

FINE SCREENING *SOLANUM* (POTATO) GERMPLASM ACCESSIONS FOR RESISTANCE TO COLORADO POTATO BEETLE

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Abstract

This study was conducted to investigate the utility of systematic screening at the genotype level within *Solanum* accessions highly resistant to the Colorado potato beetle. Evaluations of clonally replicated genotypes showed that most accessions reported to be uniform when screened as populations contained small but significant variation among genotypes for resistance to oviposition, larvae, and defoliation, differences for numbers of larvae being most common. Adult counts and percentage defoliation were not as useful in evaluating among-genotype variability in beetle resistance. Genotypes of *S. pinnatisectum* WRF 343 and *S. tarijense* PI 473227 were the most uniformly and highly resistant to Colorado potato beetle. Genotypes of *S. berthaultii* PI 473331, *S. chacoense* PI 473405, and *S. tarijense* PI 473336 were moderately to highly resistant, and genotypes of *S. bukasovii* PI 473494 and *S. canasense* PI 230511 were uniformly susceptible to Colorado potato beetle. Nonparametric correlation analyses indicated that number of egg masses, small larvae, large larvae, and defoliation scores were positively correlated, negatively correlated, or not correlated, depending on the species. One generation of selection attempting to segregate resistance and susceptibility in nearly uniform and highly resistant *S. pinnatisectum* WRF 343 resulted in "divergent" populations that could not be distinguished from each other or the base population. Thus, through genotype ("fine") screening and selection, we showed that some existing populations are virtually pure for extreme resistance. Use of individuals from such families would make screening breeding populations more efficient, and reduce the risk of losing resistance genes that have non-dominant effects. Fine screening, recurrent selection, and maintenance of such elite populations is recommended as an extension of population-based evaluation usually done by genebanks.

Compendio

El objetivo de este estudio fue investigar la utilidad de la evaluación sistemática a nivel de genotipo entre accesiones de *Solanum* con alta

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resistencia al gorgojo colorado de la papa. A pesar que muchas de las accesiones analizadas a nivel poblacional habian sido reportadas como uniformes, la evaluación de genotipos reproducidos clonalmente demostró que existe una variación significativa en la resistencia a la postura de huevos, larvas y defoliación, siendo la diferencia en el número de larvas la más común. El conteo de adultos y el porcentaje de defoliación no fue tan útil en la evaluación de variabilidad entre genotipos con resistencia al gorgojo. Los genotipos de *S. pinnatisectum* WRF 343 y *S. tarijense* PI 473227 mostraron la mayor uniformidad y resistencia al gorgojo colorado de la papa. Los genotipos de *S. berthaultii* PI 473331, *S. chacoense* PI 473405, y *S. tarijense* PI 473336 mostraron entre moderada y alta resistencia, y los genotipos de *S. bukasovii* PI 473494 y *S. canasense* PI 230511 fueron uniformemente susceptibles al gorgojo. El análisis de correlación no paramétrica indicó que el número de masas de huevos, larvas pequeñas, larvas grandes y defoliación tienen una correlación positiva, negativa, o no tienen correlación, dependiendo de las especies. El intento de utilizar una generación de selección divergente para producir segregación de resistencia y susceptibilidad en una accesión de relativa uniformidad y con alta resistencia (*S. pinnatisectum* WRF 343) no fue exitoso. En consecuencia, este estudio demuestra la existencia de poblaciones esencialmente puras para la resistencia extrema y por ello no necesitan ser previamente mejoradas para ser utilizadas en los programas de mejoramiento de germoplasma. En conclusión, la evaluación de genotipos o evaluación "fina" y selección podrían ser útiles para la identificación o el establecimiento de poblaciones en las cuales la resistencia máxima es verdadera (homozygota). La evaluación fina, selección recurrente, y el mantenimiento de dichas poblaciones sería una útil extensión de las evaluaciones basadas en poblaciones, las cuales son usualmente hechas por los bancos de germoplasma.

Introduction

The Colorado potato beetle, *Leptinotarsa decemlineata* Say (Coleoptera: Chrysomelidae), is the most important defoliator of potato in North America (13). Insecticide resistance is widespread in this species and can extend to all major classes of insecticides making control increasingly difficult and costly (8). The development of Colorado potato beetle-resistant cultivars could greatly aid in the management of this pest (3).

