# Foliar Resistance to Late Blight in Potato Clones Evaluated in National Trials in 1997

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## ABSTRACT

**Changes in the oomycete *Phytophthora infestans* in the United States and other parts of the world pose a significant threat to potato production. A continual evaluation of potato clones for resistance to late blight is necessary to identify clones with resistance and to monitor the stability of resistance in light of the emergence of new and more aggressive strains of this pathogen. Twenty-two potato clones (10 cultivars and 12 selections) were evaluated in 1997 for late blight resistance at seven U.S. locations. Seven late blight differentials ($R_1R_2R_3R_4$, $R_1R_2R_4$, $R_1R_3R_4$, $R_3$, $R_8$, $R_{10}$, and $R_{multi}$) were also included in the test at five of these locations. The US-8 strain of *P. infestans* was present at all locations. Percent infected foliage was recorded at approximately weekly intervals following the onset of disease. Area under the disease progress curve (AUDPC) was calculated. The nonparametric stability statistics mean absolute rank differences ($S^{(1)}_i$) and variances of the ranks ($S^{(2)}_i$) were used to analyze phenotypic stability. Although neither of these statistics was significant for individual clones, both of these statistics were significant when summed over clones, indicating the importance of genotype x environment interactions on the rankings of these clones across locations. The most late blight-resistant and susceptible clones were the most stable; clones in the intermediate ranges were most subject to rank changes due to genotype x environment interactions. The most late blight-resistant clones were AWN86514-2, B0692-4, B0718-3, and B0767-2. The most susceptible clones were B0811-13, B1004-8, Nor-Donna, and Krantz. AUDPC was very low for the late blight differentials $R_8$ and $R_{multi}$, moderately low for $R_{10}$ and very high for the remaining differentials. This study is important in characterizing the reaction of potato clones to new strains of *P. infestans*.**

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ADDITIONAL KEY WORDS: *Phytophthora infestans*, genotype x environment, phenotypic stability.

Abbreviations: AUDPC-area under the disease progress curve; FL-Florida; MD-Maryland; ME-Maine; MI-Michigan; MN-Minnesota; ND-North Dakota; NY-New York; PA-Pennsylvania

## INTRODUCTION

Potato late blight, caused by *Phytophthora infestans* (Mont.) de Bary, is one of the most important diseases of potatoes worldwide (Fry and Goodwin 1997). Late blight is a rapidly developing and destructive disease, capable of destroying a potato field in less than five days under conducive weather conditions. The migration of virulent and metalaxyl-resistant strains of this pathogen in the last two decades has caused epidemics in North America, Europe, and other parts of the world (Fry et al. 1993). Prior to 1980, strains of *P. infestans* outside of Mexico were the US-1 genotype (Fry et al. 1993), an A1 mating type, which was sensitive to metalaxyl, the only fungicide available that could slow the progress of an established epidemic. Resistance to metalaxyl first appeared in Europe (Davidse et al. 1981) in 1980 and was subsequently found in the United States and Canada in the late 1980's (Deahl et al. 1991). Almost concurrent with the appearance of resistant isolates was the discovery of the A2 mating type of *P. infestans* in many parts of the world (Gisi and Cohen 1996). With both mating types present in European fields, the pathogen has been shown to reproduce sexually (Drenth et al. 1995; Sujkowski et al. 1994). Sexual reproduction has the potential to greatly increase the genetic variation of this pathogen population and make control even more difficult.

Beginning in 1996, the United States Department of Agriculture, Agricultural Research Service, in cooperation with scientists in eight states, initiated a National Late Blight Germplasm Evaluation Trial to screen potato clones for resistance to these new strains of *P. infestans*. Sixteen clones were evaluated. Several selections from U.S. breeding programs were highly resistant to the US-8 genotype of *P. infestans* present at all eight test locations. No evidence for genotype x environment interactions was found on late blight reactions as measured by ranking clones by area under the disease progress curve (Haynes et al. 1998).

