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Somaclonal variation in tuber disc-derived populations of potato. II. Differential effect of genotype

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Abstract. Three somaclonal populations of potato (*Solanum tuberosum* L.), each comprised of at least 1,000 plants, were regenerated from the cultivars Kennebec, Russet Burbank, and Superior. The frequency of formation of adventitious meristems from tuber disc explants varied significantly between these potato genotypes. Only 1.0–1.3% of each somaclonal population exhibited morphological aberrations. Regenerated populations of 'Kennebec' and 'Superior', when compared to respective control populations over three asexual generations, were similarly enriched with somaclones having more elongated tubers, a higher total tuber number and weight, a higher cull tuber number and weight, and earlier maturity. Somaclones of 'Russet Burbank' also produced more elongated tubers, a higher total tuber number, and a higher cull tuber number and weight but, in contrast, these somaclones were lower in total tuber weight, lower in U.S. 1 tuber number and weight, shorter in stem length, and lower in vigor. Of the three cultivars, 'Russet Burbank' somaclones possessed the greatest variability for most traits. Besides this significant genotype effect, quantitative traits differed amongst each other in respect of relative changes resulting from somaclonal variation. Observed differences among genotypes and quantitative traits will undoubtedly affect the success or failure of plant improvement programs attempting to utilize somaclonal variation.

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Introduction

There have been many recent reports documenting the existence of somaclonal variation in the potato (see Larkin 1987). These investigations have been largely unstandardized, somaclones having been regenerated from different potato cultivars, the choice of which has depended upon the locality of the researcher. Additionally, regeneration protocols and explant types have varied widely (Larkin and Scowcroft 1983; Rietveld et al. 1987, 1991). Once plants were regenerated, the assessment of somaclonal variation by various workers has involved a variety of experimental designs, observed phenotypes, and statistical analyses, thereby making comparisons among studies difficult.

The type of explant and the genotype of the donor material may significantly influence somaclonal variation (Larkin 1987). The results of several studies with potato, while not conclusive, do seem to diminish the influence of an explant type effect (Larkin 1987). Evidence of a genotypic effect, however, has been presented for cytogenetic abnormalities in potato (Karp et al. 1982) and oats (McCoy et al. 1982) and for phenotypic variation in wheat (Larkin 1987) and *Pelargonium* spp. (Skirvin and Janick 1976). Comparative phenotypic studies among cultivars of potato that were conducted under uniform experimental conditions are lacking. Such information is necessary to maximize the efficacy of somaclonal variation as a tool for plant improvement.

We have developed an efficient method of producing very large populations of potato somaclones through adventitious regeneration from tuber disc explants (Jarret et al. 1980; Rietveld et al. 1987). One such population, regenerated from the cultivar Superior, has been extensively studied across five asexual generations and across three diverse locations (Rietveld et al. 1991). We observed statistically-significant variation for many quantitative traits including total tuber number and weight, main stem length, flower number, and tuber elongation ratio (Rietveld et al. 1991). Unidirectional mean shifts, often in a desirable direction, were observed for many traits in the somaclonal population when compared to a control population. Many replicated somaclonal lines show stability of a genetic nature across asexual generations and across diverse locations (Rietveld et al. 1991). We now present the results of studies conducted on three additional populations of somaclones, each regenerated from a different potato cultivar. These results illustrate that there is a large effect of genotype (i.e., cultivar) on the kinds of changes arising from adventitious regeneration.

Materials and methods

Regeneration of treatment and control plants

Tubers of 'Kennebec' (KEN) and 'Russet Burbank' (RB) were obtained in December 1982 from Oregon State University. These two clones were derived from single tubers in 1980. Tubers of a third cultivar, 'Superior' (SUP), were obtained in November 1981 from a commercial production established from certified seed.

Somaclones were regenerated from tuber disc explants using the method presented previously (Rietveld et al. 1991). Batches of tuber discs isolated each day were separately identified throughout these studies. Plantlets which produced roots in the third medium (Rietveld et al. 1991) were acclimated to ambient humidities under mist. After 1–2 weeks, plantlets were transplanted into 5-cm-square peat pots containing a standard greenhouse soil mix and were allowed to acclimate an additional 3 weeks under full sun prior to field establishment.

