ORGANIC FARMING RESEARCH FOUNDATION

Project report submitted to the Organic Farming Research Foundation:

Project Title:

Public Breeding for Organic Agriculture – Screening for Horizontal Resistance to Late Blight in Tomato

FINAL PROJECT REPORT

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Project Summary

We developed a reliable test to identify and quantify intermediate levels of resistance to Late blight in tomato populations as well as within exceptional individuals contained in these genetically segregating populations. Following this we made selections and attempted to make cross-pollinations between resistant individuals in the hopes of stacking favorable genetic factors for higher levels of Horizontal Resistance (HR) in subsequent populations.

Onset of Late blight disease symptoms was quite sudden and progressed swiftly. Our weekly disease severity readings were successful in statistically separating the most resistant tomato accessions from the rest of the accessions. However, we were not able to show as fine of a distinction in degree of resistance between accessions as hoped due to the severity and speed of the disease epidemic. We were successful in selecting and gathering seed from putative HR individuals that did exhibit less severe symptoms. Cross-pollinations attempted at the onset of disease were not able to mature to seed as the severity of Late blight eventually overran all plants in the test, debilitating their ability to ripen fruit. A number of logistical experimental changes were made for the continuation of the project in 2005.

Outreach was enhanced dramatically by the inclusion of students from The Evergreen State College in Olympia whose farm we used as one of our test sites. Student participation spread beyond the agro-ecology program to include students in math and statistics courses. The project was incorporated into curriculum and continuing into its second year, continues to provide a research model that was previously unavailable to farm students.

Introduction and Objectives

Late blight of tomato and potato, caused by the fungal pathogen *Phytophthera infestans,* is currently the most destructive disease of tomato (*Lycopersicon esculentum*) in the Pacific Northwest. Geographically this includes regions stretching from the San Francisco Bay in California to the coastal islands of British Columbia. The importance of this disease, which has had far-reaching effects worldwide since causing the Irish Potato Famine in the 1840s, has increased substantially in the early 1990s when new clonal lineages of the A2 mating type migrated from the Toluca Valley of Mexico (Fry and Goodwin, 1997). Previous to this only genotypes of the A1 mating type of *P. infestans* had been detected outside of the Toluca Valley. The migration of the A2 genotypes (which are able to sexually mate with A1 genotypes, thereby creating new genetically recombinant genotypes) brought a sharp increase in the number of *P. infestans* genotypes during the 1990s and 2000s in many environments where Late blight (LB) is a problem. Tomato researchers have reported an increase in both the virulence and prevalence of

many new genotypes of the pathogen from California (Nunez, 2002), Northwestern Oregon/Southwestern Washington (Miles, 2003), Skagit Valley of Washington (Inglis, 2003) and in North Carolina (Gardner, 2003).

In the Willamette Valley of Oregon, Western Washington, and Western British Columbia, most organic farmers will not attempt to grow a tomato crop in the field due to expectations of heavy losses from this disease. Growers either abandon tomatoes as a viable crop or grow the crop in high tunnels with much added expense. Early maturing tomato cultivars like 'New Hampshire Surecrop' and 'Legend' that are marketed with claims of resistance to LB have single genes for resistance (*Ph1* and *Ph2* respectively) that are often easily overcome by the new, genetically distinct genotypes of *P. infestans*. Newer tomato varieties are being released by North Carolina State University and the Asian Research and Development Center in Taiwan that combine multiple resistance genes (*Ph2* and *Ph3*) in a single breeding line or hybrid cultivar and currently confer much higher levels of resistance to Late blight. Unfortunately, the breeding lines and hybrids from these programs have two serious drawbacks: 1) This tomato germplasm is late-maturing and only suitable for the southernmost range of the northwest growers and 2) the resistance they confer is from single, "vertical resistance" (VR) genes which are often "overcome" by chance mutation of the pathogen. Hence, it is imperative that we develop fresh market tomatoes that are early enough in their maturity to take advantage of the market season and that have genetically elastic "durable resistance" that won't be easily overcome by genetic changes in the pathogen population.