This study is a continuation of the National Late Blight Germplasm Evaluation Trials. In addition to the clones tested in 1996, six clones were evaluated for the first time; three of these new clones reportedly have some resistance to late blight (B0288-17 [K.G. Haynes, pers comm], Dorita [Platt and McRae 1990], and Robijn [Colon et al. 1995]). The objectives of this study were (1) to identify clones with resistance to late blight and (2) to examine the phenotypic stability of the expressed resistance across U.S. environments in 1997.

## MATERIALS AND METHODS

Twenty-two potato clones, consisting of 12 numbered selections from U.S. breeding programs and 10 cultivars, along with seven late blight differentials ([$R_1R_2R_3R_4$= PI 215618], [$R_1R_2R_4$ = PI 215623], [ $R_1R_3R_4$ = PI 215621], [$R_3$ = PI 423653], [$R_8$ = PI 303149], [$R_{10}$ = PI 423656], and [$R_{multi}$=PI 303150]) obtained from the NRSP-6 collection at Sturgeon Bay, WI, were established in tissue culture and tested for potato viruses A, X, Y, M, S, and leafroll using ELISA, and potato spindle tuber viroid using cDNA techniques by Agdia (Agdia, Inc., Elkhart, IN). None of the viruses nor the viroid were detected, with the exception that most of the clones were infected with PVS. Plantlets were micropropagated and approximately 200 plantlets of each clone were transplanted into Jiffy Mix (Jiffy Products of America, Inc., West Chicago, IL) in the greenhouse at Beltsville, MD, during the fall of 1996. In early December, minitubers were harvested from these plants. Fifteen minitubers of each clone and differential were distributed to cooperating scientists at nine locations across the USA for planting and evaluation. A listing of the seven locations from which data were obtained, soil type at the location, the planting date, and evaluation dates for late blight is given in Table 1. No late blight developed at the California location. The results from the Wisconsin location were confounded with a severe early blight infestation and are not presented here. The differentials failed to emerge promptly in Florida and therefore, are not included in the statistical analysis of the clones.

Minitubers of the clones and differentials were planted in a randomized complete block design consisting of three replications of five hills at all sites. Every other row or every third row in the field was planted with Russet Burbank to be used as a spreader row, except for Florida, where Red LaSoda was planted in place of Russet Burbank, and New York, where no spreader rows were used. All locations inoculated the plots with their own US-8 strains of *P. infestans* (A2 mating type, metalaxyl-resistant)(Goodwin et al. 1995) except for Florida and Maine, which relied on natural infestations for late blight, caused also by the US-8 strain.

Plants were evaluated for late blight at frequent intervals, no less than weekly, during the epidemic. Late blight readings were recorded on a plot basis as either the percent infected foliage or by the Horsfall-Barratt scale (1945). Horsfall-Barratt ratings were converted to a percentage value using the Eli Lilly tables, which are statistically derived (Redman et al. 1969). Area under the disease progress curve (AUDPC) was calculated

TABLE 1—*Locations of the late blight trials in 1997, soil type, date plots were planted, date plots were inoculated, and dates plots were evaluated for late blight.*

| Location | Soil Type | Planting Date | Inoculation Date | Evaluation Dates |
|---|---|---|---|---|
| Hastings, FL | Wabasso sand | February 21 | NA | 3/25, 3/31, 4/4, 4/9, 4/16 |
| Bath, MI | muck | June 6 | 7/20 | 7/22, 7/29, 8/1, 8/4, 8/13, 8/18, 8/25 |
| Presque Isle, ME | gravelly loam | June 7 | NA | 9/11, 9/16, 9/20 |
| Rosemont, MN | silt loam | June 9 | 8/14 | 8/25, 8/29, 9/1, 9/7, 9/17 |
| Prosper, ND | clay loam | May 27 | 7/16 | 8/1, 8/8, 8/15, 8/22, 8/29 |
| Freeville, NY | gravelly loam | June 30 | 8/14 | 8/17, 8/22, 8/26, 8/29, 9/2 |
| Rock Springs, PA | clay loam | June 6 | 8/11 | 8/27, 9/3 |

NA - plots were not inoculated.