Control plants of KEN and RB were multiplied in vitro by axillary bud enhancement (Miller and Lipschutz 1984). An in-vivo procedure (Rietveld et al. 1991) was used to establish control plants of SUP. Regardless of the method, the procedures were coordinated to allow both the treatment (i.e., somaclones) and the control plants to be of similar size just prior to field establishment.

Field establishment and experimental design

Large populations of treatment and control plants of each cultivar were established in field plots (Rietveld et al. 1991). The relative proportion of treatment to control plants differed for each cultivar (Table 1). One representative tuber from each plant established from tissue culture (i.e., the A_0 generation) was used to establish one plant in the first tuber generation (i.e., A_1). With the SUP material, this process was repeated again to produce the A_2 generation (see Table 1). Putative lines were selected from treatment and control populations in the A_1 generation (A_2 for SUP) based on upper level performance for the traits of tuber elongation ratio, total tuber number and weight, and U.S. 1 tuber number and weight. The actual upper limits of selection from the distribution regions were 1.5%, 5% and 2.5% for the cultivars KEN, RB, and SUP, respectively. Up to ten plants represented each line in the A_2 generation (A_3 for SUP). Material in these advanced generations (i.e., A_1 and higher) was prepared according to the methods presented in Rietveld et al. (1991).

Table 1. Field plot specifications. Asexual generations are represented by A_x, where x = consecutive generation number (initial generation of plants from tissue culture is A_0). Designs included unreplicated (U) plantings where each line was represented by only one plant and replicated (R) plantings where each line was represented by up to ten plants divided equally between two blocks. Row widths were 91 cm and seed spacing within rows was also 91 cm. All plots were located in Wendell, Idaho, except for the A_0 generation of 'Superior' which was located in LaCrosse, Indiana

Cultivar	Generation, year, and design	Number of lines		Seed piece mass (g)
		Treatment	Control	
Kennebec	A_0-83-U	4784	502	–
	A_1-84-U	4203	441	30 ± 2
	A_2-85-R	296	41	45 ± 3
Russet Burbank	A_0-83-U	1064	201	–
	A_1-84-U	871	188	30 ± 2
	A_2-85-R	159	44	45 ± 3
Superior	A_0-82-U	1720	680	–
	A_1-83-U	1476	584	30 ± 2
	A_2-84-U	1476	584	45 ± 3
	A_3-85-R	145	56	45 ± 3

Collection and analysis of data

In the A_0 generation, data were collected from each plant for the traits of tuber elongation ratio and total tuber number and weight. Only three traits were examined because performance in the A_0 generation is influenced by regeneration and propagation artifacts (Rietveld et al. 1991). In the A_1 generation (and A_2 for SUP), data were collected for the additional traits of U.S. 1 tuber number and weight, maturity index, and flower number index. The traits of cull tuber number and weight, main stem length, plant vigor, leaf color, degree of branching, and time of blooming were added to characterize the replicated A_2 generations (A_3 for SUP). All of these traits were described earlier (Rietveld et al. 1991). Measured traits, except main stem length, were collected from each plant (up to ten plants represented each line in the replicated generations). The main stem length measurement and the ranked traits were collected from random samples representing up to 40% of the experimental units. In addition, systematic samples (Neter et al. 1978) representing 10% of the replicated lines of each cultivar were assayed in 1985 for potato viruses X, Y, and leaf roll (Rietveld et al. 1991). All traits and data analysis procedures were previously discussed in Rietveld et al. (1991).

Results

Qualitative differences

The three cultivars differed in their relative capacity to regenerate adventitiously. Discs isolated from 'Kennebec' (KEN) and 'Russet Burbank' (RB) tuber tissue produced 11% more and 72% fewer plantlets, respectively, than discs from 'Superior' (SUP) tuber tissue (data not shown). The intensity of disc greening after 2 weeks on the first medium (Rietveld et al. 1987, 1991) was highest for KEN and lowest for RB. The frequency of aberrant plants (Rietveld et al. 1987), comprising 1.1%, 1.0%, and 1.3% of the KEN, RB, and SUP populations, respectively, did not differ significantly. Flower color variants only occurred in the SUP treatment population. The normal lavender flower color of SUP was altered in a stable fashion to pure white and dark purple at frequencies of 0.12% for each change. Although no flower color variants were observed in the KEN or RB treatment populations, one line in each of these populations produced aberrant flowers with greatly enlarged sepals and a vestigial corolla and reproductive parts (see Rietveld et al. 1987; Fig. 2 C, D). Lastly, 0.1% and 0.2% of KEN and RB lines, respectively, had a yellow sectored phenotype (see Rietveld et al. 1987; Fig. 2 B). This condition was stable through all subsequent asexual generations and was not associated with viruses S, X, Y, leaf roll, or alfalfa mosaic (data not shown).

