*Euphytica* **127:** 1–9, 2002.



# Early generation selection for potato tuber quality in progenies of late blight resistant parents

Dilson A. Bisognin[1,2] & David S. Douches[1,*]
[1]*Department of Crop and Soil Sciences, Michigan State University, East Lansing, MI 48824, U.S.A.;* [2]*Sponsored by Ministry for Science and Technology – CNPq, Brazil; Permanent Address: Department of Fitotecnia, Federal University of Santa Maria, Santa Maria, RS, 97119-900, Brazil; (*author for correspondence; E-mail: douchesd@msu.edu)*

Received 2 August 2000; accepted 19 November 2001

*Key words:* chip-processing, early generation selection, *Phytophthora infestans*, potato breeding, *Solanum tuberosum*, specific gravity, tuber appearance

**Summary**

Developing disease resistant cultivars is one of the major objectives for a potato (*Solanum tuberosum* L.) breeding program, but many resistant clones have not achieved commercial acceptance because of late maturity and non-marketable tuber characteristics. Selection for tuber quality should have greater emphasis in breeding disease resistant cultivars. The objectives of this study were 1) to evaluate the ability of late blight (*Phytophthora infestans* (Mont.) de Bary) resistant parents to transmit chip-processing (tuber appearance, specific gravity, and chip-color) or tablestock (tuber appearance) quality to the offspring and 2) to compare selecting for tuber quality in single-hill versus eight-hill generations. We made crosses among eight unadapted potato cultivars (B0718-3, Bertita, Bzura, Greta, Libertas, Stobrawa, Tollocan, and Zarevo) with reported late blight resistance with adapted susceptible cultivars/breeding clones to generate 95 populations (4,750 seedlings). Approximately 10% of the progeny from each cross were selected from single-hill plots based on tuber appearance, number, shape, and internal defects. These selected clones (408) were evaluated for tuber appearance, specific gravity, and chip-color. The same evaluations in the following year were made on tuber samples from eight-hill plots. Libertas and Tollocan were the best parents for transmitting chip-color; B0718-3, Zarevo, and Tollocan for transmitting tuber appearance; and Bzura, Libertas, and Zarevo for transmitting high specific gravity to the highest percentage of the offspring. Overall, 50% and 56% of the clones based on single- and eight-hill generation, respectively, were considered to possess chip-processing quality; over 90% of the clones had acceptable tablestock quality. A total of 71% of the clones possessing acceptable chip-processing and 95% of the clones possessing acceptable tablestock quality selected in both generations were identified in single-hill plots. The evaluation of tuber quality characteristics in single-hill generation not only permitted the identification of clones with acceptable chip-processing and tablestock, but also increased the amount of clonal information for the following generation of selection. In crosses between late blight resistant and susceptible clones, selection for tuber quality traits can be initiated in single-hill generation using a moderate selection intensity and precede late blight testing.

## Introduction

Breeding for disease resistance is a common objective for many crop species. Overemphasis on improving disease resistance can limit yield and other important traits because of genetic bottlenecks (Kelly et al., 1998). In potato (*Solanum tuberosum* L.), late blight (*Phytophthora infestans* (Mont.) de Bary) is the most devastating disease worldwide (Fry & Goodwin, 1997; Kamoun et al., 1999) and genetic host plant resistance is one of the major objectives for breeding (Colon et al., 1995).

Although breeding for late blight resistance has had greater priority in the last century than for any

other pathogen, the potato market in many countries is dominated by late blight susceptible cultivars (Umaerus et al., 1983). As an example, among 147 cultivars and breeding lines evaluated against US8 genotype of *P. infestans* in greenhouse experiments, two-thirds were classified as very susceptible (Douches et al., 1997). In fact, there is no North American cultivar currently in use that has an adequate level of late blight resistance (Helgeson et al., 1998). In contrast, potato breeders have made great progress over the last century for early maturity, chip-color, tuber appearance, and specific gravity (Douches et al., 1996) and cultivars with good chip-processing quality have been released (Love et al., 1998). Since late blight resistance is not the trait that confers enough advantage for a clone to become a successful cultivar (Umaerus et al., 1983), late blight resistance needs to be combined with tuber quality, acceptable maturity, and other agronomically important traits.

In order to combine characteristics, a selection/evaluation procedure capable of identifying desirable clones at the early generation stage is required. Selection in single-hill generation reduces the cost for clonal maintenance and also permits the identification of superior parents for use in other cross combinations (Thill & Peloquin, 1995). In addition, an efficient selection strategy should be able to significantly reduce the number of selected clones and to keep superior ones for later generations of selection (Tai & Young, 1984). Since superior tuber quality has been the market-limiting trait that characterizes the cultivars released in the past century (Douches et al., 1996; Love et al., 1998), this trait should be evaluated and selected for as early as possible in a potato breeding program.