A number of plant breeders improving crop varieties for the challenges of organic cropping systems consider polygenic, quantitatively inherited disease resistance or "horizontal resistance" (HR) to be appropriate for issues of sustainability in agriculture (Jones, 2004). HR is conferred by a number of genetic factors in the host that slow the rate and extent of the disease's parasitism, limiting the ability of the pathogen to become established, grow, and reproduce (Vanderplank, 1963). The use of HR crop varieties establishes a more effective ecological balance in the field between the pathogen and host; the disease is able to survive but is present at manageable levels. Whereas the use of VR crop varieties creates an environment in which the pathogen is exposed to selection pressure that often favors more virulent genotypes within the pathogen population, potentially leading to epidemic outbreaks of disease in subsequent generations.

Materials and Methods

Field procedures: This experiment was planted in two locations with a parallel schedule of greenhouse seeding, transplanting to the field, and trellising. Locations were Old Tarboo Farm (OTF) in Quilcene, Washington and The Evergreen State College Farm (TESCF) in Olympia, Washington. The field plot layout used in this study was a Randomized Complete Block Design (RCBD) with three replications using twelve

tomato accessions (six cultivars and six breeding populations) as treatments. Accessions include five cultivars and six populations that had previously demonstrated some level of resistance to Late blight in trials conducted by Washington State University in Mt. Vernon (Inglis *et al.* 2000) and in independent trials conducted by J. Navazio in Bellingham, Washington. Each accession was represented by 12 plants per accession, planted in double rows of 6 plants at 0.5 m spacing within rows and between rows. Border rows were single rows along the east and west length of the field and three plants at the start and end of each row at the north and south ends of the experiment. Plants were staked in a standard "basket weave" pattern onto bamboo stakes that ran the length of each row. Tying of plants was done on a weekly schedule for four weeks.

The commercial tomato cultivars with putative resistance to Late blight (LB) included 'Legend', Juliette', 'Slava', 'Stupice', and 'NC03220'. 'Juliette' is a commercial hybrid bred by the Known You Seed Company of Taiwan that exhibited moderately high levels of resistance in our Bellingham trials. 'Legend' is a popular home garden variety with the Ph2 gene for LB resistance that was bred by Oregon State University. 'Legend' is touted for having "blight resistance" in regional garden seed catalogues. 'NC 03220' is an experimental hybrid from North Carolina State University that combines the Ph2 and Ph3 resistance genes for LB. It has exhibited superior resistance to LB under heavy disease pressure in the field in North Carolina (Gardner, 2003). 'Slava' and 'Stupice' are both heritage varieties from the Eastern Europe that are reported by farmers to have moderate levels of resistance. 'Siletz' is an Oregon State University release that served as our susceptible check variety. 'Siletz developed severe LB disease symptoms in evaluation trials at the Mt Vernon research station of Washington State University (Inglis *et al.* 2000). Also included were six tomato populations known as the Bellingham Late Blight Populations (BLBP). These experimental populations were derived from crosses and segregating tomato germplasm and had exhibited moderate levels of LB resistance in research conducted by J. Navazio in Bellingham, Washington[1].

Seedling plants were produced in greenhouses using standard organic cultural techniques. At six weeks of age seedling plants were transplanted to the field in both locations and grown using standard organic cultural techniques. Irrigation was applied on a weekly schedule using overhead sprinklers in the hope that it would encourage the spread of disease. Plants were checked twice weekly for disease symptoms and the onset of fruit ripening. By 2 August the first putative disease lesions were discovered on several accessions in the TESCF plot. Samples were taken and sent to the WSU Plant Clinic (WSUPC) at the WSU Puyallup Research and Extension Center in Puyallup and

[1] Previous to this study, the BLBP had gone through three cycles of selection for Late blight resistance under heavy disease pressure. These populations also have early maturity, superior culinary quality and appropriate fresh market fruit type, all of which coupled with Late blight resistance are important for organic fresh markets in the Northwest.