(Shaner and Finney 1977) and subjected to standard analysis of variance using the general linear models procedure in SAS (1987) by location. Heterogeneity of variance was tested using Bartlett's test (Bartlett 1937).

Mean AUDPC was calculated for each clone and differential at each location, but only the clones were ranked on mean AUDPC from lowest to highest within locations. These rankings were analyzed for the nonparametric measures of phenotypic stabililty developed by Huehn (1990): mean absolute rank difference and variance of the ranks. The PC-SAS program developed by Lu (1995) was utilized for these analyses. A box and whisker plot of the rankings of AUDPC within locations for each clone was then drawn (Axum 1999).

## RESULTS AND DISCUSSION

Area under the disease progress curve for the 22 clones tested was analyzed separately for each location. There were significant differences between clones for AUDPC at each location (Table 2). Bartlett's test indicated that heterogeneity of variance between locations was significant ($\chi^2 = 188$, $P<0.01$). Therefore, data were not combined across locations for further parametric analyses. The error variances ranged from a low of 1365 at PA to a high of 43,494 at ND. The coefficient of variation ranged from a low of 13 at MN to a high of 70 at ME. There was little late blight infestation in ME, which relied on natural infestation for testing. Distribution of the late blight infestation among plots at the other six sites, all of which were inoculated with *P. infestans* except FL, was more uniform than at ME.

The mean AUDPC and the ranking of the 22 clones within locations are presented in Table 3. Mean AUDPC ranged from a low of 96 in ME to a high of 1086 in MN. The low mean AUDPC in ME is again indicative of low late blight infestation, which may have been due to lack of inoculation, a lack of favorable environmental conditions for *P. infestans*, or both.

A box and whisker plot of the rankings of the clones across locations is given in Figure 1. The median ranking for each clone is indicated as a solid line within each box. For our discussion, clones were arbitrarily assigned to one of four categories based on the median rankings as resistant (median ranking < 6), moderately resistant (6< median ranking < 12), moderately susceptible (12 < median ranking < 18) and susceptible (18 < median ranking). The most late blight-resistant clones were from U.S. breeding programs (AWN86514-2, B0692-4, B0718-3, and B0767-2) (Table 3; Figure 1), in agreement with the results of the 1996 trial reported by Haynes et al. (1998). Of the three entries (B0288-17, Dorita, Robijn) that reportedly had some resistance to late blight that were new to the trial this year, the median

TABLE 2—*Analysis of variance on area under the disease progress curve (AUDPC) and the coefficient of variation by location for 22 potato clones evaluated for late blight resistance in the United States during 1997.*

| Source | FL | ME | MI | MN | NY | ND | PA |
|---|---|---|---|---|---|---|---|
| Rep | 30396 | 44715** | 31325 | 68482* | 638 | 152927* | 1081 |
| Clone | 168849** | 19250** | 498164** | 1354089** | 65614** | 492635** | 66501** |
| Error | 19241 | 4546 | 35666 | 20384 | 1811 | 43494 | 1365 |
| Coefficient of variation | 34 | 70 | 25 | 13 | 14 | 26 | 15 |