The objectives of this study were 1) to evaluate the ability of late blight resistant parents to transmit chip-processing (chip-color, tuber appearance, and specific gravity) or tablestock (tuber appearance) quality to the offspring and 2) to compare selecting for tuber quality in single-hill versus eight-hill generations.

## Materials and methods

Eight unadapted cultivars (B0718-3, Bertita, Bzura, Greta, Libertas, Stobrawa, Tollocan, and Zarevo) with reported late blight resistance were crossed with adapted susceptible cultivars/breeding clones to generate 95 populations segregating for late blight resistance, marketable tuber quality, and maturity (Table 1). For each cross, 50 seedlings (4,750 seedlings total) were transplanted at the Michigan State University Montcalm Experiment Station, MI in 1997 with 75 cm within-row spacing between plants. At harvest, approximately 10% of the best offspring from each cross were selected based on tuber appearance, number, shape, and internal defects. This selection resulted in 408 clones (8.9%) that were used in this study. These clones were grouped according to their late blight resistant parent and were planted in 1998 in eight-hill plots with 30 cm within-row spacing. In this study, family refers to half-sib progeny of the respective late blight parent (i.e. B0718-3 family, Bertita family, etc).

All tubers harvested from single-hill plots and a random sample of tubers (5.1–8.3 cm diameter) from eight-hill plots were used for tuber appearance and specific gravity evaluations. Tuber appearance was evaluated on a scale 1 to 5 of increasing defects (1 = excellent, as cultivar Atlantic; 2 = very good; 3 = acceptable; 4 = poor; and 5 = very poor). Specific gravity was measured on a minimum 2 kg sample using the formula [weight in air / (weight in air – weight in water)] with 1.080 or greater considered acceptable for chip-processing. One tuber and five-tuber samples (two slices/tuber), respectively from single- and eight-hill plots, were used for chip-color evaluation. Chip-color was evaluated on a scale 1 to 9 of increasing color darkness (1–2 = excellent; 3 = very good, as cultivars Atlantic and Snowden; 4 = acceptable; 5 = unacceptable; and 6–9 = poor). From here after, tuber quality refers to the combination of tuber appearance, specific gravity, and chip-color.

Tuber quality data were analyzed using a mixed model (SAS PROC MIXED) including families, years (single- and eight-hill generations) and the interaction family $\times$ year as fixed effects. Variance components were estimated by restricted maximum likelihood. The same analysis was done considering only years as a fixed effect. The significance of fixed effects was tested by the F type III test. Family means were compared by Fisher's least significance difference (LSD) at $\alpha = 0.05$. Pearson correlation analysis was done to compare tuber quality data from single- and eight-hill clonal generations and to estimate heritability as proposed by Frey & Horner (1957). Correlation analysis was done at the clonal level, for individual late blight families and combined analysis of all families, and at the family level (late blight family means). All these analysis were done following the procedures of SAS (SAS Institute, 1995). The expected response to

*Table 1.* Late blight resistant parents (top row) and susceptible adapted cultivars/advanced breeding clones (below) were crossed to generate segregating populations

| B0718-3 | Bertita | Bzura | Greta | Libertas | Stobrawa | Tollocan | | Zarevo |
|---|---|---|---|---|---|---|---|---|
| MSB107-1 | MSB110-3 | MSC127-3 | MSC127-3 | MSA097-1Y | MSC127-3 | MSA091-1 | MSA091-1 | MS716-15 |
| MSC122-1 | MSC084-A | MSE234-7 | MSE234-7 | MSC127-3 | MSE234-7 | Allegany | MSA097-1Y | NorValley |
| MSC127-3 | MSC108-2 | MSF077-8 | MSF077-8 | MSC135-4 | MSF134-1 | Chaleur | MSA199-1P | ND860-2 |
| MSC148-1 | MSE226-2 | ND860-2 | ND860-2 | MSE230-6 | ND860-2 | Conestoga | MSB076-2 | NY102 |
| MSD001-3Y | MS702-80 | Yukon Gold | | MSD040-4RY | Yukon Gold | Andover | MSC010-1 | NY84 |
| MSE234-7 | Reddale | | | MSF023-4 | | Krantz | MSC011-1 | Onaway |
| MSE251-1 | Spunta | | | MSF077-8 | | Lenape | MSC122-1 | Pike |
| Andover | Steuben | | | Andover | | MS716-15 | MSC127-3 | Rose Gold |
| NorValley | W877 | | | Atlantic | | NY88 | MSD040-4RY | Saturna |
| NY101 | | | | | | Pike | Allegany | Snowden |
| Pike | | | | | | Rose Gold | Andover | Spunta |
| Prestile | | | | | | Snowden | Atlantic | W870 |
| Shepody | | | | | | St. Johns | Brador | W877 |
| W870 | | | | | | Superior | B1254-1 | Yukon Gold |
| Yukon Gold | | | | | | W870 | Conestoga | |
| | | | | | | W877 | Krantz | |
| | | | | | | Sag. Gold | MS702-80 | |

selection (R) was calculated using Falconer & Mackay (1996):

$$R = i \cdot r_{xy} \cdot \sigma_p$$

where i is the selection intensity, $r_{xy}$ is the correlation between single- and eight-hill generations, and $\sigma_p$ is the square root of the phenotypic variance. The expected response to selection was then divided by $\sigma_p$ and expressed in percentage (R%) to compare different generations or selection intensities.