subsequent samples were later confirmed to be Early blight (*Alternaria solani*) by the Plant Pathology Diagnostic Clinic (PPDC) at the University of Wisconsin in Madison. Early blight (EB) was also found and confirmed on 20 August at the OTF plot. Although we had not intended to evaluate the progression of EB, we observed considerable variation between accessions in these plots for disease symptoms to this malady and decided to score for levels of resistance until LB appeared. EB had spread sufficiently through the TESCF plot by 16 August to take our first reading. Two subsequent evaluations with scores taken were completed at this plot on 23 August and 27 August before appreciable levels of LB commanded our attention. After confirming the presence of EB in the OTF plot on 20 August we were able to score EB on 28 August and 4 September at OTF.

LB was observed on 23 August at the TESCF and its identity confirmed on 27 August by PPDC. We evaluated LB at TESCF at two weekly intervals, on 30 August and on 7 September. Unfortunately scoring for LB at TESCF was discontinued one week later as most accessions had fully succumbed to the effects of the disease. LB symptoms were first noted at the OTF plot on 7 September but although LB quickly spread in several sections of the plot, the damage was highly localized and did not spread evenly across the plot. This made our ability to make meaningful comparisons impossible. Therefore no LB scoring was performed at OTF.

Scoring was done using a 1 to 9 scale; with 1 representing the most diseased accession in the experiment for that reading and 9 represented the least diseased accession in the experiment for that reading. This disease scoring is independent of other readings and is based purely on the relative extent of the disease symptoms for that particular plot, under those particular environmental conditions, for that specific day.

Analysis of data: Analyses of data for levels of resistance to EB and LB was carried out using Kruskal-Wallis test for non-parametric data. The K-W test was chosen because it does not require the data within groups to be distributed normally. K-W is a test to determine if two or more treatments differ only with respect to the distribution median and assumes that there is not difference in median values for all treatments as the null hypothesis. The K-W test is the non-parametric analog to the ANOVA test for parametric data sets. The analysis of scores for resistance to LB at the TESCF plots is represented in Table 1. Tables 2 and 3 present the analyses for resistance to EB at TESCF and at OTF respectively. To simplify the data presentation, these tables represent the mean ranks of resistance to EB and LB for all observation dates.

Results and Discussion

Late blight results: Late blight epidemics may occur quite suddenly and progress over a short period of time (Gallegly, 1952; Gardner, 2003). For this reason, researchers have

noted some of the difficulties of selecting for levels of resistance in the field (Gallegly, 1960). We experienced a different challenge to collecting data in each of our two field locations. At OTF the spread of disease tended to be quite localized and did not spread through the field in an even fashion, thereby eliminating any chance of recording accurate data on the relative resistance to disease. At TESCF the spread of the disease was even, however the rate at which LB spread through the experimental plot was too rapid to allow for more than two weekly readings. From 30 August, when we performed our first LB reading, to 14 September we performed LB readings twice at TESCF. By 18 September there was overwhelming destruction due to LB epidemic conditions with total necrosis in most accessions and it was realized that we couldn't perform a third reading due to the lack of variability for resistance between accessions. In comparison to the destruction imposed by LB over a number of seasons, this outbreak at TESCF was indeed the most rapid and severe sweep of this disease in a tomato field that the senior author had ever witnessed. Certainly this epidemic was much more rapid in its spread than in several seasons of selection of the Bellingham Late Blight Population (BLBP) in his Bellingham nursery. This LB outbreak was also considerably quicker in its spread through the TESCF plot than had been witnessed in D. Inglis' plots in Mt. Vernon in 1999 (Inglis *et al.* 2000).

