THE EFFECT OF CULTIVAR MATURITY ON THE RESISTANCE OF POTATOES TO EARLY BLIGHT CAUSED BY *ALTERNARIA SOLANI*

A. Johanson[1] and H.D. Thurston[2]

Abstract

A series of clonal variants of common potato varieties which had been selected for different maturities were screened in the field for their resistance to early blight caused by the fungus *Alternaria solani*. Maturity of these cultivars was also rated in the field. A strong correlation was found between cultivar maturity and resistance to early blight. Earlier-maturing cultivars were more susceptible, and later-maturing cultivars were more resistant. Starch gel electrophoresis of the tuber enzymes of these cultivars indicated that the maturity variants did not differ with respect to the isozymes tested. This is consistent with the hypothesis that variants of the same cultivar, differing only in maturity, had been selected. These results therefore suggest that it may be difficult to select cultivars which are both early-maturing, and resistant to early blight.

Compendio

Una serie de variantes clonales de variedades comunes de papa que habían sido seleccionadas para diferentes grados de madurez, fueron evaluadas en el campo para resistencia al tizón temprano causado por el hongo *Alternaria solani*. Se calificó también la madurez de estos cultivares en el campo. Se encontró una correlación muy grande entre la madurez del cultivar y la resistencia al tizón temprano. Los cultivares que maduraron más temprano fueron más susceptibles y aquellos más tardíos fueron más resistentes. La electroforesis de las enzimas de los tubérculos de estos cultivares en geles de almidón indicó que en cuanto a madurez las variantes no diferían con respecto a las isozimas probadas. Esto es consistente con la hipótesis que las variantes del mismo cultivar que habían sido seleccionadas diferían sólamente en madurez. Estos resultados por lo tanto sugieren que puede ser muy difícil seleccionar cultivares que sean tanto precoces como resistentes al tizón temprano.

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[1]Current address: Natural Resources Institute, Central Avenue, Chatham Maritime, Chatham, Kent ME44TB.U.K.
[2]Grad. student, Dept. of Plant Pathology; Professor, Dept. of Plant Pathology, Cornell University, Ithaca, NY 14853.
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Introduction

Genetic resistance to early blight in potato cultivars is of great importance, but little research has been directed towards this area. Advanced clones in the Cornell University potato breeding program are periodically screened for resistance to early blight at Varna, N.Y. Different levels of general resistance have been found, and results have been consistent from year to year. The resistance which has been identified appears to show a strong correlation with the maturity of the variety. Early-maturing clones, tend to be highly susceptible, and late-maturing clones tend to be highly resistant (6, 7). This has also been reported in the literature (1, 2, 4, 5, 10).

Late-maturing, or late season potato cultivars generally have an indeterminate vine-type growth habit. Such cultivars continue producing new foliage and may keep initiating new tubers until disease, or poor weather conditions stop their growth. Completion of the growth cycle requires 100 or more days. Early-maturing, or early season cultivars generally have a determinate, bush-type growth habit. In these cultivars tuber initiation and the onset of tuber growth occur earlier and they do not continue to produce new foliage throughout the growing season. Their growth cycle is completed in 60-80 days.

Due to the short growing season in the Northern U.S., and the better market prices which can be obtained early in the season, most farmers would prefer to grow early-season and mid-season varieties. At present, this is often difficult if good control of early blight is also to be achieved. Various studies were therefore carried out to determine if the association between maturity and early blight resistance is as strong as the literature suggests.

A series of supposed clonal variants of common potato varieties, which had been selected on the basis of different maturities were obtained.[3] The existence of these varieties was an opportunity to test further the theory that maturity and early blight resistance are highly correlated, since it was claimed that the only difference between these variants is their maturity.

Materials and Methods

Field Trials 1986

A field trial was set up in order to test these varieties. The trial included a "new strain" of the variety Superior, which was documented to be later-maturing than the regular Superior; a "new strain" of Norchip, later than the regular variety; and four different maturing varieties of Norgold: Norgold Super, Norgold #11, Norgold #19, and Norgold #40, all thought to be later-maturing than regular Norgold. The regular Superior and Norchip for this test were foundation seed, obtained from Dr. E.D. Jones at the Uihlein Farm, Lake Placid, NY.

