wongan Hills Research Station during the survey, IG78 consists of historic isolates, QNB58i was an isolate from eastern Australia, and the others consist of isolates collected in other regions of Western Australia (6).

Models for genotype-by-strain biplots.

Two types of GGE biplots can be constructed for a genotype-by-strain data set, depending on the research emphasis. If evaluation of pathogen strains is the primary objective, a strain-focused biplot can be constructed; if evaluation of host genotypes is the main purpose, a genotype-focused biplot can be constructed. If both are of interest, then both types of biplots are needed to thoroughly characterize the relationships within the data set.

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Strain-focused biplot. To generate a genotype-by-strain biplot appropriate for evaluation of pathogen strains, the data are first genotype-centered, i.e., the respective means of genotypes across strains are subtracted from the original data. The genotype-centered data are then subjected to singular value decomposition, which results in a number of principal components. A GGE biplot is constructed using the first two principal components (PC1 and PC2), and other smaller PCs are regarded as residues:

$$\hat{Y}_{ij} - \alpha_i = \lambda_1 \xi_{i1} \eta_{1j} + \lambda_2 \xi_{i2} \eta_{2j} + \varepsilon_{ij} \quad (1)$$

where:

$\hat{Y}_{ij}$ is the expected disease score of genotype i ($i=1$ to 13) to strain j ($j=1$ to 8),

α_i is the mean score of genotype i across all strains,

λ_1 and λ_2 are the singular values for PC1 and PC2, respectively,

ξ_{i1} and η_{1j} are the PC1 eigenvectors for genotype i and strain j , respectively,

ξ_{i2} and η_{2j} are the PC2 eigenvectors for genotype i and strain j , respectively, and

ε_{ij} is the residue for each genotype-strain combination not explained by PC1 and PC2.

Since the genotype main effects are removed, the genotype-centered data contain only strain main effects and genotype-by-strain interaction. To display PC1 and PC2 in a biplot, equation 1 needs to be written in the form of equation 2:

$$\hat{Y}_{ij} - \alpha_i = g_{i1} s_{1j} + g_{i2} s_{2j} + \varepsilon_{ij} \quad (2)$$

where g_{ik} and s_{kj} are called genotype and strain scores for PC k , respectively, and are defined as:

$$g_{ik} = c \xi_{ik}, s_{kj} = \lambda_k \eta_{kj} \quad (3)$$

where $k = 1, 2$, and c is any positive value used to make the genotype scores and the strain scores comparable in magnitude (11). The strain-focused biplot is generated by plotting g_{i1} against g_{i2} and s_{1j} against s_{2j} in a single plot. Since the entire singular value is partitioned into the strain scores,

the strain scores take the unit of the original data, whereas the genotype scores are unitless (11).

Genotype-focused biplot. Correspondent equations for constructing a genotype-focused biplot are:

$$\hat{Y}_{ij} - \beta_j = \lambda_1 \xi_{i1} \eta_{1j} + \lambda_2 \xi_{i2} \eta_{2j} + \varepsilon_{ij} \quad (1a)$$

$$\hat{Y}_{ij} - \beta_j = g_{i1} s_{1j} + g_{i2} s_{2j} + \varepsilon_{ij} \quad (2a)$$

$$g_{ik} = \lambda_k \xi_{ik}, s_{kj} = c \eta_{kj} \quad (3a)$$

where β_j is the mean disease score of strain j across all genotypes, and all other variables are the same as defined in equations 1 to 3. Since the strain main effects are removed from the data, the strain-centered data contain only genotype main effects and genotype-by-strain interactions. Equation 3a determines that the genotype scores take the unit of the original data, and strain scores are unitless.

Generation and visualization of a biplot. The genotype and strain scores can be obtained using all major statistics packages such as SAS, the output of which can be used to generate a biplot using common tools such as Microsoft Excel. Yan and Hunt (12) presented a step-by-step description for generating a GGE biplot using SAS and Microsoft Office programs. However, since this is a laborious process, the GGEbiplot software (10) was used, which substantially reduced the time needed for the analyses. All biplots presented in this paper are direct outputs of GGEbiplot.