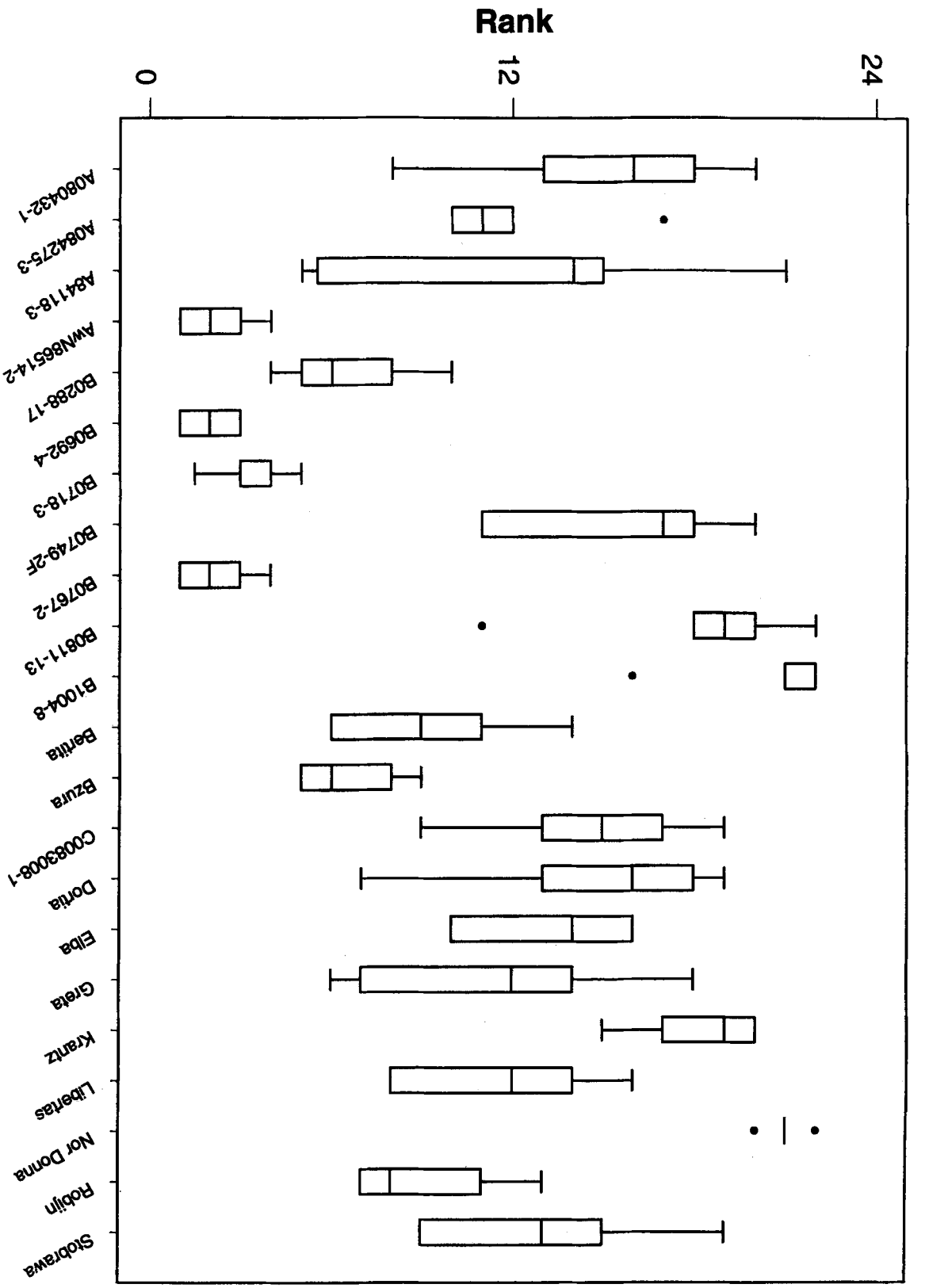


FIGURE 1.

Box and whisker plot of rank for mean area under the disease progress curve (AUDPC) of 22 clones evaluated against US-8 *Phytophthora infestans* at seven locations in the USA in 1997. For each clone, the box represents the interquartile range, the horizontal line within the box represents the median, and the whiskers represent the minimum and maximum values excluding outliers and extreme values, which are represented by solid circles.