Virus assay results

Although no visible symptoms were observed, a virus assay that tests for low titres was conducted as a precaution. Potato viruses X (PVX) and leaf roll (PLRV) were detected in this material (Table 2), but no lines tested positive for potato virus Y. Within each cultivar, differences between the frequencies of positive-testing treatment and control lines lacked significance. Infection by PLRV significantly reduced total tuber weight yield in the KEN and SUP cultivars (analysis of variance not shown). The restraint on yield

Table 2. Differences among cultivars for virus infection

Cv	Population	Frequency of lines testing positive	
		PVX	PLRV
KEN	Treatment	0.00	0.41
	Control	0.00	0.60
RB	Treatment	0.00	0.92
	Control	0.00	0.86
SUP	Treatment	0.06	0.31
	Control	0.20	0.40

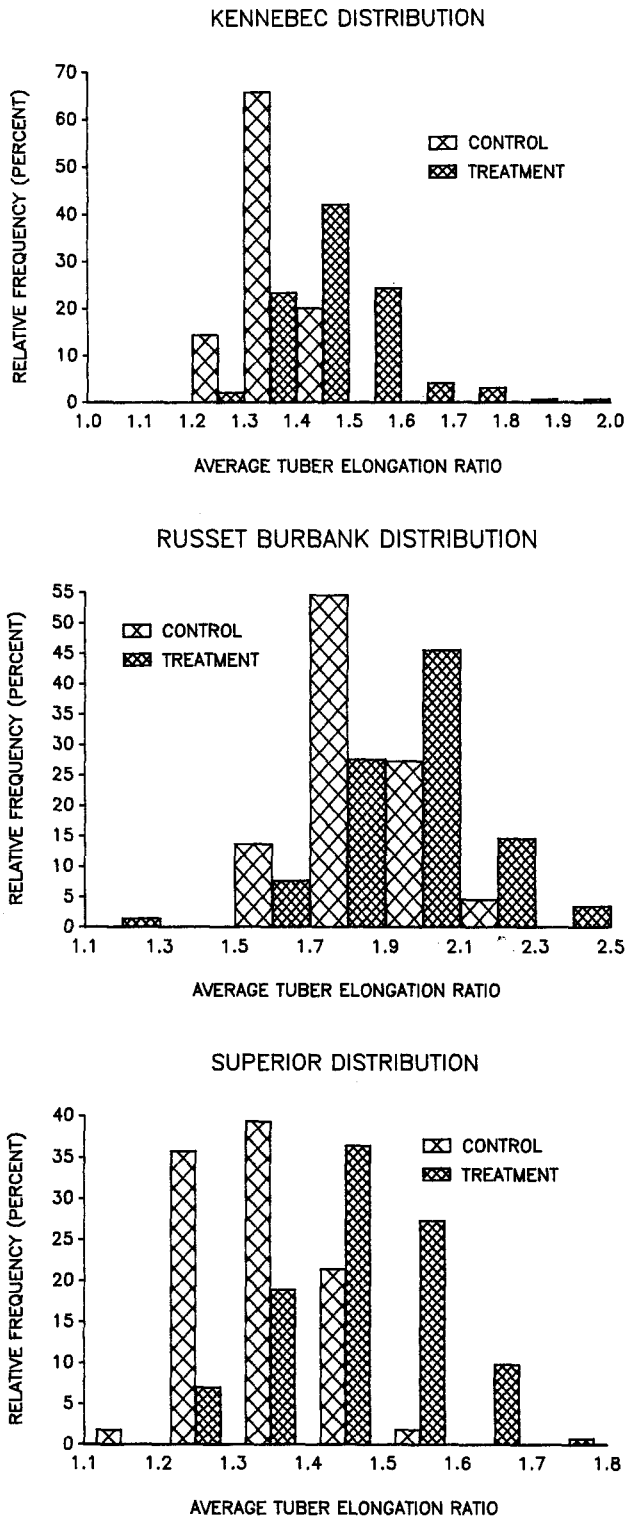

Fig. 1. Tuber elongation ratio frequency histograms for treatment and control populations isolated from three potato cultivars. These distributions included all replicated treatment and control lines in the A_2 generation of 'Kennebec' and 'Russet Burbank' and in the A_3 generation of 'Superior'

Table 3. Mean and variance results for three cultivars across successive tuber generations. Significance levels are represented by ***, **, *, ?, and NS which denote $P \leq 0.001$, $P \leq 0.01$, $P \leq 0.05$, $0.05 < P < 0.25$ (questionable significance; see Anderson and McLean 1974), and $P \geq 0.25$ (non-significance), respectively. The notations T/C and C/T designate which population, treatment or control, respectively, has the greater variance

Trait	Generation and cultivar	Treatment mean	Control mean	Mean difference		Variance difference		
				t-value	Signif.	F-value	Signif.	Dir.
Tuber elongation ratio	A_0-KEN	1.613	1.425	25.07	***	1.16	?	C/T
	A_1-KEN	1.568	1.441	17.89	***	2.10	***	T/C
	A_2-KEN	1.481	1.351	12.22	***	2.96	***	T/C
	A_0-RB	1.910	1.722	8.72	***	1.30	**	T/C
	A_1-RB	2.125	2.028	2.95	***	1.11	?	T/C
	A_2-RB	1.945	1.851	3.52	***	1.86	*	T/C
	A_0-SUP	1.706	1.362	32.76	***	5.64	***	T/C
	A_1-SUP	1.290	1.214	12.26	***	1.53	**	T/C