RESULTS

The genotype main effect, strain main effect, and genotype-by-strain interaction were 67, 2, and 31%, respectively, of the total variation of the disease scores presented in Table 1. The main effect of the pathogen is notably small, whereas the genotype-by-strain interaction is many times larger, indicating that the strains differ primarily in specific virulence to different barley line groups.

Visual evaluation of the net blotch isolate groups. The strain-focused model is used to study the virulence of the isolate groups on various barley line groups. Subjecting the data (Table 1) to equations 1 to 3 results in Table 2, where each barley LG or net blotch IG is represented by two scores for PC1 and PC2, respectively. When the PC1 score is plotted against the PC2 score, each LG or IG is displayed as a point in a biplot (Fig. 1).

The biplot explained 89% of total variation of the genotype-centered data, as indicated at the top left of the biplot. The biplot reveals three distinct clusters of isolate groups: cluster 1 consists of IG48 and IG78, cluster 2 consists of the single eastern isolate QNB85i, and cluster 3 consists of the other five isolate groups, namely, IG75, IG84, IG86, IG87, and IG88 (Fig. 1).

The polygon in Figure 1 facilitates visual identification of isolate groups that are

Table 2. PC1 and PC2 scores for 13 barley line groups (LG) and 8 *Pyrenophora teres* isolate groups (IG) used for generating a biplot

	PC1	PC2
<i>P. teres</i> IG	s_{1j}	s_{2j}
Ig86	-1.551	-0.898
Ig75	-1.571	-0.741
Ig87	-2.343	-0.506
Qnb85i	-2.292	3.493
Ig88	-1.602	-0.911
Ig84	-1.908	-0.688
Ig48	6.374	0.177
Ig78	4.893	0.074
Barley LG	g_{i1}	g_{i2}
Cameo	-0.506	-0.393
Clipper	-0.881	-0.788
Betzes	-0.684	-1.724
LG30	-0.317	0.491
LG10	1.193	0.170
LG16	0.098	-0.004
LG32	0.106	0.270
LG8	2.473	0.167
LG31	1.887	-0.855
LG17	-0.289	-0.713
LG22	-0.383	2.680
LG33	0.098	0.459
LG34	-0.312	0.556

Table 1. Mean responses of 13 barley line groups (LG) to 8 *Pyrenophora teres* isolate groups (IG) on a scale of 0 to 9, with larger values indicating greater susceptibility^a

Barley groups	Net blotch isolate groups							
	IG86	IG75	IG87	QNB85I	IG88	IG84	IG48	IG78
Cameo	6.0	4.3	5.8	5.0	4.9	6.1	4.0	4.7
Clipper	5.2	5.0	5.5	5.0	6.4	6.9	4.0	3.5
Betzes	7.7	6.3	7.3	5.0	6.9	6.4	5.0	5.2
LG30	7.6	7.1	7.9	8.0	7.1	7.4	7.2	6.5
LG10	2.1	2.0	1.9	2.0	1.9	2.0	4.9	4.0
LG16	1.8	1.8	1.9	1.9	2.1	2.0	2.3	1.9
LG32	2.3	2.1	2.3	2.8	2.9	2.8	2.9	2.6
LG8	2.3	2.0	2.0	2.0	2.3	2.2	7.8	6.8
LG31	3.6	2.7	2.7	2.0	3.6	3.6	7.4	6.4
LG17	4.7	4.6	4.8	4.0	4.9	5.0	3.9	4.2
LG22	5.1	4.1	5.0	8.0	4.7	5.0	4.6	4.7
LG33	4.5	3.6	4.5	4.7	4.2	4.1	4.6	4.4
LG34	2.8	2.7	3.5	4.0	3.8	3.8	3.0	2.6

^a Data from Gupta and Loughman (6).

most virulent to each of the line groups (13). The polygon is drawn on isolate groups that are located farthest from the biplot origin so that all other isolate groups are contained in it. Starting from the biplot origin, perpendicular lines are drawn to each side of the polygon, which divide the biplot into sectors. The isolate groups located at the vertices are either the most or the least virulent to some or all of the line groups. Isolate groups located close to the biplot origin are less specific in virulence. The polygon view of a biplot has one interesting property; it is that the vertex isolate group for a sector is the most virulent

to genotypes falling in that sector (11,13). Thus, IG48 is most virulent to LG8, LG31, and LG10; QNB85i is most virulent to LG22; and IG86 and closely located isolate groups are most virulent to cultivar Betzes. Therefore, a biplot not only classifies the isolate groups, but also shows the basis of the classification, i.e., their differential interactions with the line groups.