Previous research has characterized natural Colorado potato beetle resistance mechanisms, their inheritance, and to a limited extent, the partitioning of resistance within tuber-bearing *Solanum* species. Some species have been shown to resist Colorado potato beetle by means of glandular trichomes (5, 10), which can vary in density and composition (4). Foliar glycoalkaloids can also impart resistance to the Colorado potato beetle (14). Desirable types of and levels of glycoalkaloids often vary considerably within accessions (2, 15), and other defense mechanisms can also be present (6).

Thus, resistance to Colorado potato beetle varies among species, among accessions within species (1, 6), and within accessions (11).

The US potato genebank (NRSP-6, Sturgeon Bay, WI) has responsibility to collect, classify, preserve, evaluate and distribute germplasm of potato (*Solanum* spp.). Ideally, this includes stocks with extreme expression of useful traits (*e.g.*, Colorado potato beetle resistance). While the potato of commerce is a clonal crop, most species occur in nature as populations which reproduce by true seeds, a convenient form of preservation for genebank operations. Since most *Solanum* species are outcrossers, such populations are potentially heterozygous and heterogeneous for traits of interest.

Genebank-sponsored screening among NRSP-6's approximately 4,300 accessions comprising over 100 species has nearly always been done on seedling populations. While Flanders *et al.* (6) note that species is a useful predictor of predominant resistance or susceptibility to insect pests, their data show that substantial variability occurs among accessions. Only in *S. pinnatisectum* were all accessions classified as uniformly highly resistant to damage by the Colorado potato beetle. Resistances to other insect species were also inconsistent within potato species (6). Among researchers, inconsistent scores of resistance to Colorado potato beetle within accessions are also common. Of 1,052 NRSP-6 accessions tested for resistance to Colorado potato beetle defoliation by multiple researchers and scored as susceptible, intermediate, or resistant, different scores were reported for 425 accessions (over 40%). Nearly 140 or 13% of the accessions were reported both as resistant and as susceptible.

Inconsistent ratings of resistance among researchers could have several explanations. There may have been different methods used among researchers, or different levels of pest pressure, or different parameters measured. This could result in conflicting evaluation reports even when screening homozygous populations. When screening heterogeneous populations, additional ambiguity can result. Researchers may, by chance, screen a genetically different sample, especially when small populations are screened. Researchers may also interpret heterogeneity differently. One might score a heterogeneous accession as "intermediate" based on the average rating of individuals, while another might rate the same accession "resistant" or "susceptible" due to the presence of outstanding individuals.

The potato breeder desires that as many useful genes as possible are contributed by the wild parent, and that gametic variation with respect to resistance, and resulting need for progeny testing, is minimized. Assuming limited interactions of resistance factors and the genome or cytoplasm of the cultivated parent, this is most efficiently accomplished by using wild parents which carry all available genes for resistance in the fixed (homozygous) condition. Such stocks would also permit more efficient synthesis of superior diploids for use in breeding via 2n gametes (12). Thus, this re-

search was initiated to characterize individuals within reputedly resistant populations in order to identify existing populations with uniform maximum resistance and/or improve the uniformity of existing populations by selection.

Materials and Methods

Materials Screened, 1991—Accessions evaluated were as follows: *S. chacoense* PI 209412, *S. chacoense* PI 473405, *S. tarijense* PI 473227, and *S. tarijense* PI 473336. *Solanum chacoense* PI 209412 and *S. tarijense* PI 473227 were reported by Carter (1) to exhibit a uniformly high resistance to Colorado potato beetle defoliation. However, she tested unreplicated genotypes (seedling populations). An additional accession of *S. chacoense* and *S. tarijense* resistant to Colorado potato beetle defoliation (9) was also selected for testing.

Propagation and Evaluation, 1991—Tubers for this experiment were produced by seedlings grown during winter in a greenhouse at NRSP-6, Sturgeon Bay. Tubers of 11 to 18 genotypes per accession were planted 3 June at the University of Minnesota Agricultural Experiment Station, Rosemount. Plots of four plants were replicated five times in a randomized complete block design. Row and plant spacing were 1.0 m and 0.45 m, respectively. Rainfall was supplemented twice with 3 cm of overhead irrigation during the growing season. Plants were evaluated for resistance to second generation larvae and adults. Individual whole plants were evaluated on each observation date. On 24 July and 5 August, counts were made of small larvae (instars I and II), large larvae (instars III and IV), and adults. On 5 and 13 August, visual estimates of defoliation were made using a 0-4 scale: 0 = <3%; 1 = 3-10%; 2 = 11-25%; 3 = 26-50%; and 4 = 51-100% defoliation. Larval and adult counts, and defoliation were summed over both sample dates to determine the mean number of insects or injury per plant per date.