	A_2-SUP	1.363	1.220	26.27	***	2.54	***	T/C
	A_3-SUP	1.466	1.337	9.35	***	1.65	*	T/C
Total tuber number	A_0-KEN	16.6	9.85	22.31	***	2.07	***	T/C
	A_1-KEN	20.5	19.0	3.68	***	1.28	**	T/C
	A_2-KEN	15.9	14.3	1.71	*	2.08	**	T/C
	A_0-RB	26.0	16.3	14.61	***	3.59	***	T/C
	A_1-RB	15.8	10.6	8.14	***	2.15	***	T/C
	A_2-RB	14.6	11.1	4.00	***	4.21	***	T/C
	A_0-SUP	6.88	5.67	5.22	***	2.64	***	T/C
	A_1-SUP	14.1	10.5	13.51	***	1.44	**	T/C
	A_2-SUP	11.9	10.6	5.65	***	1.08	?	T/C
	A_3-SUP	17.3	13.6	3.61	***	2.06	**	T/C
Total tuber weight	A_0-KEN	648	655	0.44	NS	1.23	*	T/C
	A_1-KEN	2100	2200	2.98	**	1.11	?	T/C
	A_2-KEN	2180	2030	1.76	*	1.23	?	T/C
	A_0-RB	604	638	1.35	?	1.04	NS	T/C
	A_1-RB	1270	1320	1.11	?	1.68	**	T/C
	A_2-RB	1530	1850	3.76	***	1.20	?	T/C
	A_0-SUP	163	348	24.09	***	2.38	***	C/T
	A_1-SUP	1090	1030	2.94	**	1.08	?	C/T
	A_2-SUP	1310	1380	2.15	*	1.21	**	C/T
	A_3-SUP	2160	2010	1.53	?	1.12	NS	T/C
U.S. 1 tuber number	A_1-KEN	3.51	4.49	8.90	***	1.33	**	C/T
	A_2-KEN	4.67	4.66	0.02	NS	1.51	?	T/C
	A_1-RB	1.42	1.78	3.44	***	1.66	**	C/T
	A_2-RB	1.42	3.25	10.35	***	1.03	NS	C/T
	A_1-SUP	3.03	3.42	4.51	***	1.06	NS	T/C
	A_2-SUP	4.16	4.61	4.09	**	1.09	?	C/T
	A_3-SUP	5.19	5.09	0.42	NS	1.57	*	T/C
U.S. 1 tuber weight	A_1-KEN	797	1050	9.57	***	1.35	**	C/T
	A_2-KEN	1420	1440	0.30	NS	1.32	?	T/C
	A_1-RB	304	419	4.39	***	1.66	**	C/T
	A_2-RB	347	909	10.22	***	1.51	*	C/T
	A_1-SUP	569	692	6.72	***	1.12	?	C/T
	A_2-SUP	861	1030	5.94	***	1.31	**	C/T
	A_3-SUP	1430	1540	1.37	?	1.06	NS	T/C
Cull tuber number	A_2-KEN	1.60	1.08	1.60	?	3.87	***	T/C
	A_2-RB	3.22	2.18	2.66	**	2.61	***	T/C
	A_3-SUP	1.43	0.81	2.20	*	2.61	***	T/C
Cull tuber weight	A_2-KEN	251	150	3.39	***	1.80	*	T/C
	A_2-RB	582	496	1.36	?	1.29	?	T/C
	A_3-SUP	198	94.5	5.21	***	3.17	***	T/C
Main stem length	A_2-KEN	55.8	56.0	0.17	NS	1.15	NS	C/T
	A_2-RB	48.9	52.8	3.06	***	1.25	?	T/C
	A_3-SUP	52.5	51.6	0.87	?	1.01	NS	C/T
Maturity index	A_1-KEN	2.8	2.6	4.92	***	1.36	**	C/T
	A_2-KEN	1.9	1.7	2.28	*	1.91	**	T/C
	A_1-RB	2.2	2.2	0.94	?	1.03	NS	C/T
	A_2-RB	2.0	1.9	0.73	NS	1.16	NS	T/C
	A_1-SUP	2.9	2.8	2.50	**	1.30	**	C/T

