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ABSTRACT
A field study in two regions of Peru was conducted to determine how host-diversity effects on potato late blight varied geographically. Foliar disease severity was evaluated separately for the potato varieties in mixtures as well as in the single-variety plots. The TAUDPC (truncated area under the disease progress curve) and RMR (relative mixture response) for each site were analyzed separately using SAS mixed effects model procedures. While there was little difference between the sites in the 1997-1998 season, host-diversity effects were generally greater near Huancayo than near Cajamarca in the 1998-1999 season. Estimates of host-diversity effects from studies in Oregon and Ecuador were also compared with results for Peru. Host-diversity effects for reduced disease were generally greater for sites where we predicted lower levels of outside inoculum.

1. INTRODUCTION

A host-diversity effect in an epidemiological context is defined in terms of the disease level (severity or incidence) in a mixture of host varieties compared with the mean disease level in single variety populations of each of the host varieties. The levels in single-variety populations are appropriately weighted for comparison depending on the proportion of the mixture composed of the varieties. If there is a host-diversity effect, it will tend toward reduced disease in mixtures compared with single variety populations, but increased disease is possible in some circumstances. The host diversity effect on potato late blight severity in a single geographic site was previously studied by Andrivon et al. (2003), Garrett and Mundt (2000), and Garrett et al. (2001).

This field study was designed to determine whether host-diversity effects on potato late blight varied geographically. At Quito, near the equator, potatoes are grown year round and the level of outside inoculum in potato growing areas is likely to be high. Moving from Cajamarca in the north of Peru to Huancayo in central Peru, potato production becomes more seasonal and it would be expected that the amount of ambient inoculum would decline. Our hypothesis was that the likely higher level of inoculum at the lower elevation, more northerly Cajamarca sites in our study would result in a smaller host-diversity effect than would be observed at the higher elevation, more southerly Huancayo sites. The results obtained in Peru were compared to previous results obtained in the USA (Garrett and Mundt, 2000) and Ecuador (Garrett et al., 2001) using a meta-analysis approach (Cooper and Hedges, 1994). Our hypothesis was that the more seasonal the area was for potato production, the greater the host-diversity effect for reduced late blight would be.

2. MATERIALS AND METHODS

Field studies in Huancayo and Cajamarca. One to two sites in farmers' fields were established near each of Huancayo (S 12°, W 75°) and Cajamarca (S 07°, W 78°), Peru, during the 1997-1998 and 1998-1999 field seasons. The sites near Huancayo were at a higher altitude than the sites near Cajamarca, in addition to being further south of the equator. Mixture plots were planted in ¼ of a susceptible variety and ¾ of a more resistant variety, with the varieties arranged systematically to maximize the distance between susceptible varieties. The different mixtures studied are listed in Table 1. At each site, two different mixtures were planted along with the pure stands of the component varieties. Because of seed tuber limitations, the same mixtures could not be planted at every site during the first season. Research plots were arranged in a randomized complete block design with four replicates. Plots were 4 m x 4 m, consisting of 12 plants in each of four 1 m wide rows. Plots were spaced at least 4 m apart from each other on all sides and borders were planted with oats (*Avena sativa*) near Huancayo and rye (*Secale cereale*) near Cajamarca. To allow the plants to grow before the epidemic began, protective fungicides were applied at the beginning of the season. All inoculum was naturally occurring and epidemics began late in the 1998-1999 season because of unusually dry conditions.

Percentage foliar disease severity was evaluated separately for the varieties in mixtures as well as in the single-variety plots. The 90% TAUDPC (area under the disease progress curve truncated at the point when disease severity in the most susceptible variety reaches 90%) was used in this study. The rationale for using TAUDPC rather than the usual AUDPC and the formula for calculating TAUDPC were described in Garrett et al. (2001).

The design of the experiment within each site-year was a randomized complete block design. The general linear model $Y_{ijk} = s_i + b_j + \tau_k + \varepsilon_{ijk}$ was fit to the data, where Y_{ijk} is the TAUDPC for the k^{th} treatment (variety or variety mixture) within the j^{th} block in the i^{th} site, s_i represents the effect of the i^{th} site (i = 1, 2, 3, 4 in 1997-1998; i = 1, 2, 3 in 1998-1999); b_j, the effect of the j^{th} block (j = 1,…,4), and τ_k, the effect of the k^{th} treatment (i = 1, …, 8 in 1997-1998; i = 1, …, 12 in 1998-1999); and ε_{ijk}, residual error. During the 1997-1998 season, there were four single-variety treatments and two mixture treatments with two readings each (one for each of the two variety components of the mixture); during the 1998-1999 season, there were four single-variety treatments and four mixture treatments with two readings each. Because there was a tendency for the variance of the response to increase with the mean response for a given treatment, Levene's test was used to test the equality of variance among treatments. If the variances were significantly heterogeneous, then the covariance structure was specified by using the SAS MIXED procedure (SAS Institute Inc., Cary, NC). The SAS programming code used was as in Garrett and Mundt (2000): proc mixed data = dataname; class site blk cv code; model taudpc=site | trt /noint solution ddfm=kr; random blk(site); repeated/ group=code; where code is defined to be the grouping of the variances for all treatments based on the output generated from

Levene's procedure. The TAUDPC in mixtures were compared to those in monocultures for each mixture component of each mixture using planned linear contrasts. For example, a contrast statement designed for testing the TAUDPC in a mixture of K and Y to those of K and Y in monocultures was: contrast 'KY-3/4K-1/4Y' trt 1 -3/4 -1/4.