The distance from the biplot origin to the marker of a line group is a measure of its discriminating ability for the isolate groups. Thus, line groups LG8, LG31, LG10, LG22, Clipper, and Betzes, which are located away from the biplot origin

(long vectors), are more discriminating than those that are located close to the biplot origin, e.g., LG16, LG32, and LG30 (Fig. 1). Little difference among isolate groups can be seen on these latter line groups; the isolate groups are equally virulent or avirulent on these line groups. To illustrate, LG16 is resistant to all isolate groups and LG30 is susceptible to all isolate groups (Table 1).

Five Western Australian isolate groups are located closely in Figure 1, indicating that they are similar in virulence to the barley line groups. Any difference among these isolate groups can be examined by generating a biplot based on a subset consisting of only these isolate groups (Fig. 2). The five isolate groups fall into three clusters: IG86 and IG87 are similar in that they are more virulent to Clipper; IG84 and IG88 are similar in that they are more virulent to Betzes and Cameo; and IG75 is the least virulent to all line groups, particularly to Cameo. The differences among the three clusters of isolate groups in Figure 2 are small, however, relative to those among the three large clusters in Figure 1, as can be seen from the magnitude of the scales.

Small differences exist within each cluster of isolate groups. In Figure 1, although IG78 is similar to IG48, it is less virulent to LG8, LG31, and LG10. In Figure 2, IG88 is less aggressive than IG84 to almost all line groups, and IG87 is less virulent to Betzes but more virulent to Clipper, compared with IG86. The pattern displayed in Figures 1 and 2 can be summarized in a dendrogram (Fig. 3), in which both clusters of the isolate groups and the respective differential line groups are presented. The eight isolate groups were first divided into three major groups based on Figure 1, with LG22, LG8+LG31, and Betzes being the most discriminating genotypes. The large cluster with five isolate groups was further divided into three subgroups based on Figure 2, with Cameo, Clipper, and Betzes being the most discriminating genotypes.

Visual evaluation of the barley line groups. For evaluating the barley line groups, a biplot based on strain-centered data is constructed (Fig. 4). Although the isolate groups fall into two distinct clusters, clusters of barley line groups are not evident, implying that the relationship among the line groups is more complex. All isolate groups, with the exception of IG48, fall in the sector for which LG30 is the vertex. This suggests that LG30 is most susceptible to all isolate groups, with the possible exception of IG48. Opposite to LG30 and located on the other side of the biplot origin, LG16 seems to be most resistant to all isolate groups. Although LG8 is quite different from LG30, as judged by the biplot distance between them (Fig. 4), they seem to be equally susceptible to isolate groups IG48 and IG78, since the two isolate groups are located near the line that is perpendicular to the polygon side that

Fig. 1. GGE biplot based on disease scores of 13 barley cultivars or line groups (LG) inoculated with 8 net blotch isolate groups (IG). The isolate groups are used as entries (italic lowercase), and the barley line groups are used as genotypes (bold uppercase). Based on data of Gupta and Loughman (6).