## Results

### *Progeny performance for tuber quality*

Families, years (single- and eight-hill generations) and the interaction family × year as fixed effects were significant ($p < 0.01$) for all tuber quality traits, except for specific gravity between years. When year was considered as fixed effect, there was not a significant ($p > 0.05$) difference between years for chip-color and specific gravity. The performance of the late blight families for tuber quality in single-hill generation in 1997 showed that, on average, families had marginal chip-color (4.2), acceptable tuber appearance (2.6), and high specific gravity (1.087) (Table 2). The Libertas family had the best chip-color, but did not significantly differ from Zarevo, Tollocan, and Stobrawa families. For tuber appearance, the B0718-3 family had the best ratings, but did not significantly differ from the Tollocan family. The Libertas family was superior for both specific gravity and chip-color and the Tollocan family for chip-color and tuber appearance.

The average performance of the families was slightly better in eight-hill plots than in single-hill generation (Table 3). Greta and B0718-3 families had the best chip-color. The B0718-3 family had the best and the Zarevo had the second best average tuber appearance rating. For specific gravity, Libertas, Zarevo, and Bzura families had the highest values. In eight-hill generation, only the B0718-3 family performed the best for more than one trait (chip-color and tuber appearance).

The correlation analysis at the clonal level showed significant coefficients between single- and eight-hill generations for the combined analysis of all late blight families for all tuber quality traits (Table 4). Tuber appearance had the smallest (0.27) and specific gravity had the highest correlation coefficient (0.67). Considering individual late blight families, significant correlations between single- and eight-hill generations for all individual families were found only for chip-color. Libertas family for specific gravity and B0718-3, Greta, Libertas, Stobrawa, and Tollocan families for tuber appearance had no significant correlation between single- and eight-hill generations. At the late

*Table 2.* Progeny performance of eight late blight resistant parents for tuber quality in single-hill generation in 1997

| Late blight families[a] | Evaluated clones | Chip-color[b] (ratings) | Tuber appearance[c] (ratings) | Specific gravity[d] |
|---|---|---|---|---|
| Libertas | 52 | 3.7 a[e] | 2.8 cdef | 1.098 a |
| Zarevo | 92 | 4.0 ab | 2.5 bc | 1.094 b |
| Tollocan | 71 | 4.0 ab | 2.4 ab | 1.084 e |
| Stobrawa | 34 | 4.1 ab | 2.6 bcd | 1.089 cd |
| Greta | 28 | 4.3 bc | 3.0 def | 1.088 cd |
| B0718-3 | 59 | 4.3 bc | 2.2 a | 1.077 f |
| Bertita | 40 | 4.3 bc | 3.1 f | 1.080 f |
| Bzura | 32 | 4.7 c | 2.6 bcd | 1.091 bc |
| Average | 51 | 4.2 | 2.6 | 1.087 |

[a] All evaluated clones are half-sibs in relation to the late blight resistant parent.
[b] Evaluated as a scale 1 to 9 of increasing color darkness.
[c] Evaluated as a scale 1 to 5 of increasing defects.
[d] Formula [weight in air / (weight in air – weight in water)].
[e] Means in columns followed by the same letter are not significantly different using Fisher's LSD at $\alpha = 0.05$.

*Table 3.* Progeny performance of eight late blight resistant parents for tuber quality in eight-hill generation in 1998

| Late blight families[a] | Evaluated clones | Chip-color[b] (ratings) | Tuber appearance[c] (ratings) | Specific gravity[d] |
|---|---|---|---|---|
| Greta | 28 | 3.2 a[e] | 2.5 c | 1.090 b |
| B0718-3 | 59 | 3.7 ab | 1.4 a | 1.078 d |
| Zarevo | 92 | 3.8 bc | 1.7 b | 1.095 a |
| Bertita | 40 | 3.9 bcd | 2.5 c | 1.080 cd |
| Libertas | 52 | 4.0 bcde | 2.5 c | 1.094 ab |
| Bzura | 32 | 4.2 cdef | 2.5 c | 1.097 a |
| Tollocan | 71 | 4.3 def | 2.3 c | 1.082 c |
| Stobrawa | 34 | 4.4 f | 2.2 c | 1.090 b |
| Average | 51 | 3.9 | 2.2 | 1.092 |

[a] All evaluated clones are half-sibs in relation to the late blight resistant parent.
[b] Evaluated as a scale 1 to 9 of increasing color darkness.
[c] Evaluated as a scale 1 to 5 of increasing defects.
[d] Formula [weight in air / (weight in air – weight in water)].
[e] Means in columns followed by the same letter are not significantly different using Fisher's LSD at $\alpha = 0.05$.

blight family level, high correlation coefficients were found for tuber appearance ($r = 0.78$, $p < 0.05$) and for specific gravity ($r = 0.92$, $p < 0.01$), but no significant correlation was found for chip-color (data not shown).

