Evaluation of a Short-Day Adapted Tetraploid Potato Population with Horizontal Resistance to *Phytophthora infestans* under Long-Day Conditions in Northern Maine

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ABSTRACT

Phytophthora infestans **(Mont.) de Bary, the cause of late blight, has rapidly overcome major (R) gene resistance in potatoes. A population of short-day adapted tetraploid potatoes with horizontal resistance to late blight was developed at the International Potato Center in Lima, Peru. True seed from this population was obtained from the NRSP-6 Project at Sturgeon Bay, WI for the purpose of evaluating its potential to contribute to the breeding effort for late blight resistance in the United States. In 1996, 552 single hills were planted on Chapman Farm, Presque Isle, ME; only 448 tuberized. In 1997, these clones were planted on Chapman Farm for increase; 129 were saved, 53 failed to tuberize, and 266 were discarded because they were sprouted at harvest. In 1998 and 1999, 69 clones were tested for their reaction to late blight in replicated plots on Aroostook Farm, Presque Isle, ME. Percent infected foliage was estimated three times toward the end of the season and used to compute area under the disease progress curve. Broad-sense heritability for horizontal resistance to late blight was estimated as 0.78 with a 95% confidence interval of 0.64 to 0.86. Using detached leaflet assays, these clones were inoculated with US-8 strains of *P. infestans*, and the diameter of the lesion was measured 7, 8, 9, 10 and 11 days after inoculation. The correlation between field resistance and the detached leaflet assay was very low (0.18<r<0.24). Some clones from this population are highly resistant to the US-8 strain of *P. infestans* and represent another source of breeding material for developing late blight resistant varieties in the future. However, very late maturity, short dormancy, poor tuberization and low fertility levels may limit the usefulness of this germplasm in northern USA latitudes.**

RESUMEN

Phytophthora infestans **(Mont.) de Bary, causante del tizón tardío, ha vencido rápidamente la resistencia de genes mayores (R) en papa. El Centro Internacional de la Papa en Lima, Perú, ha desarrollado una población de papa tetraploide adaptada a días cortos, con resistencia horizontal al tizón. La semilla verdadera (botánica) de esta población fue obtenida del Proyecto NRSP-6 en Sturgeon Bay, WI, con el propósito de evaluar su potencial para contribuir con el mejoramiento para resistencia a tizón tardío en los Estados Unidos. En 1996, se sembraron para multiplicación 552 plantas en la granja Chapman, Isla Presque, ME, de estas, sólo tuberizaron 448. En 1997 estos clones se sembraron en la granja Chapman para incremento, 129 se guardaron, 53 no tuberizaron y se eliminaron 266 porque brotaron a la**

Accepted for publication 22 May 2007.
ADDITIONAL KEY WORDS: late blight, broad-sense heritability, *Solanum tuberosum* L.

ABBREVIATIONS: AUDPC, area under the disease progress curve; sAUDPC, square root of AUDPC; H, broad-sense heritability

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cosecha. En 1998 y 1999, se probaron 69 clones para su reacción al tizón tardío en parcelas repetidas en la granja Aroostook, Isla Presque, ME. El porcentaje de follaje infectado fue estimado por tres veces hacia el final de la campaña y usado para calcular el área bajo la curva de progreso de la enfermedad. La herencia en sentido amplio para resistencia al tizón tardío fue estimada como 0.78 con un 95% de intervalo de confianza de 0.64 a 0.86. Utilizando pruebas de foliolos desprendidos, estos clones fueron inoculados con variantes US-8 de *P. infestans* y se midió el diámetro de la lesión 7, 8, 9,10 y 11 días después de la inoculación. La correlación fue muy baja (0.18<r<0.24). Algunos clones de esta población son muy resistentes a la variante US-8 de *P. infestans* y representan otra fuente de material de mejoramiento para desarrollar variedades resistentes al tizón tardío en el futuro. Sin embargo, la madurez muy tardía, periodo de latencia corto, tuberización pobre y bajos niveles de fertilidad podrían limitar la utilidad de este germoplasma en latitudes del norte de los Estados Unidos de América.