Materials Screened, 1993—We retested most of the accessions evaluated in 1991, but the genotypes within each accession were different between years. *S. chacoense* PI 209412 was not retested because it propagated poorly via cuttings. Four additional accessions were included in 1993: *S. berthaultii* PI 473331, *S. bukasovii* PI 473494, *S. canasense* PI 230511, and *S. pinnatisectum* WRF 343. Carter (1) reported *S. pinnatisectum* WRF 343 as uniformly resistant, and *S. bukasovii* PI 473494 as uniformly susceptible (this being used as a check). *S. berthaultii* PI 473331 and *S. canasense* PI 230511, both reported resistant to Colorado potato beetle defoliation (9), were also added.

Propagation and Evaluation, 1993—Accessions were grown in spring as seedlings in the greenhouse at NRSP-6. Rooted cuttings were produced to replicate individual genotypes instead of tubers. This was done to avoid the delayed, staggered emergence of tubers experienced in 1991. On 9 June, cuttings of 14 to 18 genotypes from each of seven accessions were planted at the University of Minnesota Agricultural Experiment Station, Crookston.

Plots of four plants were replicated four times in a randomized complete block design. Fewer plants were evaluated in 1993 than in 1991 because materials were limited. Every two rows of treatments were alternated with two rows of Red LaSoda potatoes, which had been planted in mid-May to retain beetles in the field. Row and plant spacing were 1.0 m and 0.3 m, respectively. On 16 July adult beetles were collected from a nearby potato field and a single insect was placed on each treatment plant to supplement the naturally occurring population. Individual whole plants were evaluated on each observation date. On 15, 22 and 29 July, counts were made of small larvae (instars I and II), large larvae (instars III and IV), summer adults, and second generation egg masses. Counts of each life stage were averaged across sampling dates. Plants were scored for defoliation on 29 July and 12 August using the same 0-4 scale as in 1991. On the first date, individual plants were visually scored as slightly defoliated (0-2 defoliation score) or heavily defoliated (3-4 defoliation score). On the second date, visual estimates of defoliation were made using the entire 0-4 scale.

Materials Screened, 1995—We evaluated three *S. pinnatisectum* WRF 343 families: (1) the genotypes examined in 1993, (2) intermates between the most resistant genotypes identified in 1993, and (3) intermates between the most susceptible genotypes identified in 1993. In 1993, these resistant parents had no egg masses, larvae, or defoliation, and the susceptible parents averaged one egg mass per 20 plants, one larva per three plants, and suffered no defoliation. In 1993, both *S. pinnatisectum* WRF 343 and *S. tarijense* PI 473227 were highly resistant. We selected *S. pinnatisectum* WRF 343 for this study because it had exhibited significant variability from which to select resistant and susceptible parental genotypes. *Solanum tarijense* PI 473227 had slight but significant defoliation in 1991, which identified it as less extreme in resistance and therefore less desirable for further study.

Propagation and Evaluation, 1995—To produce the resistant and susceptible families screened in 1995, we planted tubers from the four most resistant and four most susceptible genotypes evaluated in 1993 and bulk intermated within each group. The resulting seeds and tubers of the original *S. pinnatisectum* WRF 343 genotypes evaluated in 1993 were grown, and cuttings were made to replicate genotypes. On 5 June, cuttings of 16 to 18 genotypes from each family were planted at the University of Minnesota Agricultural Experiment Station, Rosemount. Plots of 10 plants were replicated three times in a randomized complete block design. Row and plant spacing were 1.0 m and 0.3 m, respectively. Individual whole plants were evaluated on each observation date. On 1 August, counts were made of summer adults. On 1 and 11 August, plants were examined for the presence of larvae, second generation egg masses, and defoliation. On 4 August, adult beetles were collected from a nearby potato field that was not treated with insecticide and placed on the test plants to augment the existing beetle population. Three or four adults were placed on each of the

middle three plants of each plot, *i.e.*, 10 adults per each 10-plant plot. Plants were scored for vigor on 11 August using a 1-3 size scale: 1 = small; 2 = medium; 3 = large plants.