*Selection of clones with acceptable tuber quality in single-hill generation*

Libertas, Stobrawa, Zarevo, and Tollocan families had the highest percentage of clones with acceptable chip-color (Table 5). Greta and Bzura were the parents that transmitted chip-color to the smallest percentage of its offspring. A selection based on a light chip-color (ratings $\leq 3$) in single-hill generation eliminated 18% of the clones that would be selected in eight-hill generation. Alternatively, using the chip-color rating of 4 (acceptable quality) as a threshold for selection in single-hill generation eliminated only 7% of the clones that had ratings $\leq 3$ in eight-hill generation. The percentage of discarded clones with acceptable chip-color in eight-hill plots varied from 0% (Stobrawa family) to 25% (Greta family).

*Table 4.* Correlations at the clonal level between single- and eight-hill generations for individual late blight families and combined for all families

| Late blight families | Traits | Specific gravity (SG) | Tuber appearance (TA) | Chip-color (CC) |
|---|---|---|---|---|
| | SG | 0.43** | | |
| B0718-3 | TA | | ns[a] | |
| | CC | | | 0.28* |
| | SG | 0.56** | | |
| Bertita | TA | | 0.041* | |
| | CC | | | 0.60*** |
| | SG | 0.44* | | |
| Bzura | TA | | 0.48** | |
| | CC | | | 0.63*** |
| | SG | 0.59** | | |
| Greta | TA | | ns | |
| | CC | | | 0.43* |
| | SG | ns | | |
| Libertas | TA | | ns | |
| | CC | | | 0.38* |
| | SG | 0.68*** | | |
| Stobrawa | TA | | ns | |
| | CC | | | 0.72*** |
| | SG | 0.30* | | |
| Tollocan | TA | | ns | |
| | CC | | | 0.36* |
| | SG | 0.65*** | | |
| Zarevo | TA | | 0.25* | |
| | CC | | | 0.46*** |
| | SG | 0.67** | | |
| Combined | TA | | 0.27** | |
| | CC | | | 0.42** |

[a] ns = not significant, * $p \leq 0.05$, ** $p \leq 0.01$ and *** $p \leq 0.001$.

Stobrawa, B0718-3, Zarevo, Tollocan, and Bzura transmitted acceptable tuber appearance (ratings $\leq 3$) to more than 90% of the progeny (Table 6). An average of 32% of the clones that would have been rejected from single-hill generation for tuber appearance had good tuber appearance (ratings $\leq 2$) in eight-hill generation. However, a selection criterion of tuber appearance ratings $\leq 3$ would have eliminated only 4% of the clones that would be selected in eight-hill generation. The percentage of discarded clones with acceptable tuber appearance in eight-hill generation varied from 0% (Bzura family) to 14% (Greta family).

Bzura, Libertas, Zarevo, and Stobrawa transmitted acceptable specific gravity to more than 90% of the offspring (Table 7). The selection of clones with specific gravity $\geq 1.080$ (acceptable range) in single-hill generation resulted in 82% selection and would have eliminated only 4% of the clones that would be selected in eight-hill generation. The percentage of discarded clones that had acceptable specific gravity in eight-hill generation varied from 0% (Bzura and Stobrawa families) to 11% (Greta family).

The expected response to selection showed similar gain for specific gravity selecting in the single- or in eight-hill generation (Table 8). However, selecting in the single-hill generation resulted in slightly higher gain for chip-color and tuber appearance than in eight-hill generation, even when a higher selection intensity was used.

### *Identification of clones with acceptable chip-processing or tablestock quality*

The identification of clones with acceptable chip-processing quality was based on the threshold for selection identified for each tuber quality characteristic (Tables 5, 6, and 7). The selection was first done for chip-color ratings $\leq 4$ followed by tuber appearance ratings $\leq 3$ and a specific gravity $\geq 1.080$. Using this selection criterion, a total of 206 clones (50%) and 228 clones (56%) were identified in single- and eight-hill generations, respectively, as possessing acceptable chip-processing quality. A total of 146 clones were selected in both generations, which was 71% of the clones identified in single-hill generation. If in the single-hill generation the same selection criteria was applied followed by selecting clones in the eight-hill generation with chip-color ratings $\leq 3$, tuber appearance ratings $\leq 2$ and specific gravity $\geq 1.080$, an expected response to selection of 0.09%, –6.06% and –3.22% would be obtained (data not shown).