INTRODUCTION

Developing potatoes (*Solanum tuberosum* L.) with resistance to late blight, caused by the oomycete *Phytophthora infestans* (Mont.) de Bary, is a major focus of most potato breeding programs around the world. In the 19th century, breeding for horizontal resistance to late blight began after the blight epidemics in Europe from 1845-1847 (Ross 1958). Later breeding efforts focused on the incorporation of major R-gene resistance from hexaploid *S. demissum* Lindl. into tetraploid *S. tuberosum* (Black et al. 1953; Malcolmson and Black 1966). Breeding for horizontal resistance was largely discontinued in favor of R-gene based resistance. However, compatible races of *P. infestans* rapidly emerged and overcame this R-gene based resistance (Ross 1986; Wastie 1991), so that by the 1970s most breeders had ceased to use R-gene based resistance in their breeding efforts. Improvements in chemical control in the 1970s, coupled with the failure of R-gene based resistance, caused many breeders to abandon their breeding efforts for late blight resistance. Others focused on breeding for horizontal resistance (Umaerus et al. 1983).

The situation changed drastically again in the 1980s and 1990s with the appearance of metalaxyl-resistant isolates of *P. infestans* (Davidse et al. 1981; Dowley and O'Sullivan 1981; Deahl et al. 1993a). These were subsequently found to be a mixture of pathogenic strains that had migrated from Mexico (Goodwin et al. 1994), along with sexual recombinants among some of these strains (Goodwin et al. 1998). In the 1990s and 2000s the breeding efforts for late blight resistance have once again focused on developing horizontal resistance. Horizontal resistance is controlled by many genes and can influence a number of biological processes involved in pathogenicity (Umaerus et al. 1983).

Landeo et al. (1995) developed a tetraploid potato population with horizontal resistance to late blight at the International Potato Center (CIP). Since this population was developed in Peru, it is likely to be better adapted to short-day than long-day growing conditions. Utilizing short-day adapted germplasm for breeding purposes in the long-day northern regions of the United States has been problematic. Such germplasm may tuberize poorly, fail to bulk up, produce long stolons, produce tubers that can not easily be removed from the stolons, have deep eyes and have very short or very long dormancy (Tarn et al. 1992).

Evaluating late blight resistance in the field can only be done once a year in most parts of the United States. Various laboratory procedures for evaluating germplasm for late blight resistance have been reported in the literature (Dorrance and Inglis 1997; Vleeshouwers et al. 1999), but the test conditions were variable as were the interpretations of correlations between field and laboratory resistance.

The purposes of this study were to evaluate the performance of segregating progeny from CIP's late blight resistant population under long-day conditions in northern Maine, to test those progeny which were better adapted to northern Maine for resistance to late blight, and to determine how well field tests for late blight resistance correlated with a detached leaflet laboratory test.

MATERIALS AND METHODS

True seeds from 13 tetraploid potato families bred at CIP were obtained from the NRSP-6 Project in Sturgeon Bay, WI. These were treated with 1500 mg L^{-1} gibberellic acid (GA_3) for 24 hr, allowed to air dry, and sown in flats of Jiffy Mix (Jiffy Products of America, Inc., West Chicago, IL) in the greenhouses at Beltsville, MD in August 1995. All seedlings were transplanted into 8.9 cm clay pots two to four weeks after ger-

mination. Tubers from seedlings were harvested in December 1995. All tubers were harvested from each pot, counted, put in 900 g brown paper bags, labeled, stored at 4 C and 95% relative humidity, and subsequently shipped to Presque Isle, Maine, in the spring for planting. In all, 552 clones were harvested from these 13 families (Table 1).