Within accessions, genotypic variation was examined using nonparametric analysis of variance. We used the Kruskal-Wallis test, or Friedman's test (16) if there were significant differences among blocks. Significance of differences between accessions was determined by modified Mann-Whitney *U* test (6). Data were transformed to $\log_{10}(x + 1)$ to normalize variances. In 1993, Spearman's correlation coefficients (r) were calculated for all resistance parameters. WinSTAR (Anderson-Bell Corp., Arvada, CA, USA) software was used for all statistical analyses.

Results

Response of the Materials, 1991—All accessions were highly resistant to Colorado potato beetle defoliation. Defoliation was significantly different among genotypes of three of four accessions, however, even the most susceptible genotype averaged less than 10% defoliation. Defoliation ratings were as follows (accession mean, range of genotype means, significance value of differences among genotypes): *S. chacoense* PI 209412 (0.0, 0.0-0.1, $P > 0.05$), *S. chacoense* PI 473405 (0.1, 0.0-0.7, $P < 0.01$), *S. tarijense* PI 473227 (0.1, 0.0-0.4, $P < 0.01$), and *S. tarijense* PI 473336 (0.3, 0.0-0.8, $P < 0.05$). Only *S. chacoense* PI 473405 showed significant differences among genotypes for resistance to beetles. The number of beetles per plant in each accession was as follows (accession mean, range of genotype means, significance value of differences among genotypes): *S. chacoense* PI 209412 (0.0, 0.0-0.1, $P > 0.05$), *S. chacoense* PI 473405 (0.5, 0.0-4.7, $P < 0.01$), *S. tarijense* PI 473227 (0.0, 0.0-0.1, $P > 0.05$), and *S. tarijense* PI 473336 (0.1, 0.0-0.2, $P > 0.05$). At least one genotype in each accession had no larvae, adults, or defoliation. Few beetles were present in experimental plots although susceptible cultivars in adjacent fields were more than 50% defoliated. Adult beetles did not move readily into the field of resistant accessions, were repelled before or after ovipositing, or few larvae survived.

Response of the Materials, 1993—Again, numbers of beetles and defoliation in the resistant accessions were consistently low despite severe defoliation of the interplanted Red LaSoda. Although these accessions were selected for apparent uniformity of resistance, significant differences among genotypes within accessions were noted for at least one resistance parameter in all except one accession (Table 1, Fig. 1). Over all seven accessions, differences among genotypes within accessions were found most often in numbers of small larvae (6 accessions) and numbers of large larvae (5 accessions). Even the most susceptible accession (*S. bukasovii*) averaged fewer than 0.5 adults per plant (data not presented). On 29 July, the percentage of plants within each accession scored as heavily defoliated was as follows:

TABLE 1.—*Fine screening Solanum accessions for Colorado potato beetle resistance, 1993.*

Species, accession	Number of beetles per plant			Defoliation rating ^a
	Small larvae	Large larvae	Egg masses	
<i>S. berthaultii</i> PI 473331	2.1±0.4 C***	1.5±0.3 C**	0.3±0.0C*	0.3±0.6 C
Mean ^b	0.0 - 5.0	0.0 - 4.2	0.0 - 0.8	0.0 - 0.7
Range ^c				
<i>S. bukasovii</i> PI 473494	9.2±0.6 A*	8.7±0.6 A*	1.2±0.1 A	3.4±0.1 A
Mean ^b	4.6 - 17.1	4.4 - 12.3	0.7 - 1.9	2.3 - 4.0
Range ^c				
<i>S. canasense</i> PI 230511	8.0±0.5 B *	6.2±0.4 B*	0.5±0.0 B*	2.6±0.1 B**
Mean ^b	2.7 - 11.9	2.9 - 12.3	0.1 - 1.0	1.3 - 3.3
Range ^c				
<i>S. chacoense</i> PI 473405	0.9±0.1 D***	0.7±0.1 D***	0.1±0.0 D	0.0±0.0 D
Mean ^b	0.0 - 2.7	0.1 - 2.8	0.0 - 0.2	0.0 - 0.0
Range ^c				
<i>S. pinnatisectum</i> WRF 343	0.0±0.0 E*	0.0±0.0 E	0.0 + 0.0 E	0.0±0.0 D
Mean ^b	0.0 - 0.4	0.0 - 0.5	0.0 - 0.1	0.0 - 0.0
Range ^c				
<i>S. tarijense</i> PI 473227	0.1±0.0 E	0.0±0.0 E	0.0±0.0 E	0.0±0.0 D
Mean ^b	0.0 - 0.4	0.0 - 0.3	0.0 - 0.1	0.0 - 0.0
Range ^c				
<i>S. tarijense</i> PI 473336	1.2±0.2 D***	0.9±0.2 D***	0.1±0.0 D*	0.2±0.0 C***
Mean ^b	0.0 - 3.7	0.0 - 2.2	0.0 - 0.3	0.0 - 1.4
Range ^c				