The identification of clones for tablestock was done based solely on tuber appearance ratings $\leq 3$. A total of 367 clones (90%) and 387 clones (95%) were selected, respectively, in single- and eight-hill generations. Five parents (Zarevo, Stobrawa, B0718-3, Tollocan, and Bzura) transmitted acceptable tablestock quality to more than 90% of the progeny in both generations of selection. A total of 350 clones were selected in both generations, which was 95% of the clones identified in single-hill generation.

## Discussion

In this study we crossed unadapted late blight resistant parents with adapted susceptible clones to select

*Table 5.* Percentage comparison of clones with acceptable chip-color quality in single- and eight-hill generations

| Late blight families[a] | Chip-color ratings $\leq 3^b$ | | Chip-color ratings $\leq 4^b$ | |
|---|---|---|---|---|
| | Selected | Not selected[c] | Selected | Not selected[c] |
| Libertas | 44.2 | 9.6 | 80.8 | 1.9 |
| Stobrawa | 32.4 | 11.8 | 76.5 | 0.0 |
| Zarevo | 28.3 | 22.8 | 71.7 | 5.4 |
| Tollocan | 52.1 | 11.3 | 69.0 | 7.0 |
| Bertita | 32.5 | 17.5 | 60.0 | 7.5 |
| B0718-3 | 28.8 | 20.3 | 59.3 | 11.9 |
| Greta | 21.4 | 53.6 | 57.1 | 25.0 |
| Bzura | 21.9 | 9.4 | 56.3 | 3.1 |
| Total | 34.3 | 18.4 | 67.6 | 7.1 |

[a] All evaluated clones are half-sibs in relation to the late blight resistant parent.
[b] Evaluated on a scale 1 to 9 of increasing color darkness in single-hill plots.
[c] Not selected with chip-color ratings $\leq 3$ in eight-hill generation.

*Table 6.* Percentage comparison of clones with acceptable tuber appearance quality in single- and eight-hill generations

| Late blight families[a] | Tuber app. ratings $\leq 2^b$ | | Tuber app. ratings $\leq 3^b$ | |
|---|---|---|---|---|
| | Selected | Not selected[c] | Selected | Not selected[c] |
| Stobrawa | 35.3 | 50.0 | 100.0 | 0.0 |
| B0718-3 | 67.8 | 28.8 | 94.9 | 3.4 |
| Zarevo | 48.9 | 40.2 | 93.5 | 3.3 |
| Tollocan | 49.3 | 22.5 | 91.5 | 1.4 |
| Bzura | 50.0 | 15.6 | 90.6 | 0.0 |
| Libertas | 34.6 | 34.6 | 86.5 | 9.6 |
| Greta | 21.4 | 35.7 | 82.1 | 14.3 |
| Bertita | 22.5 | 27.5 | 72.5 | 7.5 |
| Total | 44.4 | 32.1 | 90.0 | 4.4 |

[a] All evaluated clones are half-sibs in relation to the late blight resistant parent.
[b] Evaluated on a scale 1 to 5 of increasing defects in single-hill plots.
[c] Not selected with tuber appearance ratings $\leq 2$ in eight-hill generation.

for tuber quality traits. Selection within these crosses was also done for foliar late blight resistance based upon greenhouse and field tests, in which 80 clones were identified as possessing moderate to strong late blight resistance to the US8 genotype of *P. infestans* (Bisognin et al., 2002). Cultivar releases over the past century suggest that tuber quality should be considered a market-limiting trait (Douches et al., 1996). Therefore, even in breeding disease resistant cultivars, tuber quality needs to be a high priority for selection and these results showed that selection for tuber quality could be initiated at the single-hill generation. Since Tollocan and B0718-3 transmit a higher level of late blight resistance to the highest percentage of the offspring (Bisognin et al., 2002), these two parents offer the best chance for combining resistance with tuber quality traits. Tollocan and B0718-3 are also the best candidates to apply the strategy proposed here, in which selection for tuber quality precedes selection for late blight resistance.

The selection of parents for their potential to transmit important traits to the offspring is an important step in a potato breeding program (Tai & Young, 1984; Thill & Peloquin, 1995). In this study we identified late blight resistant parents that also transmit tuber quality traits to the offspring. B0718-3 and Tollocan

*Table 7.* Percentage comparison of clones with acceptable specific gravity quality in single- and eight-hill generations

| Late blight families[a] | Specific gravity ≥ 1.080[b] | |
|---|---|---|
| | Selected | Not selected[c] |
| Bzura | 100.0 | 0.0 |
| Libertas | 98.1 | 1.9 |
| Zarevo | 96.7 | 1.1 |
| Stobrawa | 91.2 | 0.0 |
| Greta | 89.3 | 10.7 |
| Tollocan | 76.1 | 8.5 |
| Bertita | 55.0 | 7.5 |
| B0718-3 | 52.5 | 6.8 |
| Total | 82.1 | 4.4 |

[a] All evaluated clones are half-sibs in relation to the late blight resistant parent.
[b] Formula [weight in air / (weight in air – weight in water)].
[c] Not selected with specific gravity ≥ 1.080 in eight-hill generation.