Meta-analysis comparing results from Peru, Corvallis and Quito. Meta-analysis refers to the statistical analysis of a large collection of analysis results from individual studies for the purpose of integrating the findings (Cooper and Hedges, 1994). We considered the results of the studies near Cajamarca and Huancayo in combination with results from studies of host-diversity effects on late blight near Corvallis, Oregon, USA (Garrett and Mundt, 2000), and near Quito, Ecuador (Garrett et al., 2001). From the studies in Peru, we had 20 mixture-site-year combinations. We selected the treatment from the Quito study that was most directly analogous to the Peruvian treatments: a mixture of ¾ Santa Catalina (resistant) and ¼ Uvilla (susceptible). This mixture was studied at three different sites near Quito. The Corvallis study was of a mixture of ¾ resistant breeding selection A90586-11 and ¼ susceptible Red LaSoda. This mixture was studied for two imposed inoculum patterns (focal and general) in two different years near Corvallis, for a total of four inoculum pattern-year combinations. From these studies we can see an overall tendency for a host-diversity effect for reduced late blight.

First, we considered how the likely level of outside inoculum may have influenced the host-diversity effect. To this end, we used what Garrett et al. (2001) termed the relative mixture response (RMR) defined as ((TAUDPC in mixture)/(weighted mean TAUDPC in single-genotype stands)) as the response variable. The RMR allows for comparisons between host-diversity effects in settings that may have very different overall levels of disease. Since we did not measure the inoculum levels directly, we could only predict them based on the degree of seasonality of the different areas and the weather conditions of the year being studied. For this analysis, we ranked the locations, in order of increasing predicted inoculum levels, as Corvallis, Huancayo, Cajamarca, and Quito. These levels also reflect the distance from the equator. In addition, Huancayo's greater altitude makes seasonality relatively more apparent there. For comparisons of years, we assumed that drier years would experience lower inoculum levels. For Corvallis, 1998 was drier than 1997; for Huancayo and Cajamarca, the 1998-1999 season was drier than the 1997-1998 season. Note that our ranking of the predicted inoculum level in a wet season in Corvallis vs. a dry season in Huancayo is somewhat arbitrary. We used a weighted regression analysis to analyze RMR as a function of predicted inoculum level where the weight is the inverse of the standard error for estimating RMR for each site year. In other work, we also considered the influence of the difference in resistance between the two mixture components and these results will be discussed in more detail in another publication (Garrett et al., in preparation.)

3. RESULTS AND DISCUSSION

Peruvian field studies. Results based on the TAUDPC for the four sites in the 1997-1998 did not show any significant site and variety interaction effects ($P = 0.16$). We therefore tested the host-diversity effect averaged over the four sites for each variety mixture. The P-values for tests of equal variety means were reported in Table 2. No significant host-diversity effects were found at a 0.05 significance level. This may be partly because we inadvertently selected some mixtures for Huancayo (Chagllina-Yungay and Chagllina-Tomasa) that had relatively small differences in resistance to the local pathogen population.

In the 1998-1999 season, a set of mixtures, selected for large differences in resistance between components, was studied at all three sites. Due to the significant site and variety interaction effect ($P < 0.0001$), host-diversity effects were tested within each site for all variety mixtures with the P-values listed in Table 3. In this season, both sites near Huancayo showed approximately equal or greater evidence of host-diversity effects for reduced disease than the Cajamarca site. This difference between sites probably resulted at least in part because the epidemics at Huancayo were delayed longer by drought than the epidemic at Cajamarca. The difference between disease severity in resistant and susceptible varieties in single-variety stands was also much greater at Huancayo than at the Cajamarca site in that year.

Meta-analysis comparing Peru, Corvallis, and Quito. Results based on the weighted regression analysis for RMR showed that there was a general tendency for greater host-diversity effects (lower RMR) for reduced disease severity at the sites where we expected lower levels of outside inoculum (Fig. 1). The test for no relationship between RMR and the predicted outside inoculum level yielded a P-value of 0.0008. Responses were quite variable for some locations, however, particularly for Cajamarca in 1998. In other work there was a clear trend toward greater host-diversity effects for reduced disease for mixtures with greater differences in levels of resistance among components (Garrett et al., in preparation).