Asterisks indicate significant differences among genotypes within accessions (Kruskal-Wallis 1-way ANOVA): * $P \leq 0.05$; ** $P \leq 0.01$; *** $P \leq 0.001$. Accession means within columns followed by the same letter are not significantly different ($P > 0.05$), modified Mann-Whitney U test. Means transformed to $\log_{10}(x + 1)$ before analysis; detransformed means presented.

^aBased on 0-4 rating scale, see text for description.

^bAccession mean \pm standard error.

^cRange of genotype means.

S. chacoense, *S. pinnatisectum*, and *S. tarijense* PI 473227 = 0%; *S. tarijense* PI 473336 = 3.4%; *S. berthaultii* = 6.6%; *S. canasense* = 46.6%; and *S. bukasovii* = 68.4%. Results of the 29 July and 12 August defoliation evaluations were highly correlated ($r_s = 0.92$, $P < 0.05$).

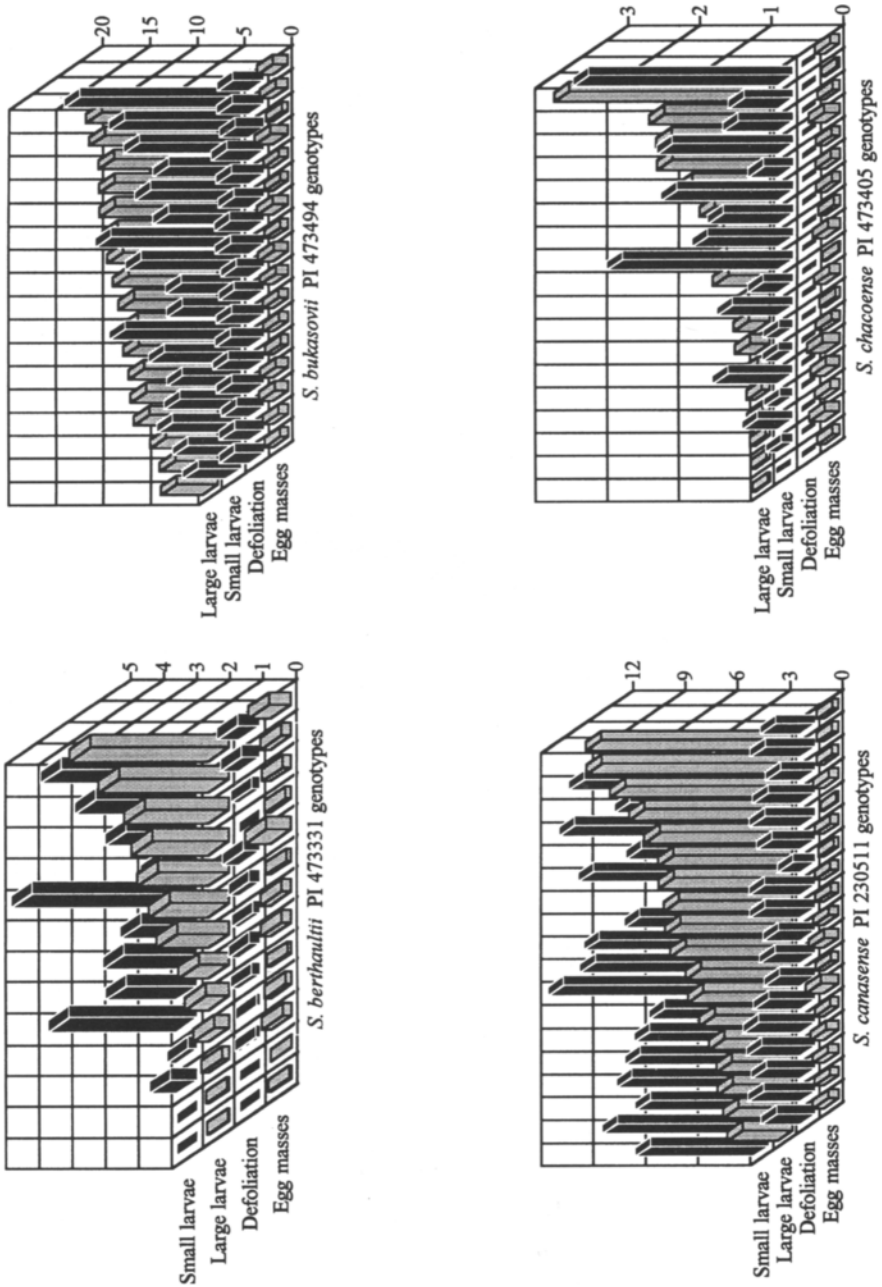
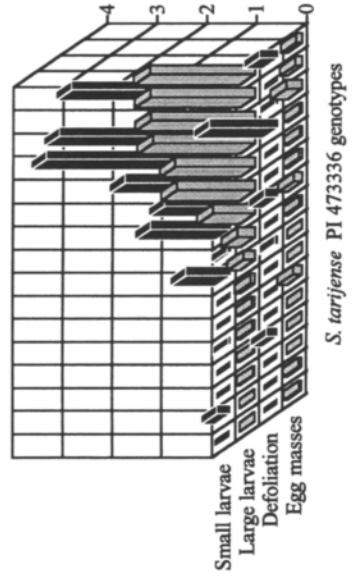
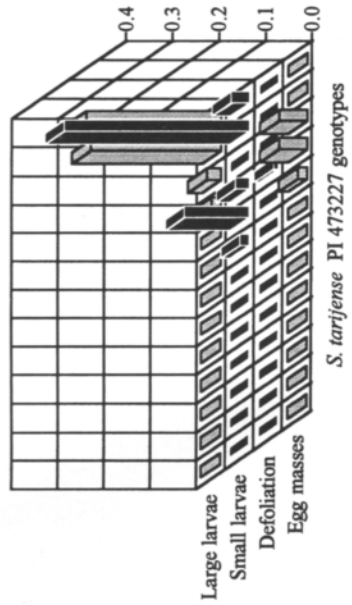
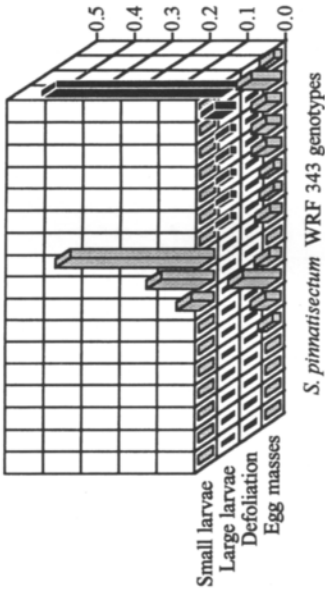