*Table 8.* Percentage of expected response to selection (R%) in single- and eight-hill clonal generations of potato tuber quality traits

| Tuber quality traits | Single-hill | Eight-hill |
|---|---|---|
| Chip-color ≤ 3[a] | –13.18 | –11.87 |
| Chip-color ≤ 4 | –7.21 | –5.77 |
| Tuber appearance ≤ 3[b] | –7.71 | –6.45 |
| Tuber appearance ≤ 2 | –1.76 | –1.34 |
| Specific gravity ≥ 1.080[c] | 0.29 | 0.25 |

[a] Evaluated as a scale 1 to 9 of increasing color darkness.
[b] Evaluated as a scale 1 to 5 of increasing defects.
[c] Formula [weight in air / (weight in air – weight in water)].

families had the highest tuber appearance ratings in single-hill generation. The B0718-3 family also had the highest tuber appearance rating average and the highest percentage of selected clones with a tuber appearance rating ≤ 2. Bzura, Zarevo, and Libertas families had the highest specific gravity in both generations of selection and the highest percentage of selected clones. The fact that late blight resistant parents were crossed with a different number and, in most cases, to different susceptible parents might have influenced family performance. Therefore, all family differences found in this study should not be attributed solely to the late blight resistant parent, but it was clear that those parents do differ in tuber quality traits transmitted to the offspring. Bzura and Stobrawa were crossed to the same susceptible parents and Greta was crossed to four out of five susceptible parents. Greta family had the highest chip-color rating and Bzura family had the highest specific gravity in eight-hill generation. Moreover, late blight family differences can not be attributed to the phenotypic selection done at harvest time, since the same selection intensity was applied to all crosses.

Considering only the percentage of selected clones, Libertas, Stobrawa, Zarevo, and Tollocan were the best parents for transmitting chip-color; B0718-3, Stobrawa, Zarevo, and Tollocan for transmitting tuber appearance; and Bzura, Libertas, Zarevo, and Stobrawa for transmitting specific gravity to the highest percentage of the offspring. The Stobrawa family, for chip-color, and the Stobrawa and Bzura families, for tuber appearance and specific gravity, had all selected clones identified in single-hill generation, but the Greta family had the highest percentage of non-selected clones for all traits. Stobrawa, Bzura and Greta have similar contribution of susceptible parents. Therefore, the percentage of selected clones was effective in showing differences among late blight families when selection for tuber quality was applied at the single- or eight-hill generations. Interaction between parents with years would increase the percentage of discarded clones as in the case of Greta family.

Attempting to breed for tuber quality traits in potato, a phenotypic selection based on tuber appearance, number, shape, and internal defects at harvest time in single-hill generation was able to reduce the number of evaluated clones from 4,750 to 408. Comparing with other traits considered for phenotypic selection, Tai (1975) determined that tuber appearance was the only trait to directly affect selection and Neele et al. (1991) found tuber yield to be the decisive component for selection. From the 408 clones, 68% possessed acceptable chip-color, 90% possessed acceptable tuber appearance, and 82% possessed desirable specific gravity in single-hill generation. If a moderate selection, based upon tuber appearance ratings ≤ 3 for tablestock, were employed no more than 4% of the clones discarded in eight-hill generation would have been selected for each trait (chip-color, tuber appearance, and specific gravity) in eight-hill generation.

The high percentage of clones selected in both generations is supported by the significant coefficients of correlation obtained between single- and eight-hill generations and by the expected response to selection. Correlation was considered the best estimate to determine relationship between early generations of

selection in potato breeding (Maris, 1988). Chip-color and tuber appearance had smaller correlation coefficients than specific gravity at the clonal level, while at the family level, there was no correlation between generations for chip-color. As a consequence, with higher correlation coefficients, 96% of clones with desirable specific gravity ($\geq$ 1.080) in eight-hill could be identified in single-hill generation using the same selection criteria. High correlation was expected for specific gravity because this trait has been previously reported to have a small genotype $\times$ environment interaction (Killick & Simmonds, 1974). Haynes & Wilson (1992) also found high positive correlation for specific gravity between the two first generations in the field.