[3]Seed obtained from Mr. G. Shaver at Nationwide Seed Sales Incorporated, Nebraska.

Two fields were used. One was to be kept free from early blight, in order to determine the maturity of the cultivars under local conditions in the absence of disease. In the other field the resistance of the cultivars to early blight was investigated. The field in which maturity was to be rated was situated at West Lampkin, near Varna, N.Y., and the early blight field was on Turkey Hill, also near Varna. The fields were identical in shape and layout. Rows were two meters apart and approximately 30 meters in length. Each experimental unit consisted of ten seed pieces, each planted 0.5 meters apart. A space of one meter was left between the plots. The experiment was set up as a randomized complete block design with five blocks, each of five rows representing a different block. In addition to the five rows of experimental material, three spreader rows of regular Superior, which is highly susceptible to early blight, were planted. Both fields were planted by hand on June 10, 1986, with half the normal recommended rate of Nitrogen fertilizer (113 Kg/ha 10-20-20), and the normal rate of Di-syston (22.5 kg/ha) to control insect pests.[4]

The spreader rows of Superior were inoculated with dried leaf inoculum in the evening of July 15. Early blight ratings were made using a modification of the Horsfall-Barratt scale on September 8, September 17, and September 28.

The maturity of the varieties was rated on September 10. A simple scale of 1-5 was devised, where one represents green, upright plants, still in flower, and five represents completely senescent plants. None of the plants had completely senesced at the time of rating.

Starch-Gel Electrophoresis of Tuber Isozymes

It was thought possible that the different maturity variants in these field trials might not be true genetic variants, but simply be the result of mixing of cultivars or mislabelling during planting, harvesting, handling, or shipment. Such mixing of cultivars is not thought to be a common occurrence, but has been shown occasionally, by testing tubers of the same variety from different sources around the United States, using these procedures (12, 11). This theory was therefore investigated by isozyme analysis.

Since potato cultivars are usually derived from a single tuber and propagated vegetatively, each plant should be identical. Electrophoresis has been shown to be a useful technique with which to identify single gene differences, and in the potato, several enzymes have been identified which are stable and have a predictable genetic basis (14). This makes them suitable for use as genetic markers. Isozyme variation for these enzymes can be examined by standard horizontal starch gel electrophoresis of the tuber extracts. The information produced is a genetic "fingerprint" which can be used to identify a particular variety.

[4]Cornell Recommendations for Commercial Potato Production, New York, 1987.

Sample preparation was carried out following the procedures of Desborough and Peloquin (3). Standard horizontal gel electrophoresis was then carried out following the procedures of May, *et al.* (12), and May (11) for the enzymes alkaline phosphatase (AKP), glucosephosphate isomerase (GPI), and maleic dehydrogenase (MDH).[5]

Results

Area Under the Disease Progress Curve

The early blight ratings were converted to the mean of the Horsfall-Barratt range and the area under the disease progress curve was calculated for the eight varieties. An analysis of variance was then performed on these data. The overall F-statistic was highly significant, and Fisher's Least Significant Difference procedure was used to examine all the pairwise comparisons between the varieties (Table 1).

TABLE 1.—*Resistance to early blight of varieties tested at Turkey Hill, 1986. Resistance expressed as area under the disease progress curve (AUDPC).*

Variety	Mean AUDPC*	Standard Dev.**
Norgold, Super	3624.5 a	425.37
Superior, regular	2580.0 b	438.18
Norchip, regular	1541.5 c	316.02
Norgold, #11	1011.4 d	327.33
Norchip, New Strain	897.2 de	189.84
Superior, New Strain	890.1 de	257.54
Norgold, #19	740.5 de	147.54
Norgold, #40	574.1 e	217.76

*Means followed by the same letter are not significantly different at P = 0.05 according to Fisher's Protected Least Significant Difference.
**Standard deviation from the mean of 5 replicates.