The results of our rankings for severity of LB symptoms (Table 1) across two scoring dates demonstrated a significant block effect due in part to exogenous factors (see conclusions) in the experiment. For this reason we used the Kruskal-Wallis (K-W) test for non-parametric data. From this test we get a clear indication that 'NC 03220' (411), 'Juliet' (407), and 'Stupice' (410) are more resistant to LB than other accessions in the test. The 'NC 03220' hybrid, with the *Ph2* and *Ph3* genes combined, was logically the most resistant at this time although its resistance was eventually overwhelmed by late September. 'Juliet' (from the Known You Seed Company in Taiwan) also has strong resistance, presumably from some combination of Ph genes (we have attempted to contact the company for information, thus far to no avail). 'Juliet' also succumbed to the disease by late September. 'Stupice' has had numerous anecdotal reports of exhibiting moderate levels of resistance by organic farmers in our region across the past several years. While 'Stupice' did have LB lesions soon after LB was first noted on 23 August in the TESCF plot, the lesions were slower to develop, were smaller in size (diameter), and did not spread as rapidly through this accession. These results were also noted for the other Eastern European variety 'Slava' (409) and for 'Legend' (408), both of which along with several of the BLBP accessions did exhibit a continuum of less disease symptoms than our susceptible check 'Siletz' (412).

Samples of tomato leaf tissue with LB symptoms were taken on two occasions at the TESCF plots and sent to W.E. Fry's laboratory at Cornell University for genotype identity. In both cases the results from Dr. Fry's lab with DNA fingerprint analyses using

gel electrophoresis revealed that the genotype of our samples was US-11. The US-11 genotype has been shown to be much more aggressive on tomato than any of the other genotypes of *Phytophthera infestans* (US-7, US-8, or US-14) that have been found in Western Washington in the last decade (Dorrance *et al*., 1999).

The disappointing showing from Bellingham Late Blight Population (BLBP) accessions for LB resistance in this experiment (Table 1; accessions # 401 – 406) might be explained by the extreme aggressiveness of the pathogen in comparison to the *P. infestans* isolates that these accessions had been selected for resistance to in Bellingham. In 2001 the senior author had unsuccessfully submitted leaf samples with Late blight symptoms to WSU in an attempt to identify a genotype of the pathogen in the Bellingham nursery, but the sample was mislaid and the identity of the isolate was never identified. The BLBP accessions however always appeared much less affected by the Bellingham *P. infestans* populations.

For a researcher evaluating this material for potential LB resistant breeding stock there was variation in resistance to LB in a number of accessions that is not revealed in the data means as reported. There were individual plants of 'BLBP-1' (401) and 'Legend' that had considerably more resistance to LB in this test than the population mean across the three replications. Hand-pollinated crosses were made with these "more resistant" individuals (within and between populations); however due to the rapid progress of the disease these hybridized fruits were not able to mature seeds before disease caused net necrosis and death in all selected plants. Fortunately, these individual plants were marked and seed was saved from these resistant plants (tomatoes are primarily naturally self-pollinated) and will constitute new breeding stock, possibly making crosses in the greenhouse this winter. Ultimately, this material will constitute new accessions in future LB screening plots.

Early blight results: As previously stated the appearance of EB in our plots was unexpected and initially viewed as a potential hindrance to our work with LB. The occurrence of EB in western Washington is rare, although its appearance in commercial tomato fields does seem to be on the rise in the last few years (Inglis, 2003). By 16 August the EB had spread evenly through the TESCF plot, affecting ten of the twelve accessions to some degree. As we noted a range in the degree of disease symptoms across these accessions, we decided to score for levels of resistance until the advent of LB. As previously described we also scored for EB in the OTF plot. The results garnered from these data indicate that six accessions in each plot exhibited significantly higher levels of resistance than the other accessions. In the TESCF plot 'BLBP-1' (401), 'BLBP-2' (402), 'BLBP-3' (403), 'BLBP-6' (406), 'Juliet', and 'NC 03220' were resistant (Table 2), while in the OTF plot 'BLBP-1', 'BLBP-2', 'BLBP-5' (405), 'Juliet', 'Legend', and 'NC 03220' were resistant (Table 3). By comparing the accessions with the highest mean