Where available, four hills of each of the 552 clones comprising the tetraploid population with horizontal resistance to late blight were planted on Chapman Farm, Presque Isle, Maine, on 4 June 1996 on a Caribou silt loam soil (fine-loamy, mixed, frigid Typic Haplothod) following a plowed-down timothy-clover sod. Tubers of a given clone were spaced 23 cm within the row, with a 69 cm space between plots, in rows 91 cm apart. The site was fertilized with 1200 kg ha^{-1} of 14-14-14 N-P-K banded in-row at planting. Cultural practices were similar to those used on commercial farms in the area. No irrigation was available. Plots were harvested with a single-row digger on 17 September 1996. Four tubers were saved from each plot for replanting on Chapman Farm in 1997. Only 81% (448/552) of the original population tuberized in the field under the long-day conditions of northern Maine (Table 1).

These 448 clones were planted on 4 June 1997 on Chapman Farm under the same conditions as employed in 1996. Flower color and female fertility, based on the presence or absence of fruit, were recorded during the growing season. Sprouting at harvest was a significant problem, and only clones with non-sprouted tubers were saved at harvest on 4 September. In all, 264 (59%) clones were not saved because of sprouting at harvest, and another 55 (12%) were not saved because they failed to tuberize. Specific gravity was determined using the weight in air and water method (Murphy and Goven 1959) for all saved clones.

On 20 May 1998, 129 clones were planted in eight hill plots on Chapman Farm under the same conditions as previously described. Flower color and female fertility were again recorded during the growing season. All tubers were harvested from each plot on 28 August. Yield and specific gravity were recorded. Five tubers of intermediate size and free of defects were placed in paper bags and stored at 10 C until processed into chips on 9 December. A 1.6 mm slice was taken from the cross-section of each tuber, rinsed in water and placed on paper towels to remove excess moisture. Chips were then fried in Primex vegetable shortening (Ach Food, Memphis, TN) until bubbling ceased. They were removed from the oil and scored for color on a 1 to 10 scale, with ≤7.0 considered acceptable color. The remaining tubers were stored at 10 C and 95% relative humidity.

The late blight field disease nursery was planted on 13 May 1998 with 121 clones from the CIP population and two standard check varieties, 'Atlantic' and 'Russet Burbank'. Four hills of each clone were planted in a randomized complete block design with two replications on Aroostook Farm, Presque Isle, Maine, on a Caribou silt loam soil. Tubers of a given clone were spaced 23 cm within the row, with a 69 cm space between plots, in rows 91 cm apart. Every third row was planted with Russet Burbank as a spreader row. Cultural practices were similar to those used on commercial farms in the area, with the exception that no fungicides were applied. No irrigation was available. Late blight (US-8) occurred naturally. The percent of late blight infected foliage was estimated visually on 5 and 19 August and 7 September. Area under the disease progress curve (AUDPC) was calculated (Shaner and Finney 1977).

On 17 May 1999, 126 CIP clones were planted in eight hill plots on Chapman Farm under the same conditions as previously described. Flower color and fertility notes were once again recorded. All tubers were harvested

TABLE 1—*List of tetraploid families from the International Potato Center evaluated in Presque Isle, Maine, and the number of clones planted each year during the course of this study.*

Family	Number of Clones Planted			
	1996[1]	1997[2]	1998[3]	1999[3]
CIP 391004 (PI584493)	5 (1)	4 (0, 1)	3, 3	3, 3
CIP 391008 (PI584494)	12 (6)	6 (2, 2)	2, 2	2, 2
CIP 391013 (PI583331)	185 (10)	175 (94, 7)	74, 69	72, 45
CIP 391018 (PI583332)	2 (1)	1 (0, 1)	0, 0	0, 0
CIP 391019 (PI583333)	9 (0)	9 (8, 1)	1, 1	1, 1
CIP 391021 (PI583334)	127 (40)	87 (66, 13)	8, 7	8, 3
CIP 391044 (PI583335)	8 (0)	8 (6, 0)	2, 2	2, 1
CIP 391046 (PI583336)	8 (0)	8 (3, 1)	4, 4	4 ,2
CIP 391053 (PI583337)	3 (0)	3 (0, 2)	1, 1	1, 1
CIP 391054 (PI583338)	3 (0)	3 (1, 0)	2, 2	2, 1
CIP 391057 (PI583340)	20 (3)	17 (8, 2)	7, 7	7, 3
CIP 391137 (PI583341)	151 (36)	115 (71, 20)	24, 22	23, 7
CIP 391139 (PI584495)	19 (7)	12 (6, 5)	1, 1	1, 0
Total	552 (104)	448 (264, 55)	129, 122	126, 69