Fig. 2. GGE biplot based on disease scores of 13 barley cultivars or line groups (LG) inoculated with 5 net blotch isolate groups (IG) from Western Australia. The isolate groups are used as entries (italic lowercase), and the barley line groups are used as genotypes (bold uppercase). Based on data of Gupta and Loughman (6).

connects LG30 and LG8. Moreover, since LG31 is located on the polygon side that connects LG8 and LG30, it should be equally susceptible to IG48 and IG78. As a rule, all line groups that are located on the polygon side should have the same susceptibility to an isolate group that is located on the line perpendicular to the polygon side. To all isolate groups, the susceptibility of LG31 should always be intermediate between that of LG8 and LG30, in proportion to its relative position between LG8 and LG30. These interpretations can be extended to visualizing susceptibility of all line groups that are located on any straight line. Similarly, based on Figure 4, the susceptibility/resistance of Betzes should be intermediate between LG30 and Clipper to all isolate groups; the susceptibility/resistance of LG10 should be intermediate between LG8 and LG16 to all isolate groups; and the susceptibility/resistance of LG34 should be intermediate between LG16 and Clipper to all isolate groups. LG33 is located near the biplot origin, suggesting that its susceptibility to all isolate groups is close to the average across the line groups.

When isolate groups IG48 and IG78 are deleted from Figure 4, the difference between the single eastern isolate QNB85i and the five western isolate groups becomes obvious (Fig. 5). Figure 5 suggests that LG30 is the most susceptible barley line group to all six isolate groups, but LG22 is equally susceptible to QNB85i, because QNB85i is located on the line that is perpendicular to the polygon side that connects LG22 and LG30. Figure 5 also suggests that LG8, LG10, and LG16 are equally resistant to all six isolate groups since they are closely clustered at the left end of the biplot.

When QNB85i is further deleted, Figure 5 is transformed into Figure 6. PC1 in this biplot explained 97% of the strain-centered data. Moreover, there is no apparent variation among the isolate groups in terms of PC1. Therefore, PC1 should exclusively represent the mean susceptibility of the line groups across the five isolate groups. Two conclusions can be drawn from Figure 6. First, the five western net blotch isolate groups are almost the same in virulence to the barley line groups tested. Second, resistance to these five isolate groups varies continuously among the barley line groups: LG30 being the most susceptible, followed by Betzes, Clipper, Cameo, etc. On the other hand, LG16, LG10, and LG8 are the

most resistant, followed by LG32, LG31, and LG34. The line groups probably have similar major genes for vertical resistance but vary in minor resistance genes to these isolate lines.

DISCUSSION

Pathology research and disease surveys generate large quantities of data in the form of a host genotype-by-pathogen strain two-way table or a geographical location-by-pathogen strain two-way table, or a mixture of the two. Thoroughly understanding such a large data set can be a major challenge to researchers. A common practice in treating such a large data set is to reduce the original data dimensions

Fig. 4. GGE biplot based on disease scores of 13 barley cultivars or line groups (LG) inoculated with 8 net blotch isolate groups (IG) from Western Australia. The barley line groups are used as entries (italic lowercase), and the isolate groups are used as testers (bold uppercase). Based on data of Gupta and Loughman (6).

Fig. 3. Dendrogram showing clusters of isolate groups based on their differential virulence to barley genotypes and line groups. Based on data of Gupta and Loughman (6).

using cluster analysis or principal component analysis. Cluster analysis of a genotype-by-strain two-way table clusters host genotypes or pathogen strains (races) or both into a few groups, as was done in Gupta and Loughman (6). The result of cluster analysis is still a two-way table; it is a reduced host group by pathogen group two-way table such as Table 1. Interpretation of this reduced data set remains a difficult task, as the table is still quite large. Principal component analysis (PCA) summarizes a two-way data set in a few principal components (PC) if the host genotypes or the pathogen strains are somehow correlated. After PCA, the number of host genotypes and the number of pathogen strains remain the same, but each genotype or strain is represented by fewer dimensions or PC. If PC1 and PC2 sufficiently approximate the original data, then the original data can be visually analyzed using a biplot as illustrated in this paper. Such a biplot still summarizes the most important patterns of the data set, even if it explains only a small fraction of the total variation. We used the results of cluster analysis of Gupta and Loughman (6) as input for biplot analysis; it should also work if the original data set were used as input.

