Potato Research 33 (1990) 357–364

Performance and stability of nine 4x clones from 4x-2x crosses and four commercial cultivars

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Accepted for publication: 24 January 1990

Additional key words: 2n gametes, Phureja, *S. tarijense*.

Summary

Nine clones from 4x-2x crosses were evaluated along with four cultivars in six Wisconsin environments. The 4x clones from 4x-2x crosses had as their 2x parents hybrids with haploid Tuberosum and either Group Phureja or *Solanum tarijense*. The 2x hybrids produced 2n pollen by first division restitution. The traits evaluated were marketable yield, mass density and chip color. Stability analysis was conducted by determining the linear relationships between mean yield of individual clones and environmental mean yields. Mean square deviations from linear regression (s^2_d) were used to evaluate phenotypic stability and regression coefficients (b) as environmental response parameters. Three 4x clones from 4x-2x crosses were more stable and not significantly different for yield than cv. Atlantic; some also had superior specific gravity and chip color. The results suggest that the 4x × 2x breeding method is very efficient for the production of high yielding, stable clones with superior processing qualities, particularly since the 4x clones from 4x-2x crosses originated from very small source populations.

Introduction

The 4x × 2x first division restitution (FDR) breeding method has been utilized in potato where the 4x parent is a *Solanum tuberosum* Group Tuberosum clone and the 2x parent is a 2n pollen producing hybrid of haploid Tuberosum and a diploid wild or cultivated relative of Tuberosum. When 2n pollen is produced by means of parallel spindles (genetically equivalent to FDR, about 80 percent of the heterozygosity and most of the epistasis of the 2x parent is transmitted to the 4x progeny (Peloquin, 1983; Douches & Quiros, 1987). 4x clones generated by this method may be identified as parallel spindle-derived 4x (PSD-4x) clones.

The heterozygosity and allelic diversity of 4x progeny are efficiently increased with this method, and epistatic interactions are transmitted from the 2x parent to the 4x progeny. Nonadditive genetic variance is primarily responsible for yield in tetraploid asexually propagated potatoes, and involves both interlocus (epistasis) and intralocus (heterozygosity) interactions (Mendoza & Haynes, 1974; Tai, 1976; Mendiburu & Peloquin, 1977). Normal meiotic processes in the tetraploid disrupt favorable interations; this disruption is reduced when the 2n gamete is formed by FDR, leading to an increased transmission of epistasis.

The 4x progeny from 4x × 2x (FDR) crosses can be significantly higher yielding than their 4x cultivar parents (Mok & Peloquin, 1975; DeJong & Tai, 1977). Further, potato improvement and cultivar development may be more efficient with the 4x × 2x method than with conventional 4x × 4x crosses. High yielding 4x clones have been obtained from small populations of 4x × 2x progeny (DeJong et al., 1981). There is also some evidence that the more highly heterozygous PSD-4x clones may be more stable in performance in different environments.

The purpose of this research was to evaluate nine 4x clones from 4x-2x crosses and four commercial cultivars for marketable yield (yield of A-sized ware tubers) and processing quality (mass density and chip color) in six environments in Wisconsin. The PSD-4x clones were compared to the cultivars for these traits and for stability over environments.

Materials and methods

Clonal performance trials. Nine clones from 4x-2x crosses and four commercial cultivars (Atlantic, Superior, Norland, Norchip) were grown in six environments in Wisconsin. The source of the nine hybrid clones was several small populations of 4x hybrids from 4x-2x crosses. The parentage and source populations of these 4x clones are given in Table 1. The 2x parents of the 4x clones produced 2n pollen by first division restitution, via parallel spindles (*ps*). Four of the parallel spindle-derived 4x (PSD-4x) clones had Phureja-haploid Tuberosum hybrids as their 2x parents and five had haploid Tuberosum-*S. tarijense* hybrids as their 2x parents.

The thirteen clones were planted in a randomized complete block design, with two replications per environment. Entries were planted in single row plots of 20 plants per plot. Spacing was 30 cm between hills, 90 cm between rows. The Wisconsin environments were: Hancock, 1987 and 1988; Rhinelander, 1987 and 1988; Spooner, 1988 and Antigo, 1988. Commercial cultural practices were followed. Harvest and grading were by machine.

The traits evaluated included: yield of A-sized tubers (marketable yield), kg/hill;

Table 1. Parentage and source populations of PSD-4x clones.

PSD-4x clone	Parentage of 4x clone (2x parent)	Source population
J8 J14	New Haig × M5 (an I × J hybrid); I = Phureja × 'Katahdin' haploid US-W1, J = Phureja × 'Chippewa' haploid US-W42	16 clones selected from 4x × 2x progeny families as single hills ('random selection')
S436 S438 S473 S477 S487	W231 × (Tuberosum haploid × *S. tarijense*)	53 full- and half-sib seedlings which were increased for evaluation in 1986, 1987 without prior selection
D45 D55	Ak37-19 × ['Superior' × (J19)] JI9 = I × J hybrid Ak37-19 × ['Oneida' × (J)]	38 clones of diverse origin, but all with Phureja, which had some prior selection, but little evaluation

mass density, calculated as [(wt. in air)/(wt. in air − wt. in water)]; and chip color, with a visual rating of 1 = light, 10 = dark, acceptable ≤4.0.