[1]For 1996 the number of tubers planted (failed to tuberize) given.
[2]For 1997 the number of clones planted (sprouted at harvest, failed to tuberize) given.
[3]For 1998 and 1999 the number of clones planted on CF, in late blight field nursery given.

from each plot on 1 September. Specific gravity was determined again as well.

Sixty-nine CIP clones were planted in the late blight disease nursery along with several resistant clones (AWn86514-2, B0692-4, 'Stobrawa') (Haynes et al. 1998, 2002) and susceptible clones (Atlantic, 'Red LaSoda', Russet Burbank) (Haynes et al. 2000, 2001) in a randomized complete block design with two replications on 27 May 1999 on Aroostook Farm. Each plot consisted of four hills of a clone. Every third row in the field was planted with Russet Burbank as a spreader row. Late blight (US-8) moved in naturally after 19 August. The first blight readings were taken 1 September, at which time two of the susceptible checks, Atlantic and Red LaSoda, were already dead. Percent infected foliage was also recorded on 6 and 11 September and AUDPC was calculated.

TABLE 2—*Mean AUDPC by family and the number of clones significantly more resistant and more susceptible than AWn86514-2 and B0692-4 in 1999.*

Family	Mean AUDPC	AWn86514-2 R	AWn86514-2 S	B0692-4 R	B0692-4 S	Number Clones
CIP 391004	410	0	2	1	1	3
CIP 391008	288	0	1	1	0	2
CIP 391013	207	9	11	22	2	45
CIP 391018	—	—	—	—	—	0
CIP 391019	638	0	1	0	1	1
CIP 391021	734	0	3	0	3	3
CIP 391044	313	0	0	0	0	1
CIP 391046	303	0	0	0	0	2
CIP 391053	754	0	1	0	1	1
CIP 391054	150	0	0	1	0	1
CIP 391057	450	0	2	0	2	3
CIP 391137	273	0	3	2	1	7
CIP 391139	—	—	—	—	—	0
Atlantic	1000					
AWn86514-2	225					
B0692-4	394					
Red LaSoda	1000					
Russet Burbank	760					
Stobrawa	363					

AUDPC was analyzed by year using the general linear models procedure in SAS (SAS 1990) and subsequently transformed with the square root transformation (sAUDPC) so that they could be combined over years. Least squares means were calculated and compared to AWn86514-2 and B0692-4, two late blight resistant clones, in 1999 using the pdiff option (Saxton 1997). All effects were considered random.

Estimates of the clonal (σ^2_C), year x clone (σ^2_{YC}), and the error (σ^2_e) variances were calculated using the mixed procedure in SAS (SAS 1999). Broad-sense heritability (H) was calculated from these estimates of variances as:

$$H = \sigma^2_C / (\sigma^2_C + \sigma^2_{YC} / 2 + \sigma^2_e / 4)$$ (Nyquist 1991)

and a 95% confidence interval on H was calculated from the mean squares (Knapp et al. 1985).

The detached leaflet assay of Liu et al. (1998) was used. Tubers were planted in 22 cm plastic pots containing a steam-treated mixture of peat, perlite and soil (1:1:1, v/v/v) and plants were grown in the greenhouse for 8 to 10 weeks. Four terminal leaflets from each clone were excised. Leaflets, abaxial side down, were placed on a plastic net with petioles inserted into water in individual 27 x 40 x 9.3 cm clear plastic containers. The center portion of each leaflet was inoculated with a drop of a sporangial suspension (3-7 x 10^4 sporangia/ml) of a US-8 isolate of *P. infestans*, and then the container was placed in a dark growth chamber for 24 h. A randomized complete block design with four replications was placed under fluorescent light (12 h) and dark (12 h) regime in a growth chamber at 16 to 18 C and high relative humidity. Lesion diameter (mm) was measured 7, 8, 9, 10 and 11 days after inoculation. Mean lesion diameter was analyzed by days after inoculation using the general linear models procedure in SAS (1990). The correlations of mean sAUDPC for each year with mean lesion diameter each day after inoculation were calculated (SAS 1990).