Table 3. (*Continued*)

Trait	Generation and cultivar	Treatment mean	Control mean	Mean difference		Variance difference		
				t-value	Signif.	F-value	Signif.	Dir.
Maturity index (*continued*)	A_2-SUP	2.9	2.9	0.49	NS	1.25	**	T/C
	A_3-SUP	2.2	2.1	2.63	**	6.10	***	T/C
Flower number index	A_1-KEN	0.10	1.3	34.86	***	7.28	***	C/T
	A_2-KEN	0.87	1.1	2.73	**	1.06	NS	C/T
	A_1-RB	0.27	0.92	11.41	***	2.11	***	C/T
	A_2-RB	0.28	0.80	6.05	***	1.15	NS	C/T
	A_2-SUP	1.1	0.91	8.05	***	1.34	***	T/C
	A_3-SUP	1.3	1.0	4.97	***	5.46	***	T/C
Plant vigor	A_2-KEN	3.2	3.2	0.06	NS	1.23	?	C/T
	A_2-RB	3.2	3.5	2.75	**	1.46	?	T/C
	A_3-SUP	3.1	2.9	2.33	*	1.29	?	T/C
Leaf color	A_2-KEN	2.0	2.0	0.37	NS	2.31	**	T/C
	A_2-RB	2.1	2.1	0.17	NS	1.31	?	T/C
	A_3-SUP	2.0	1.9	2.69	**	2.01	**	T/C
Degree of branching	A_2-KEN	2.6	2.5	1.69	*	1.13	NS	C/T
	A_2-RB	2.7	2.8	1.25	?	1.18	NS	T/C
	A_3-SUP	2.7	2.6	1.56	?	1.74	**	C/T
Time of blooming	A_2-KEN	2.4	2.3	1.42	?	1.85	**	T/C
	A_2-RB	1.2	1.5	3.34	***	1.26	?	C/T
	A_3-SUP	2.0	2.0	0.70	NS	1.28	?	T/C

was statistically equal for the treatment and control populations in the SUP study. In the KEN populations, the control lines were more adversely affected by PLRV than were the treatment lines.