The overall effect of variety on early blight resistance, as expressed by AUDPC, was highly significant. The blocks did not prove to be a significant factor in the analysis. Disease progress curves for the two variants of Superior showed that the regular, early-maturing variety had the greatest disease severity in terms of percentage defoliation due to early blight compared to the later-maturing variety, throughout the growing season. The overall area under the disease progress curve was, as expected, significantly greater for the regular variety than for the new, later-maturing strain.

[5]This investigation was carried out by Dr. B.M. May, Department of Ecology and Systematics, Cornell University, Ithaca, N.Y.

The same pattern was observed for the two variants of Norchip. The regular, early-maturing variety had the greatest disease severity throughout the growing season. The overall area under the disease progress curve was significantly greater for regular Norchip than for the later-maturing strain.

Fisher's Least Significant Difference test showed that Norgold #40 and Norgold #19 were not significantly different in terms of their resistance to early blight. These two were, however, significantly more resistant than the other three varieties. Norgold #11 was also significantly more resistant to early blight than Norgold Super, the most susceptible of the four varieties.

Maturity Ratings

An analysis of variance was then performed on the maturity ratings. The overall F-statistic was highly significant, and Fisher's Least Significant Difference procedure was then used to examine all the pairwise comparisons between the varieties (Table 2).

Regular Superior was, as expected, significantly earlier in maturity than the new strain. Regular Norchip was, also as expected, significantly earlier than the new strain. The Norgold clones behaved much as expected in term of maturity. Norgold Super was the earliest variety, followed by Norgold #11. Norgold #19 and Norgold #40 were not significantly different from each other, but slightly later than Norgold #11.

Regression of AUDPC on Maturity

A simple linear regression analysis was performed on the data to determine the relationship between AUDPC and maturity. The regression of early blight rating on the natural log of the AUDPC was highly signifi-

TABLE 2.—*Maturity ratings of varieties in West Lampkin, 1986.*

Variety	Mean maturity rating*	Standard Dev.**
Norgold, Super	2.75 a	0.50
Superior, regular	3.00 a	0.00
Norchip, regular	3.00 a	0.00
Norgold, #11	1.80 b	0.45
Norchip, New Strain	2.20 b	0.84
Superior, New Strain	1.60 cd	0.55
Norgold, #19	1.40 cd	0.55
Norgold, #40	1.20 d	0.45

Maturity ratings made on 1-5 scale (1=green, upright, flowering; 5=senesced)

*Means followed by the same letter are not significantly different at P=0.05 according to Fisher's Protected Least Significant Difference.

**Standard deviation from the mean of 5 replicates.

cant (Figure 1). Therefore, for these varieties, a high proportion of the variation in resistance to early blight can be explained by a linear relationship with the maturity of the variety. The later-maturing the variety, the greater is its resistance to early blight.

Isozyme Analysis

This procedure revealed that the maturity variants do not differ with respect to the isozymes investigated. By these criteria, at least, the variants appear to be the same variety. Although this is not a definitive test, these results are consistent with the hypothesis that variants of the same variety, differing principally only in maturity have been selected.