RESULTS AND DISCUSSION

In 1997 more than half (264/448) of the CIP clones planted were sprouted at harvest. We attributed this to premature sprouting rather than heat sprouting (Lugt 1960) for two reasons. None of the long-day adapted *S. tuberosum* clones in surrounding plots, which were planted and harvested within a day or two of the CIP clones, were sprouted at harvest. Also, there were very few days of high temperatures. The average maximum temperatures in June, July and August were 22.5, 26.0 and 23.4 C, respectively, with average minimum temperatures of 7.6, 12.9 and 11.4 C, respectively. The daily maximum temperature exceeded 29 C for three, five and three days in June, July and August, respectively. The daily minimum temperature never exceeded 19 C the whole growing season. Unless this CIP

germplasm is subject to heat stress at much lower temperatures than our long-day adapted germplasm, sprouting is more likely due to premature sprouting rather than heat sprouting.

In 1998 rainfall during June, July and August in Presque Isle, Maine, was 8.3, 14.0 and 6.3 cm, respectively. There was an extended dry spell during late July and August. The average maximum temperatures during June, July and August were 21.9, 25.8 and 25.4 C, respectively. There was a four-day stretch in July (14-17) and again in August (8-11) when the maximum temperatures exceeded 29 C. The average minimum temperatures during June, July and August were 11.7, 13.6 and 11.7 C, respectively. There was a four-day stretch in July (15-18) and a three-day stretch in August (9-11) when the minimum temperature exceeded 18 C, but it never exceeded 21 C. Late blight started in early August and developed very slowly through mid-August. In the latter part of August and early September conditions were more conducive to the spread of late blight, and by 7 September, the date of the third blight reading, the susceptible checks, Atlantic and Russet Burbank, were dead. Mean AUDPC for all 122 CIP clones was 441, ranging from 5 to 1760, and for the 69 clones common to both years mean AUDPC was 416, ranging from 7 to 1760. Mean AUDPC of the susceptible checks, Atlantic and Russet Burbank, were 1379 and 1554, respectively.

In 1999 rainfall during June, July and August was 10.4, 6.4 and 11.4 cm, respectively. During July and August no rainfall was recorded for several weeks. The average maximum temperatures during June, July and August were 26.2, 26.3 and 24.1 C, respectively. On seven days in June, six days in July, and two days in August the maximum temperature exceeded 29 C. The average minimum temperatures during June, July and August were 12.1, 14.1 and 11.7 C, respectively. On one day in June and four days in July the minimum temperature exceeded 18 C, but it never exceeded 22 C. No late blight was observed as late as 19 August 1999. However, by the time the first late blight readings were taken 1 September, the susceptible checks Atlantic and Red LaSoda were already dead. Estimated percent infected foliage in the intermediate check Stobrawa was 20 to 25%. In the resistant checks, AWn86514-2 and B0692-4, estimated percent infected foliage was 10 to 25%. Mean AUDPC for the 69 clones evaluated in 1999 was 265 and ranged from 13 to 750. Mean AUDPC for AWn86514-2 and B0692-4 were 225 and 394, respectively. In 1999, 17 and 35 of the CIP clones were significantly more resistant to late blight than AWn86514-2 and B0692-4, respectively (Table 2).

There were significant differences among the CIP clones for sAUDPC, and the year x clone interaction was also significant (Table 3). From the mixed procedure, σ^2_C, σ^2_{YC} and σ^2_e were estimated as 49.65, 22.11 and 13.27, respectively. Broad-sense heritability for AUDPC in these 69 clones was estimated as 0.78 with a 95% confidence interval of 0.64 to 0.86.