Mean and variance differences

Table 3 contains the results of statistical inferences on the means and variances of the traits for each cultivar across asexual generations. The test statistic *t* was used to determine differences between two independent means for both equal and unequal variances, and the inferences concerning variances were calculated with the test statistic *F* (Neter et al. 1978). These parameters were computed separately for the treatment and control populations in each study. Lines were represented by only one plant except in the A_2 generation for KEN and RB and in the A_3 generation for SUP (Table 1). In these replicated generations, up to five plants in each of two blocks represented each line.

For tuber elongation ratio, the greater variability in the treatment populations is diagrammatically presented in Fig. 1. Mean shifts and variance differences between the populations within a given cultivar are marked. The total tuber number distributions were more similar among cultivars, but mean shift, variance, and skewness differences between the populations within each cultivar were obvious (data not shown). Treatment population skewness for total tuber number was to the high end of the distribution for all three cultivars [measured by Pearson's Coefficient of Skewness (Neter et al. 1978); data not shown].

Table 4. Coefficient of variation results for three cultivars. This statistic was calculated (Neter et al. 1978) for the treatment population in the replicated generations (i.e., A_2 for KEN and RB and A_3 for SUP)

Trait	Coefficient of variation (%)		
	KEN	RB	SUP
Tuber elongation ratio	6.8	9.9	7.1
Total tuber number	47	55	48
Total tuber weight	27	35	30
U.S. 1 tuber number	35	72	33
U.S. 1 tuber weight	40	79	37
Cull tuber number	210	99	170
Cull tuber weight	93	70	90
Main stem length	13	17	12
Maturity index	34	32	26
Flower number index	66	170	35
Plant vigor	16	17	18
Leaf color	21	21	21
Degree of branching	14	14	13
Time of blooming	22	36	11

Variability differences among cultivars

The coefficient of variation statistic (Neter et al. 1978) allows direct comparisons among cultivars and among separate traits to determine those with the greatest variability. These coefficients are presented in Table 4. RB appeared to be more variable than the other two

cultivars for many traits. KEN and SUP had somewhat equal coefficients of variation for most traits. Coefficient of variation differences among traits within a cultivar in part reflected the differential response of the various traits to the effects of adventitious regeneration.

Assessment of stability

Replicated trials were examined for one generation and, therefore, only an initial assessment can be made of stability across asexual generations. Regressions between the generations that were not replicated were mostly significant in the treatment populations for all three cultivars (data not shown). Significance was generally lacking in the control populations for the same comparisons. Significant slope differences occurred between the treatment and control populations in about one-half of the regressions between these generations, especially for the tuber elongation ratio (data not shown).

The pattern of stability changed when the selected, replicated generations were compared to the preceding generations (i.e., A_1 vs A_2 for KEN and RB; A_2 vs A_3 for SUP). Regressions were often significant for both the treatment and control populations for RB and SUP (data not shown). Significant slope differences, occurring in either direction in respect to the treatment and control populations, were observed for about one-half the traits analyzed. In the KEN generations, however, significant regressions for the treatment population occurred for all five traits analyzed. Control population regressions for KEN were significant only for tuber elongation ratio and U.S. 1 tuber number. The slopes of the KEN treatment population regression lines were significantly greater than those of the controls for total tuber number and weight (data not shown).

Discussion

It is not possible to draw conclusions from the literature regarding the influence of genotype on somaclonal variation in potato. Although different cultivars have been regenerated through tissue culture techniques, the experimental methods differed vastly. Somaclones have been studied that were regenerated from protoplasts isolated from leaf mesophyll tissue (Secor and Shepard 1981; Austin et al. 1986), from protoplasts isolated from axenic shoot cultures (Sree Ramulu et al. 1984), from cell suspension cultures (Austin and Cassells 1983), from callus derived from leaf, rachis, and stem tissue (Evans et al. 1986), and from direct regeneration from tuber discs (Rietveld et al. 1991). Karp et al. (1982) examined chromosome number variation in potato somaclones regenerated from protoplasts isolated from axenic shoot cultures. Two cultivars were included in this study, and it was determined that they differed in the frequency of regenerates with aberrant ploidy levels. Jarret et al. (1980) and Wheeler et al. (1985) noted differential regenerative abilities among the potato cultivars in their studies that characterized new regeneration protocols. The systematic field study of Evans et al. (1986), which was a continuation of the work presented by Wheeler et al. (1985), was confined to the cultivar Desiree. In addition, only a few studies (Skirvin and Janick 1976; Larkin 1987) have examined the effect of genotype on somaclonal variation in species other than potato. The work presented here is the first report of a systematic, large-scale study assessing the effect of genotype (i.e., cultivar) on the nature of somaclonal variation.