FIG. 1. Mean number of small larvae, large larvae, egg masses, and defoliation score of each genotype within an accession ranked on number of large larvae, 1993. Note that scales vary widely among accessions.



Of the six pair-wise correlations between number of small larvae, large larvae, egg masses, and defoliation score, *S. bukasovii*, *S. canasense*, and *S. chacoense* each had one significant correlation. *Solanum tarijense* PI 473336 had three significant correlations. *Solanum berthaultii* had six significant correlations. *Solanum canasense* exhibited the only significant negative correlation. No significant correlations were found in *S. pinnatisectum* or *S. tarijense* PI 473227 because of very low insect counts and negligible defoliation.

Response of the Materials, 1995—All three families (original genotypes, and intermates of resistant and susceptible genotypes) were highly and uniformly resistant. No egg masses, larvae or defoliation were found on 1 and 11 August. On 1 August, the number of adult beetles per plant (mean \pm SD) in each family was almost identical ($P = 0.80$): original genotypes = 0.9 ± 1.2 , resistant intermates = 0.9 ± 1.2 , susceptible intermates = 0.9 ± 1.1 . Within families there was no significant variation among genotypes for number of adult beetles ($P > 0.10$). Plant size and number of adults were not significantly correlated within families (original family: $r_s = 0.006$, $P > 0.50$, $n = 18$ genotypes; resistant family: $r_s = 0.105$, $P > 0.50$, $n = 16$ genotypes; susceptible family: $r_s = 0.250$, $P > 0.25$, $n = 18$ genotypes).