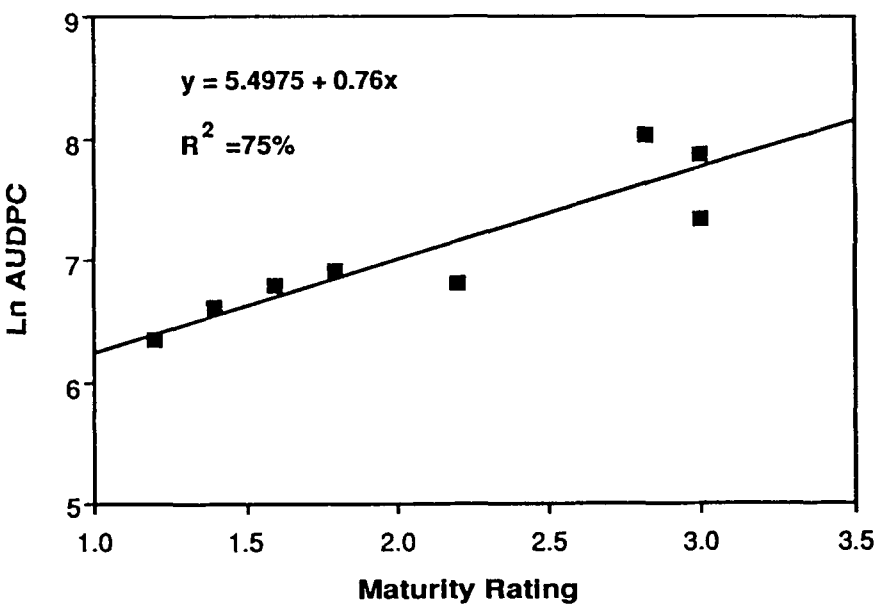

FIG. 1. Simple regression analysis of early blight rating (In AUDPC) on maturity rating of varieties in field trial, 1986.

Discussion

From these investigations it seems that the correlation of early blight resistance and maturity is, indeed, very strong. These findings substantiate previous work which has suggested that it may be very difficult to identify resistance to early blight in early or mid-season clones (1, 2, 4, 5, 10). If the only major difference between the varieties in this study is maturity, then it can be assumed that the differences in resistance to early blight observed between them is due only to this, and not to "true" genetic resistance.

Further research is needed to indicate whether the moderate levels of resistance which have so far been identified in potato varieties, is true resistance. Work is presently underway to develop a seedling screening test which may be useful in eliminating the confounding effects of maturity.

The reason for the high correlation between resistance to early blight and maturity is not clear. However, early blight is known to be a disease that primarily affects physiologically old or weakened plants (2). This can be readily observed both in the field and greenhouse. The fungus generally attacks most severely the lowermost, oldest leaves on a plant while the uppermost leaves appear symptomless. Leaves in the middle of the canopy show tiny, black, necrotic flecks. Despite the lack of macroscopically-visible symptoms, many of these top leaves, do contain the pathogen (13). It appears that this "apparent immunity" of young leaf tissue is, therefore, not due to the failure of the fungus to penetrate the host, but rather to a physiological mechanism that inhibits subsequent development of the pathogen in the plant.

Under field conditions primary lesions seem to appear at the same time on all varieties, regardless of their resistance to early blight. In addition, secondary spread, as measured by spore trapping and leaf isolations, begins almost simultaneously in different varieties. Subsequent heavy spore production after the beginning of secondary spread on the early cultivars suggests that this is the stage at which differences in resistance are expressed (8). This has serious implications for the role of early maturing varieties as sources of inoculum for later ones, when varieties with different maturities are planted in close association. Other factors, such as temperature, moisture, light intensity and daylength may be involved in breaking the "temporary plant resistance," and allowing initial lesions to develop, thus affecting secondary spread of the pathogen (8).

Although most reports of field trials document this high correlation between maturity and resistance, there are exceptions. Douglas and Pavek (4) found that although all the late clones they tested were highly resistant, not all the earlier clones were highly susceptible. They also observed one clone which approached an intermediate maturity, yet was quite resistant. From this, they suggested that breeders should concentrate their efforts in the area of the medium-to-early-maturing clones where such exceptions can be found.

In an epidemiological investigation, Holley, *et al.* (9), observed that the three cultivars Kennebec, Chieftain, and Norchip, which matured at approximately the same rate in their trials, responded very differently to infection by *Alternaria solani*. From this, they concluded that the differences in resistance observed were not simply an artefact resulting from the different crop maturation rates. Although disease began at the same time in all cultivars, the rate of disease development differed among them. They proposed that Kennebec and Chieftain do possess true "rate-reducing" resistance

to early blight. However, the maturity ratings of these three varieties have been disputed.

Conclusions

Resistance appears to be highly correlated with cultivar maturity. Earlier varieties are more susceptible, and later varieties more resistant. Evidence does suggest that some early and mid-season varieties may possess moderate levels of rate-reducing resistance. At this point, however, the prospect of selecting varieties which are both early in maturity, and highly resistant to early blight does not seem encouraging.

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