All three cultivars included in these experiments – 'Kennebec' (KEN), 'Russet Burbank' (RB), and 'Superior' (SUP) – were successfully regenerated using the tuber disc method (Jarret et al. 1980; Rietveld et al. 1987) without modification. Relative differences in regenerative ability were detected among cultivars, and RB had the lowest success rate. Jarret et al. (1980) reported lower regenerative abilities for RB and KEN, but in our hands regeneration from KEN tuber discs was most prolific. Since other cultivars, besides the three studied here, were successfully regenerated without modification by Jarret et al. (1980), the tuber disc system is a comprehensive procedure to produce large populations of potato somaclones. The desirability of the tuber disc procedure is further enhanced by the low incidence (1.0–1.3%) of grossly aberrant plants, which apparently occurred independent of cultivar.

Although grossly aberrant plants were infrequent, much variability was detected for quantitative, horticulturally-important traits (Table 3). When compared to control populations, the magnitude and often the direction of somaclonal variation for these traits differed among the cultivars examined (see Table 5). The differences between KEN and SUP were limited to only a few traits – total tuber number, flower number, plant vigor, and leaf color. It is unlikely that the 1-year span between the regeneration of the two cultivars was responsible for these few differences, since these traits were statistically different in the advanced, replicated tuber generations. Both cultivars are somewhat recent in origin – KEN was released in 1948 and SUP in 1961 (Howard 1970). These two cultivars share a common parent, USDA selection B96-56 (Rieman 1962), and this perhaps explains the relative uniformity of response to adventitious regeneration.

Somaclonal populations of SUP, normally an early-maturing cultivar, and KEN, normally having late maturity (Thornton and Sieczka 1980), both show shifts to earlier maturity (Table 3). These shifts to

Table 5. A summary of population distribution shifts for somaclones of three potato cultivars. These observations were made in the selected, replicated generations (i.e., A_2 for KEN and RB and A_3 for SUP)

Trait	Shift in somaclonal population vs control		
	'Kennebec'	'Russet Burbank'	'Superior'
Tuber elongation ratio	Much larger	Much larger	Much larger
Total tuber number	Slightly higher	Much higher	Much higher
Total tuber weight	Slightly higher	Much lower	Possibly higher
U.S. 1 tuber number	No difference	Much lower	No difference
U.S. 1 tuber weight	No difference	Much lower	Possibly lower
Cull tuber number	Possibly higher	Higher	Slightly higher
Cull tuber weight	Much higher	Possibly higher	Much higher
Main stem length	No difference	Much shorter	Possibly longer
Plant maturity	Slightly earlier	No difference	Earlier
Flower number	Lower	Much lower	Much higher
Plant vigor	No difference	Lower	Slightly higher
Leaf color	No difference	No difference	Darker
Degree of branching	Higher	Possibly lower	Possibly higher
Time of blooming	Possibly later	Much earlier	No difference

earlier maturity are not supportive of the suggestion by Sanford et al. (1984) that much of the phenotypic variation in somaclonal populations is the result of plants acquiring a bolter phenotype, which characteristically shows later maturity. Furthermore, for all three cultivars, the treatment population means significantly exceeded those of the controls for the traits of tuber elongation ratio and total tuber number (Table 3). This response occurred although there are major phenotypic differences among these cultivars for tuber elongation ratio. RB characteristically produces elongated tubers, tubers of SUP are mostly round, and the shape of KEN tubers falls between RB and SUP (Thornton and Sieczka 1980).

Somaclonal populations of KEN and RB differed greatly for most traits when compared to their respective control populations (Table 5). Except for total tuber number, the response of these same traits differed between RB and SUP (Table 5). Since the distinguishing characteristics of the RB cultivar are different from either KEN or SUP, and because RB is a much older cultivar (released in 1876), differences between RB and KEN (or SUP) are credible.