Within all three families however, there was significant variation among genotypes for plant size ($P < 0.005$), indicating significant heterozygosity for plant vigor. Plant size (mean \pm SD) of the original family (2.52 ± 0.58) and the family derived from intermated susceptible genotypes (2.48 ± 0.57) was not different, but the family derived from intermated resistant genotypes was slightly, but significantly smaller (2.38 ± 0.59).

Discussion

Fine screening revealed that within accessions previously identified as uniformly and highly resistant some genotypes deviated significantly from the accession mean for one or more resistance parameters. These populations apparently segregate for factors which cause individuals to differ significantly in their resistance phenotypes. Thus, unless all of the resistance parameters have no dominance, even the best phenotypes could be heterozygous and of less than optimal breeding value.

Adult counts were not useful in gauging differences in Colorado potato beetle resistance among accessions or genotypes. Adults are very mobile and, in small plot experiments, tend to leave or avoid heavily defoliated plants. Moreover, the presence of adults on plants does not necessarily mean that oviposition will occur. In 1995, *S. pinnatisectum* WRF 343 averaged almost one adult per plant on 1 August, and that population was supplemented at the rate of one beetle per plant on 4 August, however, no oviposition occurred.

Detailed studies of nonpreference by ovipositing adults and survival of larvae inform our understanding of the causes of resistance. However, for the purpose of screening many plants, number of larvae best differentiates among genotypes because larval counts combine the effects of oviposition and survival. Indeed, significant differences among genotypes within accessions were most often found for numbers of larvae. We observed that genotypes of equal susceptibility to oviposition were not equally supportive of larval growth and survival, *e.g.*, *S. bukasovii* and *S. chacoense* (Fig. 1). Number of small larvae represents the cumulative effect of adult oviposition and early instar survival. Number of large larvae represents the cumulative effect of adult oviposition, early and late instar survival, and larval dispersal.

Timing of defoliation assessments is critical, since potatoes have the capacity to replace lost foliage. That capacity varies greatly among *Solanum* species and to varying degrees among accessions (6). In these highly resistant accessions, differences in defoliation among genotypes were already small and difficult to detect.

Fine screening revealed that the direction and magnitude of correlations among resistance parameters varies among species. Correlation between oviposition and numbers of larvae was positive (resistant *S. berthaultii*), negative (susceptible *S. canasense*), or nonsignificant (susceptible *S. bukasovii* and resistant *S. chacoense*). If resistance parameters are highly correlated, selection could emphasize the most influential resistance parameter. However, if resistance parameters are not correlated, one must measure all important parameters to identify the best genotypes for inclusion in breeding programs.

Small but significant differences in numbers of both eggs and larvae differentiated genotypes of *S. pinnatisectum* WRF 343 in 1993. In 1995, there were no detectable differences between these genotypes or families derived from them. Either the differences of 1993 were artificial, or the 1995 test environment did not allow real differences to be detected. If the differences in 1993 were artificial, the 1995 trial served only to confirm that this accession is very pure for high resistance. If the genotype differences seen in 1993 were real, the 1995 test must have been less differentiating. However, the 1995 challenge was ostensibly severe, so the fact that no susceptibility could be detected even in a family derived from the most susceptible individuals in WRF 343 suggests that this accession does not contain very much susceptibility. Thus, although small significant variation was detected in 1993, the preexisting populations WRF 343 (and *S. tarijense* PI 473227) approximate the ideal of pure, stable, maximum resistance in a true seed family. Such sources of resistance would be easy to maintain, and would not require prescreening to identify superior parents. In addition to their breeding value, such uniformly resistant families would also be useful for studies of the physiological and genetic bases of resistance. Less beetle-resistant

accessions and species may be desirable for other reasons, *e.g.*, ease of crossing with *S. tuberosum*, high yield, or yield-tolerance to defoliation. In such cases, fine screening could be helpful for identifying the most beetle-resistant genotypes within segregating accessions (*e.g.*, *S. tarijense* PI 473336, Fig. 1), and facilitate synthesis of even more uniformly resistant subpopulations.

Although *S. pinnatisectum* WRF 343 appears to have been naturally selected for near homozygous resistance, this has had no apparent deleterious inbreeding effects. One generation of divergent selection for resistance using only four selected parents did not significantly reduce heterogeneity for plant size within sub-populations. Family means for plant size were only slightly reduced in the selected populations. Thus, artificial selection for homozygous resistance should not severely detract from the beneficial allelic diversity and heterosis a wild species may contribute to cultivar breeding.