TABLE 3—*Mean area under the disease progress curve (AUDPC) for each of 22 potato clones evaluated for percent foliar late blight at seven locations across the United States in 1997 and the rankings of AUDPC (RANK) within locations.*

| | FL | | ME | | MI | | MN | | NY | | ND | | PA | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Clone | AUDPC | RANK | AUDPC | RANK | AUDPC | RANK | AUDPC | RANK | AUDPC | RANK | AUDPC | RANK | AUDPC | RANK |
| AO80432-1 | 315 | 8 | 230 | 20 | 951 | 13 | 1486 | 16 | 401 | 18 | 774 | 13 | 356 | 18 |
| AO84275-3 | 468 | 12 | 143 | 17 | 845 | 10 | 1157 | 10 | 315 | 11 | 698 | 10 | 275 | 12 |
| A84118-3 | 179 | 5 | 41 | 5.5 | 1163 | 21 | 1437 | 15 | 338 | 14 | 685 | 9 | 328 | 15 |
| AWN86514-2 | 51 | 3 | 5 | 4 | 20 | 2 | 7 | 1 | 85 | 3 | 247 | 2 | 6 | 1 |
| B0288-17 | 191 | 6 | 55 | 10 | 84 | 4 | 506 | 6 | 161 | 5 | 669 | 8 | 78 | 5 |
| B0692-4 | 32 | 2 | 2 | 3 | 14 | 1 | 26 | 2 | 63 | 1 | 303 | 3 | 7 | 2.5 |
| B0718-3 | 131 | 4 | 1 | 1.5 | 188 | 5 | 27 | 3 | 95 | 4 | 315 | 4 | 15 | 4 |
| B0749-2F | 673 | 20 | 68 | 11 | 1021 | 17 | 1180 | 11 | 387 | 17 | 964 | 18 | 338 | 16 |
| B0767-2 | 15 | 1 | 1 | 1.5 | 38 | 3 | 50 | 4 | 73 | 2 | 190 | 1 | 7 | 2.5 |
| B0811-13 | 434 | 11 | 242 | 22 | 1123 | 19 | 1772 | 18 | 511 | 20 | 1280 | 19 | 391 | 19 |
| B1004-8 | 771 | 21 | 126 | 16 | 1181 | 22 | 2018 | 22 | 559 | 22 | 1741 | 22 | 496 | 22 |
| BERTITA | 220 | 7 | 97 | 14 | 507 | 6 | 1150 | 9 | 281 | 9 | 535 | 6 | 257 | 11 |
| BZURA | 368 | 9 | 41 | 5.5 | 773 | 8 | 488 | 5 | 234 | 7 | 403 | 5 | 112 | 6 |
| COO83008-1 | 489 | 15 | 96 | 13 | 840 | 9 | 1787 | 19 | 329 | 13 | 957 | 17 | 341 | 17 |
| DORITA | 592 | 18 | 206 | 19 | 681 | 7 | 1653 | 17 | 355 | 16 | 859 | 15 | 286 | 13 |
| ELBA | 382 | 10 | 102 | 15 | 1012 | 16 | 1230 | 12 | 297 | 10 | 925 | 16 | 292 | 14 |
| GRETA | 481 | 14 | 82 | 12 | 1043 | 18 | 839 | 8 | 218 | 6 | 766 | 12 | 149 | 7 |
| KRANTZ | 550 | 17 | 198 | 18 | 988 | 15 | 1903 | 20 | 486 | 19 | 1369 | 20 | 414 | 20 |
| LIBERTAS | 538 | 16 | 52 | 8 | 942 | 12 | 1411 | 14 | 325 | 12 | 788 | 14 | 188 | 8 |
| NORDONNA | 910 | 22 | 236 | 21 | 1145 | 20 | 1995 | 21 | 544 | 21 | 1493 | 21 | 420 | 21 |
| ROBIJN | 477 | 13 | 44 | 7 | 851 | 11 | 597 | 7 | 270 | 8 | 650 | 7 | 252 | 10 |
| STOBRAWA | 637 | 19 | 54 | 9 | 958 | 14 | 1377 | 13 | 348 | 15 | 705 | 11 | 251 | 9 |
| MEAN | 405 | | 96 | | 744 | | 1086 | | 303 | | 787 | | 239 | |

ranking of B0288-17 and Robijn were among the moderately resistant clones along with AO84275-3, Bertita, and Bzura. The median ranking of Dorita placed it among the moderately susceptible clones along with AO80432-1, A84118-3, B0749-2F, COO83008-1, Elba, Greta, Libertas, and Stobrawa. There was little variation for the ranking of NorDonna across locations; it was consistently ranked in the susceptible category along with B0811-13, B1004-8, and Krantz.