The two predictors are confounded, though, since the Huancayo sites (in 1999) and the Corvallis sites, sites with predicted lower levels of inoculum, tended to have greater differences between components. Likewise, the Quito and Cajamarca sites, sites with predicted high levels of inoculum, tended to have smaller differences between components. It may be that sites with higher levels of outside inoculum will tend to have smaller differences in resistance between varieties, especially if the resistance of the resistant variety is based on lowered inoculum production. Greater host-diversity effects than predicted might occur if there are race-specific differences in resistance between the components; in that case, even components with the same TAUDPC in single variety stands may experience reduced disease in mixture. Smaller host-diversity effects than predicted might occur because of effects such as competition between potato varieties.

4. CONCLUDING REMARK

The host-diversity effect for reduced disease was generally greater at the sites where we predicted lower levels of outside inoculum.

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REFERENCES

1. Andrivon, D., Lucas, J.-M., and Ellissèche, D. 2003. Development of natural late blight epidemics in pure and mixed plots of potato cultivars with different levels of partial resistance. Plant Pathology 52:586-594.
2. Cooper, H., and Hedges, L. V., 1994. The Handbook of Research Synthesis. Russell Sage, New York.
3. Federer, W. T. 1993. Statistical Design and Analysis for Intercropping Experiments. Volume I: Two Crops. Springer-Verlag, New York.
4. Garrett, K. A., and Mundt, C. C. 1999. Epidemiology in mixed host populations. Phytopathology 89:984-990.
5. Garrett, K. A., and Mundt, C. C. 2000. Effects of planting density and cultivar mixture composition on stripe rust of wheat: an analysis accounting for limits to the replication of controls. Phytopathology 90:1313-1321.
6. Garrett, K. A., and Mundt, C. C. 2000. Host diversity can reduce potato late blight severity for focal and general patterns of primary inoculum. Phytopathology 90:1307-1312.
7. Garrett, K. A., Nelson, R. J., Mundt, C. C., Chacon, G., Jaramillo, R. E., and Forbes, G. A. 2001. The effects of host diversity and other management components on epidemics of potato late blight in the humid highland tropics. Phytopathology 91:993-1000.
8. Garrett, K. A., Zúñiga, L. N., Roncal, E., Forbes, G. A., Mundt, C. C., Su, Z., and Nelson, R. J. In preparation. Host-diversity effects on potato late blight: a meta-analysis of effects in Peru and along a geographic gradient.
9. Littell, R. C., Milliken, G. A., Stroup, W. W., and Wolfinger, R. D. 1996. SAS System for Mixed Models. SAS Institute Inc., Cary, North Carolina.

Table 1. Potato variety mixtures included in the study of host-diversity effects on potato late blight near Huancayo and Cajamarca, Peru. The degree of resistance and susceptibility is indicated in parentheses (HS = highly susceptible, S = susceptible, MS = moderately susceptible, MR = moderately resistant, R = resistance, HR = highly resistant).

Resistant variety	Susceptible variety
¾ Kory (R)	¼ Liberteña (MS)
¾ Chagllina (MR)	¼ Yungay (S)
¾ Chagllina (MR)	¼ Tomasa (HS)
¾ Perricholi (R)	¼ Tomasa (HS)
¾ Amarilis (HR)	¼ Yungay (S)
¾ Amarilis (HR)	¼ Tomasa (HS)
¾ Kory (R)	¼ Tomasa (HS)
¾ Kory (R)	¼ Yungay (S)

Table 2. P-values from testing the null hypothesis of no host-diversity effect. Results are shown for four sites in the 1997-1998 season.

Variety mixture	P-value
Chagllina and Yungay	0.9641
Kory and Liberteña	0.2471
Chagllina and Tomasa	0.6434
Perricholi and Tomasa	0.6182
Amarilis and Yungay	0.6566

Table 3. P-values for testing the null hypothesis of no host-diversity effect. Results are shown for three sites in the 1998-1999 season.

Site	Sicaya (Huancayo)	Pazos (Huancayo)	Santa Clotilde (Cajamarca)
Variety mixture		P-value	
Amarilis and Tomasa	<0.0001	0.0017	0.0019
Amarilis and Yungay	0.0078	0.2092	0.3214
Kory and Tomasa	<0.0001	0.0005	0.0009
Kory and Yungay	0.0046	0.1857	0.1528

Figure 1. The relative mixture response (RMR; ratio of late blight severity in mixture over late blight severity in single-variety stands) based on the TAUDPC with d=90 for each site-mixture-year combination versus the predicted level of outside inoculum. If there was no host-diversity effect, the expected RMR was equal to one. The level of inoculum was predicted qualitatively based on the climate of an area and the degree of seasonality of potato production there. Squares indicate Huancayo sites in 1997-1998, diamonds indicate Huancayo sites in 1998-1999, triangles indicate Cajamarca sites in 1997-1998, and circles indicate the Cajamarca site in 1998-1999. Observations from previous studies (Garrett and Mundt 2000 and Garrett et al. 2001) are also included: stars indicate Quito sites, '--'s indicate Corvallis sites with general inoculum, and '-'s indicate Corvallis sites with focal inoculum.