All of the CIP clones were very late in maturity judging by the green haulms even after vine kill. There are numerous reports in the literature of the correlation between late blight resistance and late maturity (Visker et al. 2004; Umaerus et al. 1983). Major QTLs for late blight resistance and late maturity are also linked (Collins et al. 1999; Oberhagemann et al. 1999; Visker et al. 2005). It remains to be seen if the levels of late blight resistance in this CIP germplasm can be passed on to progeny when this material is crossed into *S. tuberosum* germplasm adapted to the northern latitudes.

There were no significant differences among clones for lesion diameter in the detached leaflet test for any of the five days of testing post-inocula-

TABLE 3—*Analysis of variance on the square root of area under the disease progress curve for 69 CIP potato clones derived from a short-day adapted tetraploid population with horizontal resistance to late blight evaluated under long-day conditions in Presque Isle, Maine, in 1998 and 1999.*

Source	d.f.	M.S.[1]	Estimate of the Variance Component[2]
Year	1	287.80	
Rep (year)	2	464.76	
Clone	68	253.69**	49.65**
Year x clone	68	56.83**	22.11**
Error	133	13.24	13.27**

** Significant at the 1% level.
[1]Results using the general linear models procedure in SAS (SAS 1999).
[2]Results using the mixed models procedure in SAS (SAS 1990).

TABLE 4—*Analysis of variance on mean lesion diameter for detached leaflets seven, eight, nine, ten and eleven days post-inoculation with US-8* Phytophthora infestans *in the laboratory test conducted in 1999.*

Source	d.f.	day 7	day 8	day 9	day 10	day 11
Experiment	3	59.99**	187.07**	362.74**	549.61**	798.19**
Clone	67	18.78	43.88	75.73	103.85	138.02
Error	200	14.48	36.62	61.62	82.81	103.70

**Significant at the 1% level.

TABLE 5—*Other characteristics of the 17 CIP clones significantly more resistant to* Phytophthora infestans *than the resistant clone AWn86514-2.*

	1997		1998				1999	
Clone	Fert[1]	SG[2]	Fert	SG	Chip[3]	Spt[4]	Fert	SG
CIP391013-2	N	1.058	N	1.061	8.4	6	N	1.062
CIP391013-3	N	1.077	N	1.083	6.0	0	N	1.084
CIP391013-8	N	1.064	N	1.074	8.0	25	N	1.072
CIP391013-38	N	1.048	N	1.055	9.8	0	N	1.057
CIP391013-46	N	1.058	N	1.077	8.0	1	N	1.068
CIP391013-53	N	1.056	N	1.071	9.0	0	N	1.063
CIP391013-56	N	1.053	N	1.070	8.0	51	N	1.062
CIP391013-67	N	1.059	N	1.079	7.8	51	N	1.065
CIP391013-69	N	1.067	N	1.078	9.0	13	N	1.073
CIP391013-89	N	1.058	N	1.068	7.0	1	N	1.065
CIP391013-95	N	1.055	N	1.075	9.0	13	N	1.053
CIP391013-122	N	1.057	N	1.071	7.6	25	N	1.068
CIP391013-132	N	1.061	Y	1.086	7.6	38	N	1.071
CIP391013-158	N	1.068	N	1.083	8.4	0	N	1.077
CIP391013-162	N	1.053	N	1.070	8.0	6	N	1.060
CIP391013-171	N	1.065	N	1.074	8.2	25	N	1.062
CIP391137-83	N	1.082	N	1.080	6.0	51	N	1.070

[1]Fertility observed as fruit set in the field.
[2]Specific gravity.
[3]Chip color on a 1 to 10 scale; ≤7.0 is considered acceptable. Chipped on December 9, 1999, following approximately three months storage at 10 C.
[4]Sprout length in mm on tubers chipped December 9, 1999, following approximately three months storage at 10 C.