Two nonparametric statistics developed by Huehn (1990) are independent of the genotypic value, namely $S^{(1)}_i$, which measures the mean absolute rank differences of a clone over all locations, and $S^{(2)}_i$, which measures the common variance of the ranks. Neither of these statistics was significant for individual clones (Table 4); however, when summed across clones they were significant, indicating that there was genotype x environment interaction on the rankings of the clones. The importance of genotype x environment interactions in this study is apparent in Figure 1. In six of the clones the interquartile range, indicated in Figure 1 as the length of the box, was greater than five rank positions: A84118-3, B0749-2F, Elba, Greta, Libertas, and Stobrawa. The whiskers on the boxes, which indicate the distribution of the ranks across locations minus outliers, further indicated the variability of the rank distributions in this particular test, and hence, the importance of genotype x environment interactions. The whiskers for AO80432-1, COO83008-1, and Dorita exceed the length of their respective interquartile range, indicating the tremendous variation in response among the rankings across locations.

Seven late blight differentials were evaluated at five locations (Table 5). $R_8$ and $R_{multi}$ were relatively resistant to the US-8 genotype. $R_{10}$ was moderately resistant. The remaining differentials, involving different combinations of $R_1$, $R_2$, $R_3$ and $R_4$ genes were moderately susceptible to susceptible.

Clones that were common to both the 1996 and 1997 study show that there was a greater interquartile range in the moderately resistant to moderately susceptible clones in the 1997 study than in the 1996 study (Haynes et al. 1998). The interquartile range of the most resistant clones (AWN86514-2, B0692-4, B0718-3 and B0767-4) was similar between years. A comparison of the interquartile range of the most susceptible clones is not

TABLE 4—*Mean area under the disease progress curve for 22 potato clones evaluated for percent late blight infected foliage at seven locations in the National Potato Germplasm Late Blight Evaluation Trial in 1997, and the tests of significance for mean absolute rank differences ($Z^1_i$) and variance of the ranks ($Z^2_i$).*

| Clone | MAUDPC | $S^{(1)}_i$ | $Z^{(1)}_i$ | $S^{(2)}_i$ | $Z^{(2)}_i$ |
|---|---|---|---|---|---|
| AO80432-1 | 645 | 5.52 | 1.26 | 23.81 | 1.04 |
| AO84275-3 | 557 | 3.24 | 6.51 | 7.24 | 4.17 |
| A84118-3 | 596 | 8.86 | 0.93 | 53.24 | 0.65 |
| AWN86514-2 | 60 | 10.29 | 3.45 | 76.62 | 5.07 |
| B0288-17 | 249 | 7.52 | 0.02 | 46.81 | 0.16 |
| B0692-4 | 64 | 9.05 | 1.17 | 61.90 | 1.80 |
| B0718-3 | 110 | 8.38 | 0.44 | 55.48 | 0.89 |
| B0749-2F | 662 | 5.81 | 0.89 | 23.81 | 1.04 |
| B0767-2 | 53 | 10.00 | 2.81 | 72.90 | 4.08 |
| B0811-13 | 822 | 8.29 | 0.37 | 48.24 | 0.24 |
| B1004-8 | 985 | 10.48 | 3.90 | 79.14 | 5.79 |
| BERTITA | 435 | 6.57 | 0.22 | 31.00 | 0.33 |
| BZURA | 346 | 8.76 | 0.82 | 58.90 | 1.33 |
| COO83008-1 | 691 | 7.62 | 0.04 | 43.33 | 0.04 |
| DORITA | 662 | 4.95 | 2.19 | 18.95 | 1.74 |
| ELBA | 606 | 6.19 | 0.50 | 26.90 | 0.68 |
| GRETA | 511 | 5.81 | 0.89 | 24.62 | 0.94 |
| KRANTZ | 844 | 8.57 | 0.61 | 62.81 | 1.95 |
| LIBERTAS | 606 | 4.19 | 3.83 | 12.14 | 3.03 |
| NORDONNA | 963 | 10.00 | 2.81 | 69.90 | 3.37 |
| ROBIJN | 449 | 6.00 | 0.68 | 25.90 | 0.79 |
| STOBRAWA | 619 | 7.14 | 0.01 | 34.24 | 0.14 |
| SUM | | | 34.35* | | 39.24* |