ratings for resistance to EB in both plots it becomes evident that there are three standout accessions that scored the highest in both tests, 'BLBP-1', 'Juliet', and 'NC 03220' (Tables 2 & 3). The high level of resistance to EB in 'NC 03220' is due to a high level of HR to EB that was transferred into the parental lines of this hybrid from 'Campbell 1943' at the NCSU Mountain Horticultural Crops Research and Extension Station in Fletcher, NC (Gardner, 2004). The source of resistance in 'Juliet' from the Known You Seed Company in Taiwan is unknown (again, we have attempted to contact the company for information, thus far to no avail). While the HR type of resistance in BLBP-1 (as well as 'BLBP-1', 'BLBP-2', 'BLBP-3', 'BLBP-5', and 'BLBP-6') was first noted when these materials were screened (and selected) by J. Navazio in a disease nursery for the EB-Septoria leaf spot complex in Iowa City, Iowa in 2002, selections or crosses of plants specifically for their ability to resist EB were not made during these experiments. However, individual segregating plants of 'BLBP-1' and 'Legend' that were more susceptible to EB and therefore had more necrotic leaf tissue from earlier EB lesions were definitely selected against when we did LB resistant selections in these accessions during the LB epidemic.

Conclusions

The success of this experiment is in demonstrating that there is tomato germplasm that has levels of resistance to a very pathogenic genotype of LB under field conditions. Resistance to the US-11 genotype of Late blight was found in both 'NC 03220' with two known resistance genes (*Ph2* and *Ph3*), and in 'Stupice' which has a significant level of HR to LB ('Juliet' was also resistant but from as yet unidentified factors.) 'NC 03220' and 'Juliet' were extremely late maturing in western Washington, which is a serious hindrance to their use as breeding stock for the Northwest. 'Stupice' however is well adapted to the Northwest's short growing season and has a consistent and early yield of 2 to 3 ounce fruits. It exhibited considerable genetic variation for HR, fruit shape, and flavor and would be an excellent population to select within for increased HR and superior quality attributes. LB resistant selections were made for further testing among segregating 'BLBP-1' plants that exhibited resistance at the TESCF plots. LB resistant segregants were also found among 'Legend' plants at a fairly advanced stage of the epidemic and seed was saved for further testing.

Overall, however, the LB evaluation phase of the trial was much too fleeting as the time between our initial reading of the disease symptoms and the point at which the disease had grown to epidemic proportions did not allow us take an adequate number of observations. In evaluating for HR, it is very important to monitor how the putative resistant plant holds up to disease pressure and if the resistance is able to significantly slow the progress of the disease over time. Therefore in future LB work in the field we will collect data on a much more frequent schedule to assure a more accurate appraisal of the progression of disease which will translate into a more robust statistical analysis.

This experiment also successfully identified a range of materials that are resistant to EB. Among the most resistant were 'NC 03220' and 'Juliet' which were also at the top for LB resistance. 'NC 03220' showed little or no EB symptoms through the duration of the experiment. But as stated above both 'NC 03220' and 'Juliet' were much too late maturing in the coastal Northwest. Several BLBP accessions did have significant resistance to EB, notably 'BLBP-1', which also has HR for LB and will be selected for resistance to both diseases in future experiments.

As the analysis for this experiment was difficult due to a significant block effect there are a number of design changes that could be made to minimize the effects of exogenous factors in future tests. The present design of the TESCF experimental site included two unexpected perpendicular gradients across the plot. Isolation of each gradient and its influence on each replication's treatment response was limited because of extremely rapid disease progression and a resultant lack of data. Modification recommendations for future site profiles and larger data sets will help identify and eliminate background gradient noise from the experimental treatment responses. These modifications will transform random external factors (gradients) to fixed experimental factors and make data analysis much more reliable.