The correlation between single- and eight-hill generations suggests that moderate selection intensity should be applied in single-hill generation for tuber appearance and chip-color. Tuber appearance had lower correlation coefficients at the clonal level than chip-color and had no significant correlations between single- and eight-hill generations for five individual families. Tuber appearance was also the only trait significantly affected by year (single- and eight-hill generations). Chip-color had significant correlations for all individual late blight families, but small correlation (0.42) for all combined families. As opposed to specific gravity, selecting clones with desirable tuber appearance (ratings $\leq$ 2) and chip-color (ratings $\leq$ 3) would eliminate a significant percentage of clones that would have desirable quality based on eight-hill generation. However, selecting clones with acceptable tuber appearance (ratings $\leq$ 3) and chip-color (ratings $\leq$ 4) in single-hill generation would discarded a very small percentage of clones that would be selected in eight-hill generation with desirable quality. The expected response to selection in the single- and in the eight-hill generations also supports that selection can be initiated in the single-hill generation. Since the combined expected response to selection in the single and eight-hill generations (–1.76% and –3.22% for tuber appearance, –7.21% and –6.06% for chip-color) would be similar to the usual procedure of selecting only in the eight-hill generation, the best procedure is to use moderate selection intensity for tuber appearance and chip-color in the single-hill generation. Tai (1975) also found low correlation for tuber appearance at the clonal level, but medium to high correlations at the family level. Neele et al. (1991) found high heritability estimates for tuber appearance components such as tuber shape (0.61), regularity of tuber shape (0.60), skin color (0.86), eye depth (0.69), number of tubers (0.54), and average tuber weight (0.64).

The fact that clones with desirable quality, for specific gravity, and clones with acceptable quality (moderate selection intensity), for chip-color and tuber appearance, can be applied at single-hill generation is very important, since there is a gain of one year in the selection process for tuber quality. Thill & Peloquin (1995) reported that selection decisions for cold chip-processing at the single-hill generation did not differ from those in late generations and could potentially save four years in the breeding cycle. A low to moderate selection pressure in early generations was found in other studies as the best choice to reach a balance between gain from selection and elimination of valuable clones (Tai & Young, 1984; Maris, 1988). Neele et al. (1989) determined that phenotypic selection in early generations was optimized when about 32% of the clones were selected in the first clonal generation. Anderson & Howard (1981) found a higher number of discarded than selected clones comparing the first two generations of selection. In comparison, the post-harvest selection used here reduced the initial number of clones from 4,750 to 206, through selection for chip-processing quality (4.3% of selected clones), and to 367, through selection for tablestock quality (7.7% of selected clones). However, the evaluation in single- and eight-hill generations has some key differences that should be considered in the selection process. The performance of plants grown either from small greenhouse tubers or from transplants is often very distinct from that of the same plants grown from regular sized seed tubers (Davies & Johnston, 1974). In addition, difference in the in-row spacing (75 cm vs. 30 cm) may influence plant competition. These factors can reduce the heritability in single-hill generation for many traits resulting in poor selection efficiency (Tai & Young, 1984). Sample size is another concern for evaluations in single-hill generation. The accuracy of the specific gravity estimation decreases rapidly for samples smaller than 10 tubers (Lulai & Orr, 1979).

Different traits are of primary importance when developing cultivars with chip-processing or tablestock quality. Chip-color is the most important trait for the chip-processing industry (Thill & Peloquin, 1995) followed by tuber appearance (freedom from internal and external defects) and high dry matter. For tablestock cultivars, tuber appearance is the most important trait (Dale & Mackay, 1994). If the objective is to develop cultivars for chip-processing industry and tablestock, the tuber quality information from single-hill genera-

tion could be used to assist in making better decisions in later generations of selection for other traits including disease resistance. Also, multitrait selections based on data from different environmental conditions might increase the probability of identifying clones possessing an acceptable balance of key agronomic traits. Haynes & Wilson (1992) found that the probability of selecting the same clone in the later generation was 1.7 and 1.9 times higher for clones selected based on horticultural characteristics than on specific gravity.

In summary, moderate selection intensity for tuber quality traits (chip-color ratings $\leq 4$, tuber appearance ratings $\leq 3$ and a specific gravity $\geq 1.080$) can be initiated at the single-hill generation in crosses to select for late blight resistance. The identification of superior clones for tuber quality in single-hill generation reduces each selection cycle in one year and reduces the number of clones for late blight testing. Intermating selected clones, a higher percentage of clones possessing acceptable chip-processing or tablestock quality is expected in following cycles of genotypic recurrent selection. Moreover, Tollocan and B0718-3 are the best parents for improving late blight resistance and offer the best opportunity for the application of tuber quality selection in advance of disease resistance selection for combining desirable traits. The progenies of Tollocan and B0718-3 could also be combined with the offspring of other high valuable sources of late blight resistance for the development of cultivars with durable resistance.

## References


Anderson, J.A.D. & H.W. Howard, 1981. Effectiveness of selection in the early stages of potato breeding programmes. Potato Res 24: 289–299.