Cluster analysis followed by biplot analysis has been referred to as "pattern analysis" (2,3). In this notation, the two are not competing methods; they are two successive steps toward a thorough understanding of a large two-way or multivariate data set. Cluster analysis can classify the pathotypes and/or the genotypes into groups, but it does not indicate specific interactions between pathotypes and genotypes. Biplot analysis classifies both pathotypes and genotypes simultaneously, and at the same time it also shows how individual pathogens and genotypes interact. Therefore, cluster analysis may or may not tell the whole story, whereas biplot analysis does, as the interactions are clearly displayed and easily interpreted.

Two types of GGE biplots are presented for visualizing a genotype-by-strain data set. If the research emphasis is on pathogen strain evaluation, a GGE biplot based on genotype-centered data is appropriate (Figs. 1 and 2). With such a biplot, the following questions can be visually addressed. First, are there crossover genotype-by-strain interactions? Alternatively, is the virulence of the strains specific to host genotypes? If there is no crossover genotype-by-strain interaction, all genotypes will fall in a single sector, which

means that a single strain is most virulent to all genotypes and there is no race differentiation within the pathogen (assuming both the host and the pathogen are well represented in the data). Crossover interaction, and hence virulence specificity, are indicated if host genotypes fall into different sectors (Figs. 1 and 2). When there is virulence specificity, a second question can be addressed: what are the most discriminating host genotypes? In our example, Figure 1 reveals that barley lines LG8, LG31, LG10, LG22, and Betzes are the most discriminating genotypes, and Figure 2 reveals that Clipper and Cameo are additional discriminating genotypes.

Biplots based on strain-centered data are appropriate if the emphasis is on the evaluation of host genotypes (Figs. 4 to 6). The following questions can be visually addressed. First, are there apparent clusters of pathogen strains? If yes, it suggests race specifications within the pathogen; if not, either there is no race specification within the pathogen or the pathogen is highly specified so that each strain is different. A second question will clarify this: are there crossover genotype-by-strain interactions? If not, there is probably no race differentiation within the pathogen, and a single host genotype can be selected that is most resistant to all strains. If there are clear race specifications but there are no crossover genotype-by-strain interactions (e.g., Figs. 4 to 6), a genotype exists (e.g., LG16) that carries all genes needed to be resistant to all strains. Crossover interactions suggest that genes resistant to different strains exist in different genotypes and should be pyramided.

The advantage of graphical analysis using biplots over conventional analysis is obvious, even for a small data set. As an example, biplot analysis (figure not shown) of the data in Table 2 of Gupta and Loughman (6), a small table that contains five genotypes by five pathotypes, clearly showed that isolate 95NB117 differentiated the six-row barleys (Atlas, Harbin, Steptoe) from the two-row barleys (Betztes and Herta) in that this isolate was avirulent on the two-row barleys but virulent on the six-row barleys. In contrast, the other races were avirulent on the six-row but virulent on the two-row barleys. The biplot also showed that Betztes and Herta gave distinctly different reactions, in that Betztes was most susceptible to isolate 95NB104 while Herta was most susceptible to the remaining three isolates (95NB97, 95NB106, and 95NB155). These relationships were not evident from even this simple table.

Biplots may be used in other types of data relevant to pathology research and plant breeding. For example, it would be particularly interesting to use GGE biplots to analyze seedling versus adult plant reactions of a group of genotypes to a series of isolates to evaluate the interactions and the groupings that may be present among

Fig. 5. GGE biplot based on disease scores of 13 barley cultivars or line groups (LG) inoculated with 6 net blotch isolate groups (IG) from Western Australia. The barley line groups are used as entries (italic lowercase), and the isolate groups are used as testers (bold uppercase). Based on data of Gupta and Loughman (6).

Fig. 6. GGE biplot based on disease scores of 13 barley cultivars or line groups (LG) inoculated with 5 net blotch isolate groups (IG) from Western Australia. The barley line groups are used as entries (italic lowercase), and the isolate groups are used as testers (bold uppercase). Based on data of Gupta and Loughman (6).

genotypes and among isolates. Biplots could possibly identify resistance sources that were specific to a development stage and others that may have a similar reaction at all development stages. They could also give an indication of the distribution and frequency of isolates with similar or different virulence and/or aggressiveness to barley at different growth stages. This could be of considerable use in developing breeding strategies and selecting isolates to use in screening breeding materials.

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