Due to difficulties with LB overwhelming the TESCF plot in three weeks and the problem of not collecting data in the OTF plot because of an uneven spread of the disease, we are considering conducting a series of disease screenings in growth chambers at The Evergreen State College. In these experiments we would inoculate young plants of each of the experimental accessions with LB in order to determine relative levels of resistance. The selected individuals could then be intermated and resulting progeny screened in the field. Through identifying the most resistant segregants for HR to LB from among the best parental stock that we have identified it is certainly possible to increase the quantitative levels of this resistance among the subsequent generations of the tomato germplasm we are breeding. If we can indeed couple this resistance with HR for EB in suitable fresh market tomatoes in subsequent experiments then we will be on task in supplying organic farmers in the Northwest with tomato varieties that can be produced in the field.

Continuation

We have made several changes to the tomato project for the 2005 season. We are working with 16 cultivars conducting 4 randomized replicated plots that contain 16 plants each (1,024 plants in total). We are working with North Carolina NC0332 (F1) as our resistant check and the cultivar "Siletz" as our susceptible. Out of the 12 accessions we tested in 2004, 6 were rejected for further testing for reasons of either demonstrating high susceptibility to Late blight or because they were poor types lacking desirable

characteristics. We have added 10 new accessions to the field along with the 6 carry-overs from 2004. Several of the accessions (various F4 combinations derived from crosses of Grape x Cherry) planted in 2004 had some plants that were segregating for moderate levels of resistance to Late blight. From these plants we selected these segregates and saved seed. They will be further selected in 2005.

Outreach

The test plots at both TESC and at Old Tarboo were incorporated into a number of ongoing Organic Seed Alliance farmer education projects as well as classes at TESC. OSA brought over 40 farmers from British Columbia, Washington and Oregon through the plots as a component of our "Fundamentals of Plant Improvement" workshops. We also hosted a group of university and organic industry researchers on a field tour at the Old Tarboo Farm location including staff from Oregon State University, Washington State University, and Small Planet Foods. As noted in the introduction, student involvement far surpassed any projections we had at the time of developing the proposal. As shown on the TESC web site: (http://www.evergreen.edu/cell/projects/tomato.htm) the project became for them, "Organic Seed: Participatory Plant Breeding & Crop Botany". Students scored evaluations, collected data, performed statistical analysis, and led tours of the test plots. They collected data beyond the scope of our project, including fruit count, fruit weight, and Briggs. They were proud of their disease nursery; what before had been a hindrance – the overwhelming incidence of Late blight – was in the end seen as a potential for improvement. In 2005 this project became an integral part of the curriculum for "Practice Sustainable Agriculture" in 2005 with 15 students participating in weekly maintenance, evaluation, scoring, and other components of practical research. This was perhaps the greatest outcome of the project; new farmers learning the basics of on-farm research/plant improvement.

Finally, we hope publish this project and create a poster for conferences at the end of the 2006 season when we have more conclusive data and improved germplasm. We also have agreed to make the germplasm available to the Cornell Organic Seed Partnership for evaluation at regional sites throughout the country. We plan on having sufficient seed stock for these evaluations at the end of the 2006 season.

Table 1. Kruskal-Wallis Test for Mean Late Blight ranks at Evergreen. Treatments 11, 7 and 10 were significantly resistant to Late blight compared to the population.

Treatment	N	Median	Mean Rank	Z
11	3	8	33.8	2.63
7	3	5.5	23.8	0.92
10	3	6	21.5	0.52
8	3	4.5	20.3	0.31
9	3	5	18.8	0.06
4	3	5	17.5	-0.17
5	3	5	16.7	-0.31
2	3	4.5	15.8	-0.46
1	3	4.5	15.5	-0.52
3	3	4	13.8	-0.8
6	3	2	12.3	-1.06
12	3	3	12	-1.12

H = 11.85, DF = 11, P = 0.456 (when adjusted for ties)

Table 2. Kruskal-Wallis test for Mean Early Blight at Evergreen. Treatments 7, 11, 1, 2, 3 and 6 were significantly resistant to Early blight compared to the population. This indicates a great deal of variation within the replications.