Fine screening would be beneficial not only for Colorado potato beetle resistance, but for any desirable traits for which inbreeding is not deleterious. Whether homozygous populations are identified or synthesized, establishing them requires that individuals within outstanding accessions be screened with replication at the genotype level. Such work would help to close the current gap between the general information provided by accession-based screening and the specific needs of germplasm enhancers and breeders for superior parents, facilitating the use of exotic germplasm for potato cultivar improvement.

Literature Cited

1. Carter, C.D. 1987. Screening *Solanum* germplasm for resistance to Colorado potato beetle. *Am Potato J* 64:563-568.
2. Deahl, K.L., S.L. Sinden, and R.J. Young. 1993. Evaluation of wild tuber-bearing *Solanum* accessions for foliar glycoalkaloid level and composition. *Am Potato J* 70:71-76.
3. Dimock, M.B. and W.M. Tingey. 1985. Resistance in *Solanum* spp. to the Colorado potato beetle: mechanisms, genetic resources and potential. *In: D. Ferro and R. Voss (Eds.)*. *Proc Symp Colorado Potato Beetle, XVIIth Int Congr Entomol, Mass Exp Sta Res Bull* 704, pp. 79-106.
4. Dimock, M.B. and W.M. Tingey. 1987. Mechanical interaction between larvae of the Colorado potato beetle and glandular trichomes of *Solanum berthaultii* Hawkes. *Am Potato J* 64:507-515.
5. Dimock, M.B. and W.M. Tingey. 1988. Host acceptance behavior of Colorado potato beetle larvae influenced by potato glandular trichomes. *Physiol Entomol* 13:399-406.
6. Flanders, K.L., J.G. Hawkes, E.B. Radcliffe, and F.I. Lauer. 1992. Insect resistance in potatoes: sources, evolutionary relationships, morphological and chemical defenses, and ecogeographical associations. *Euphytica* 61:83-111.
7. Fligner, M.A. and G.E. Policello. 1981. Robust rank procedures for the Behrens-Fisher problem. *J Am Stat Assoc* 76:162-168.
8. Forgash, A.J. 1985. Insecticide resistance in the Colorado potato beetle. *In: D. Ferro and R. Voss (Eds.)*. *Proc Symp Colorado Potato Beetle, XVIIth Int Congr Entomol, Mass Exp Sta Res Bull* 704, pp. 33-52.

9. Hanneman, R.E. Jr. and J.B. Bamberg. 1986. Inventory of tuber-bearing *Solanum* species. Wis Agric Exp Sta Bull 533, 216 pp.
10. Neal, J.J., J.C. Steffens, and W.M. Tingey. 1989. Glandular trichomes of *Solanum berthaultii* and resistance to the Colorado potato beetle. Entomol Exp Appl 51:133-140.
11. Neal, J.J., R.L. Plaisted, and W.M. Tingey. 1991. Feeding behavior and survival of Colorado potato beetle, *Leptinotarsa decemlineata* (Say), larvae on *Solanum berthaultii* Hawkes and an F6 *S. tuberosum* L. X *S. berthaultii* hybrid. Am Potato J 68:649-658.
12. Ortiz, R., S.J. Peloquin, R. Freyre, and M. Iwanaga. 1991. Efficiency of potato breeding using FDR 2n gametes for multitrait selection and progeny testing. Theor Appl Genet 82:602-608.
13. Radcliffe, E.B., K.L. Flanders, D.W. Ragsdale, and D.M. Noetzel. 1991. Pest management systems for potato insects. In: D. Pimentel (Ed.), CRC Handbook of Pest Management in Agriculture. Second edition. Vol 3. pp. 587-621.
14. Sinden, S.L., L.L. Sanford, and S.F. Osman. 1980. Glycoalkaloids and resistance to the Colorado potato beetle in *Solanum chacoense* Bitter. Am Potato J 57:331-343.
15. Sinden, S.L., L.L. Sanford, and K.L. Deahl. 1986. Segregation of leptine glycoalkaloids in *Solanum chacoense* Bitter. J Ag Food Chem 34:372-377.
16. Zar, J.H. 1984. Biostatistical analysis. 2nd ed., Prentice-Hall, Inc., Englewood Cliffs, N.J. 679 pp.