Bisognin, D.A., D.S. Douches, K. Jastrzebski & W.W. Kirk, 2002. Identification and selection of potatoes resistant to the US8 genotype of *Phytophthora infestans* from crosses between resistant and susceptible clones. Euphytica (In press).

Colon, L.T., D.J. Budding, L.C.P. Keizer & M.M.J. Pieters, 1995. Components of resistance to late blight (*Phytophthora infestans*) in eight South American *Solanum* species. European J Plant Pathol 101: 441–456.

Dale, M.F.B. & G.R. Mackay, 1994. Inheritance of table and processing quality. In: J.E. Bradshaw & G.R. Mackay (Eds.), Potato Genetics, pp. 285–315. CAB International, Cambridge, 552 p.

Davies, H.T. & G.R. Johnston, 1974. Reliability of potato selection in the first clonal generation. Amer Potato J 51: 8–11.

Douches, D.S., D. Maas, K. Jastrzebski & R.W Chase, 1996. Assessment of potato breeding progress in the USA over the last century. Crop Sci 36: 1544–1552.

Douches, D.S., W.W. Kirk, K. Jastrzebski, C. Long & R. Hammerschmidt, 1997. Susceptibility of potato varieties and advanced breeding lines (*Solanum tuberosum* L.) to *Phytophthora infestans* (Mont.) de Bary in greenhouse screenings. Amer Potato J 74: 75–86.

Falconer, D.S. & T.F.C. MacKay. 1996. Introduction to Quantitative Genetics. Fourth edition. Prentice Hall, 464 p.

Frey, K.J. & T. Horner, 1957. Heritability in standard units. Agron J 49: 59–62.

Fry, W.E. & S.B. Goodwin, 1997. Resurgence of the Irish potato famine fungus. Bioscience 47: 363–371.

Haynes, K.G. & D.R. Wilson, 1992. Correlations for yield and specific gravity between potato tuberling and second year field generations. Amer Potato J 69: 817–826.

Helgeson, J.P., J.D. Pohlman, S. Austin, G.T. Haberlach, S.M. Wielgus, D. Ronis, L. Zambolin, P. Tooley, J.M. McGrath, R.V. James & W.R. Stevenson, 1998. Somatic hybrids between *Solanum bulbocastanum* and potato: a new source of resistance to late blight. Theor Appl Genet 96: 738–742.

Kamoun, S., E. Huitema & V.G.A.A. Vleeshouwers, 1999. Resistance to oomycetes: a general role for the hypersensitive response? Trends Plant Sci 4: 196–200.

Kelly, J.D., J.M. Kolkman & K. Schneider, 1998. Breeding for yield in dry beans (*Phaseolus vulgaris* L.). Euphytica 102: 342–356.

Killick, R.J. & N.W. Simmonds, 1974. Specific gravity of potato tubers as a character showing small genotype-environment interactions. Heredity 32: 109–112.

Love, S.L., J.J. Pavek, A. Thompson-Johns & W. Bohl, 1998. Breeding progress for potato chip quality in North American cultivars. Amer J Potato Res 75: 27–36.

Lulai, E.C. & P.H. Orr, 1979. Influence of potato specific gravity on yield and oil content of chips. Amer Potato J 56: 379–390.

Maris, B., 1988. Correlations within and between characters between and within generations as a measure for the early generation selection in potato breeding. Euphytica 37: 205–224.

Neele, A.E.F., H.J. Nab, M.J. de Jongh de Leeuw, A.P. Vroegop & K.M. Louwes, 1989. Optimizing visual selection in early clonal generations of potato based on genetic and economic considerations. Theor Appl Genet 78: 665–671.

Neele, A.E.F., H.J. Nab & K.M. Louwes, 1991. Components of visual selection in early clonal generations of a potato breeding programme. Plant Breed 106: 89–98.

SAS Institute, 1995. The SAS System for Windows. Release 6.12. SAS Institute, Cary, NC.

Tai, G.C.C., 1975. Effectiveness of visual selection of early clonal generation seedlings of potato. Crop Sci 15: 15–18.

Tai, G.C.C. & D.A. Young, 1984. Early generation selection for important agronomic characteristics in a potato breeding program. Amer Potato J 61: 419–434.

Thill, C.A., S.J. Peloquin, 1995. A breeding method for accelerated development of cold chipping clones in potato. Euphytica 84: 73–80.

Umaerus, V., M. Umaerus, L. Erjefalt & B.A. Nilsson, 1983. Control of *Phytophthora* by host resistance: problems and progress. In: D.C. Erwin, S. Bartnicki-Garcia & P.H. Tsao (Eds.), *Phytophthora infestans*: Its Biology, Taxonomy, Ecology, and Pathology, pp. 315–326. The American Phytopathological Society. St. Paul, Minnesota.