Treatment	N	Median	Mean Rank	Z
11	3	8	34.3	2.72
1	3	7.33	31	2.15
7	3	7	30	2
2	3	5.33	20.2	0.29
3	3	5.33	20.2	0.29
6	3	5.33	19	0.09
4	3	5	17.2	-0.23
5	3	4.67	16.8	-0.29
8	3	4.33	15.8	-0.46
10	3	3.33	8.7	-1.69
9	3	2.67	5.5	-2.23
12	3	1.67	3.1	-2.63

H = 28.84, DF = 11, P = 0.002 (adjusted for ties)

Table 3. Kruskal-Wallace Test for Mean Early Blight at Old Tarboo. Treatments 7, 11, 1, 8, 5 and 2 were significantly resistant to Early blight compared to the population.

Treatment	N	Median	Mean Rank	Z
7	3	9	34.2	2.69
11	3	8	31.5	2.23
1	3	6	25.8	1.26
8	3	6	24.5	1.03
5	3	5	20.3	0.31
2	3	5	19.7	0.2
4	3	5	18	-0.09
6	3	4.5	14.8	-0.63
10	3	4.5	13.5	-0.86
12	3	4.5	10	-1.46
9	3	4	6	-2.15
3	3	3	3.7	-2.55

H = 27.32, DF = 11, P = 0.004 (adjusted for ties)

For More Photos and Data:
http://www.evergreen.edu/cell/projects/tomato.htm
"Organic Seed: Participatory Plant Breeding & Crop Botany"

References

Literature Cited:

Barnham, W.S. and D.E. Ellis. 1951. Sources of resistance to late blight and southern bacterial wilt. Tomato Genet. Coop. Rpt 1:2

Black, L.L., T.C. Wang, P.M. Hanson, and J.T. Chen. 1996. Late blight resistance in four wild tomato accessions: Effectiveness in diverse locations and inheritance of resistance. Phytopathology 86:S24 (abstr.).

Derie, M.L. and D.A. Inglis. 2001. Persistance of complex virulences in populations of Phytophthora infestans in western Washington. Phytopathology 91:606-612.

Dorrance, A.E., D.A. Inglis, M.L. Derie, C.R. Brown, S.B. Goodwin, W.E. Fry, and K.L. Deahl. 1999. Characterization of Phytophthora infestans populations in western Washington. Plant Dis. 83:423-428.

Fry, W.E. and S.B. Goodwin. 1997. Re-emergence of Potato and Tomato Late blight in the United States. Plant Dis. 81:1349-1357.

Gallegly, M.E. 1952. Sources of resistance to two races of the Tomato Late blight fungus. Phytopathology 42:466.

Gallegly, M.E., 1960. Resistance to the late blight fungus in tomato. In Proceedings Plant Science Seminar-1960, p. 113-135. Campbell Soup Company, Camden, New Jersey.

Gardner, R. 2003. Personal communication. North Carolina State University.

Goodwin, S.B., L.S. Sujkowski, and W.E. Fry. 1996. Widespread distribution and probable origin of resistance to metalaxyl in clonal genotypes of Phytophthora infestans in the U.S. and western Canada. Phytopathology 86:793-800.

Inglis, D.A., E. Vestey, M.L. Derie, B. Gundersen, and V. Creel. 2000. Evaluation of heirloom tomato cultivars for resistance to Late blight, 1999. Biol. Cult. Tests 15:125-126.

Inglis, D.A. 2003. Personal communication. Washington State University, Mount Vernon.

Jones, Stephen. 2004. Personal communication.

Miles, C. 2003. Personnel communication. Washington State University, Vancouver.

Nunez, J. 2002. Early and Late blight diseases of tomatoes. U.C. Coop. Ext. Veg. Res. Info. Center. Veg. Notes On Line, April 2002.

Robinson, R.A. 1996. Return to Resistance: Breeding Crops to Reduce Pesticide Dependence. AgAccess. Davis, Calif.

Vanderplank, J.E. 1963. Plant Diseases: Epidemics and Control. Academic Press. New York.