tion (Table 4). Mean lesion diameter was 1.92, 2.87, 3.76, 4.38 and 4.96 mm at 7, 8, 9, 10 and 11 days after inoculation, respectively. The detached leaflet test was not able to discriminate among clones for their reaction to *P. infestans*. The correlations of mean lesion diameter with mean sAUDPC ranged from 0.20 to 0.24 in 1998 and 0.18 to 0.24 in 1999. None of these correlations was significantly greater than zero. This indicates that there was no relationship between the field and laboratory evaluations. This agrees with the results of Lozoya-Saldaña et al. (2006), who reported that 'Rosita' and 'Norteña' were resistant to late blight in the field under natural conditions in the Toluca Valley, but were as susceptible as the susceptible control in detached leaflet tests. They questioned the usefulness of detached leaflet tests for screening or predicting field resistance to late blight. Vleeshouwers et al. (1999) also found that some wild *Solanum* genotypes were resistant in the field, but their detached leaves were partially susceptible. Other researchers have also found that detached leaf assays are not as good as greenhouse inoculations of whole plants in discriminating overall reactions to late blight among clones (Dorrance and Inglis 1997). However, detached leaf assays can prove useful for measuring specific components of resistance (Dorrance and Inglis 1997) or for identifying virulence loci in populations of *P. infestans* (Deahl et al. 1993b; Tooley et al. 1986).

There may be several reasons why the correlation between detached leaflet assays and field tests are variable. Vleeshouwers et al. (1999) reported that the conditions under which detached leaf assays were conducted made a difference: detached leaves incubated in covered trays at high relative humidity were more susceptible than detached leaves kept in open trays. Visker et al. (2003) found that apical leaves were more resistant to late blight than basal leaves. Differences between induced local and systemic protection may explain some of the observed variation in field-grown vs detached leaf assays. Cohen et al. (1993) found that treating potato plants with jasmonic acid led to both local and systemic protection against *P. infestans*, whereas Coquoz et al. (1995) found that treating potato plants with arachidonic acid resulted in a local, but not a systemic, accumulation of a pathogenesis-related-like protein.

The 17 clones that were significantly more resistant to late blight than AWn86514-2 (Table 5) tended to have low to moderate specific gravity in the three years they were evaluated for specific gravity. Specific gravity ranged from 1.048 to 1.082 in 1997, 1.061 to 1.086 in 1998 and 1.053 to 1.084 in 1999. In 1998 when tubers of these 17 clones were chipped out of 10 C following three months' storage, the chip scores were generally unacceptable: only three clones chipped acceptably (≤7.0). Fertility in these clones was poor. Only one clone produced fruit in the field in 1998, and none of the clones produced any fruit in the field in either 1997 or 1999. These 17 clones still had a relatively short dormancy. Three months following storage at 10 C, 13 of them had already sprouted, with the longest sprouts being about 5 cm.

CONCLUSIONS

The short-day adapted CIP population evaluated in this study had high levels of resistance to *P. infestans*, presumably free of R genes, although this assumption was not tested in this

study. The levels of resistance in a large percentage of the clones were as good as those currently found in AWn86514-2 and B0692-4, two of the most late blight resistant tetraploid clones in the United States, with a small percentage even more resistant than AWn86514-2 and B0692-4. However, the population also had several undesirable traits, the three most negative being very late maturity, the lack of a suitable dormancy period for northern latitude production systems, and low yields. Out of the original 552 clones comprising the population, 48% were discarded because they were sprouting at harvest and another 28% were discarded because they failed to tuberize, all before testing for their reaction to late blight. Nevertheless, most of the 69 clones that were finally evaluated for late blight resistance for two years had good levels of resistance.

This population has the potential to contribute valuable genes for resistance to late blight in the United States. It remains to be seen if there are any genetic linkages between resistance to late blight and short dormancy, low specific gravity, low female fertility and poor chipping color, and if earlier maturing germplasm with late blight resistance can be derived from this germplasm. Intercrossing this population with long-day adapted *S. tuberosum* populations in northern United States potato breeding programs will help answer these questions.

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