*The Z statistics are measures of stability. The tests of significance of the sum of the $Z^{(1)}_i$ or $Z^{(2)}_i$ are compared to $\chi^2$ value of 33.92. Individual $Z^{(1)}_i$ or $Z^{(2)}_i$ are compared to a $\chi^2$ value of 9.32.

possible since three of the most susceptible clones were evaluated only in 1997. However, it does appear from both the 1996 and 1997 studies that the interquartile range of the most resistant and the most susceptible clones in any given year is less than the interquartile range of the moderately resistant and moderately susceptible clones. In general, clones that were resistant in one location were resistant in all. Clones that were susceptible in one location were susceptible in all. The greatest variation occurred in the intermediate categories, as might be expected. It is in these categories that minor differences due to environment, host genotype, pathogen genotype or combinations of any of these factors, will have the best chance of being expressed. It is also in these categories, where the differences in the absolute values of the ratings are small, that minor fluctuations in the estimation of percent infected foliage will be magnified using a ranking system. A 5% variation in estimating AUDPC in the mid-ranges could translate into a much different ranking from a 5% variation in estimating AUDPC in the low ranges. However, Jeger and Viljanen-Rollinson (2001) have suggested that for typical sigmoid disease-progress curves, an estimate of AUDPC based on two data points from distinct growth stages provides as much information as from repeated measurements. The variations that occur in the intermediate ranges of resistance and susceptibility might be of interest to pathologists studying various mechanisms of partial resistance, but for classifying the reactions of clones to infection, the present method is completely satisfactory. Studies involving different mechanisms of partial resistance would not be conducted in the same manner as this study to classify the reactions of the clones to the pathogen.

In contrast to the results of the 1996 study, there was evidence for genotype x environment interactions on the rankings of AUDPC for these 22 clones. This may have been the result of having more clones in the test, and therefore, greater ability to find significant differences; it may indicate that there was more variability in the US-8 strains used to inoculate these plots; or it may indicate that there was greater environmental variation across the locations in 1997 which affected the host-pathogen interaction. Although no single clone contributed significantly to this variation, it was possible to surmise from the box and whisker plot, that this significant overall interaction was arising because there was less variation in the rankings across environments for the resistant and susceptible clones compared to the

TABLE 5—*Mean area under the disease progress curve for seven late blight differentials evaluated against US-8* Phytophthora infestans *at six locations in the United States during 1997.*

| Late Blight Differential | ME | MI | MN | NY | ND | PA |
|---|---|---|---|---|---|---|
| $R_1R_2R_3R_4$ | 95 | 645 | 1528 | 460 | 1016 | 467 |
| $R_1R_2R_4$ | 81 | 906 | 1707 | 342 | 1051 | 391 |
| $R_1R_3R_4$ | 51 | 745 | 1262 | 299 | 602 | 286 |
| $R_3$ | 110 | 1037 | 1899 | 560 | 1538 | 403 |
| $R_8$ | 5 | 59 | 0 | 20 | 23 | 2 |
| $R_{10}$ | 28 | 459 | 355 | 280 | 473 | 61 |
| $R_{multi}$ | 11 | 35 | 0 | 13 | 0 | 0 |

moderately resistant and moderately susceptible clones. This is compelling evidence of the need for national tests of this kind.

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