The general effect of adventitious regeneration with RB material was a reduction in yield-related traits (Table 5). These results agree with those published by Secor and Shepard (1981), also with RB. In addition, Secor and Shepard (1981) observed a similar, marked reduction in flower number and an increase in total tuber number.

Opportunities to select lines possessing desirable alterations are greater using the cultivars KEN and SUP (Table 5). Mean shifts observed in the SUP treatment population (Table 5) principally occurred in the same directions as reported in Rietveld et al. (1991) for another regenerated population of SUP. One difference between the initial and current regenerated populations of SUP involves tuber size and quality aspects. The intial treatment population produced fewer U.S. 1 tubers by count and weight, but there were no significant differences between the treatment and control populations for cull tuber count and weight (Rietveld et al. 1991). In the current SUP treatment population, no significant differences in U.S. 1 tuber numbers were detected in the A_3 generation, but the treatment population was enriched for lines producing greater numbers of cull tubers (Table 3).

Regressions of the SUP control populations were often significant, making slope differences between the treatment and control populations mostly non-significant (data not shown). These results were similar to those observed in the initial SUP study (Rietveld et al. 1991). Selection occurred twice in the initial SUP experiment (Rietveld et al. 1991) – prior to the A_1 and A_3 generations. Most regressions involving generations following the second selection were significantly different between the treatment and control populations. In this current investigation, selection occurred only once, but this was delayed until the A_3 generation (A_2 for KEN and RB). We hypothesized that delaying selection would diminish the environmental influences on variability resulting from in-vitro culture, thereby making selection more effective. It appears, however, that an initial, moderate selection immediately following the initial generation should be followed by more stringent selection in a later generation (A_1 or A_2). This selection strategy would reduce the frequency of low-performing control plants (also comparative treatment

plants) that demonstrate a type of stability across asexual generations. We believe that low-performing control lines are at least partly responsible for significant control regression coefficients and control population variances statistically equal to or larger than treatment population variances. We have offered several explanations of successive generations of low-performing control lines in Rietveld et al. (1991).

An infection of leaf roll virus (PLRV) in the KEN study was the only virus detected that caused a differential response between the treatment and control populations. Values for yield-related traits in the control population were more reduced than in the treatment population because of PLRV infection (data not shown). This unequal influence by PLRV would have the potential to contribute to the differences reported between the two KEN populations. Since the responses of the KEN and SUP populations were similar, the influence of PLRV was not perceived to have been a major factor.

At least a portion of the variability in the traits, which was measured by the coefficient of variation (Table 4), was the direct result of adventitious regeneration. Statistically larger variances for the treatment populations for most traits (Table 3) provide support for this statement. More importantly, the coefficients of variation for nearly all treatment population traits exceeded the corresponding coefficients for the control population (data not shown). Certain traits such as tuber elongation ratio, total tuber number, cull tuber number and weight, and flower number were highly variable in the treatment population. Possible explanations for highly-variable traits resulting from adventitious regeneration were previously discussed in Rietveld et al. (1991).

We have presented results of systematic studies that demonstrate a significant genotype effect on somaclonal variation. Although at this time we do not know the molecular basis of these genotypic differences, factors such as differences in hormone levels or responsiveness between genotypes may affect genetic alterations that can control phenotypic traits, as was observed for habituation phenotypes (Meins 1982). We also show that the effects of adventitious regeneration on phenotypic variability are not equivalent among traits of horticultural interest. This new variability in quantitative traits occurs unidirectionally for most characteristics, and thus offers unique possibilities for plant improvement. The effect of genotype, however, adds another dimension to the successful implementation of somaclonal variation techniques. Some cultivars (i.e., genotypes) such as Russet Burbank may respond negatively to adventitious regeneration. Depending upon the trait of interest, this makes improvement less likely. Cultivars such as Kennebec and Superior result in somaclonal populations enriched for individuals offering possibilities for genetic advance. Consequently, investigators working with an untested cultivar may want to screen a small population of somaclones for the trait(s) of interest before committing themselves to a large and possibly unproductive study. Since many of these changes are stable through vegetative propagation, judicious selections of a beginning cultivar and specific traits for which variability is desired may well result in appreciable varietal improvement.

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