Stability analysis. Stability analysis on the three traits evaluated was made using the technique of regression, where entry mean yields were linearly regressed on the average of all entries in each environment. The regression provides two parameters for each entry, the linear regression coefficient, b, and the deviation from regression mean square, s^2_d (Eberhart & Russell, 1966). If there is significant deviation from regression, the linear regression coefficient may not be an appropriate indicator of genotype stability response over environments. Therefore, the regression coefficient, b, was considered not as a measure of stability per se, but as an indication of the average responsiveness of a genotype to environmental conditions (Eberhart & Russell, 1969; Becker & Leon, 1988). The deviation from regression means squares was taken as the stability parameter. In this interpretation of the parameters derived from linear regression, a significant deviation from regression mean squares (tested using the pooled error mean square) indicated that a clone was unstable, independent of the value of the regression coefficient. The regression coefficient was interpreted such that $b < 1$ indicated responsiveness to low (unfavorable) environments and $b > 1$ indicated responsiveness to high (favorable) environments, with the descriptor low or high being associated with the average performance of all of the clones in a given environment (Haufe & Geidel, 1978). A desirable genotype had $s^2_d = 0$, and mean performance above the grand mean.

Results and discussion

Environments, genotypes and genotypes × environment interaction were significant ($P \leq 0.05$) to very significant ($P \leq 0.01$) for the three traits evaluated based on the analysis of variance. The linear components of regression and deviations from regression were significant to highly significant ($P \leq 0.001$). For all three traits the linear component MS was significantly greater than the pooled deviations.

Yield of A-sized tubers. Five of the nine PSD-4x clones had a non-significant mean square deviation from regression for yield of A-sized tubers, indicating high phenotypic stability (Table 2). One of the four cultivars, Superior, had a significant mean square deviation, indicating lack of stability; this may have been due to unusual heat and drought stress of the 1987 and 1988 growing seasons. Two other cultivars, Atlantic and Norchip, had deviations from regressions which were significant only at the 10 percent level, indicating that they may also have relatively less stability than five of the PSD-4x clones. The two highest yielding PSD-4x clones, J8 and S487, were not significantly different from the highest yielding cultivar, Atlantic, for yield of A-sized tubers.

Each individual clone mean yield was plotted against its regression coefficient, b. Clones which were marked with either ** or * had significant deviation from mean squares (s^2_d) at the 1 and 5 percent levels, respectively (Figure 1). Figures 2 and 3, to be discussed later, were plotted in the same manner for the other traits evaluated. Figures were constructed as done by Stofella et al. (1984). Grand genotype mean yield ($\bar{x}$ = 1.02 kg/hill) was indicated with a vertical line, and mean slope (b = 1) with a horizontal line. A desirable clone should have high phenotypic stability (nonsignificant s^2_d) and a mean performance which is above the grand mean. Six of the nine PSD-4x

Table 2. Means of three traits and their stability parameters (s^2d,b) for 13 clones grown in six environments (1987, 1988).

4x clone	Yield A-sized tubers (kg/hill)			Mass density			Chip color		
	mean	b'	s^2d	mean	b	s^2d	mean	b	s^2d
J8	1.32	1.34	0.02	1.064	0.05	191	5.1	1.25	0.26*
J14	1.03	0.17	0.21**	1.070	1.38	79	4.0	0.90	0.18
S436	1.09	1.15	0.01	1.069	1.49	187	3.5	0.19	0.24+
S438	1.05	0.50	0.06*	1.079	1.11	167	3.1	0.41	0.05
S473	0.83	0.66	0.06*	1.080	0.70	92	4.5	1.41	0.26*
S477	0.79	0.05	0.11**	1.091	1.04	225+	4.8	1.67	0.30*
S487	1.19	0.95	0.02	1.078	1.10	231+	6.2	1.46	0.32*
D45	1.00	1.27	0.01	1.080	1.68	97	3.6	0.49	0.10
D55	1.08	1.33	0.03	1.079	0.97	68	3.7	0.64	0.08
Atlantic	1.24	1.33	0.04+	1.079	1.75	157	3.8	0.69	0.08
Superior	0.82	1.46	0.06*	1.065	0.67	159	5.1	1.49	0.56**
Norland	0.95	1.46	0.01	1.056	0.42	337**	6.4	1.69	0.66**
Norchip	0.91	1.37	0.04+	1.072	0.77	137	3.6	0.72	0.14
Grand mean	1.02	1.00	-	1.074	1.00	-	4.4	1.00	-
LSD 0.05	0.15	-	-	0.004	-	-	0.4	-	-
Pooled error	-	-	0.02	-	-	100	-	-	0.10

+, *, ** indicates significance at the 10, 5 and 1 percent levels, respectively for deviation means squares from regression (s^2d)
' regression coefficient, (b)

clones had higher than the grand mean for yield of A-sized tubers; four of these had high phenotypic stability. Atlantic was the only cultivar with yield greater than the grand mean. The PSD-4x clones which had high stability, high yield and responsiveness to favorable environments were J8, S436 and D55. S487 had high stability, high yield and equal responsiveness to high and low (favorable and unfavorable) environments. The clones with relatively low yield and high stability were cvs Norland, Norchip and D45; they all had responsiveness to favorable environments. S473, S477 and Superior had relatively low yield and stability, with the cultivar showing responsiveness to favorable environments and the PSD-4x clones showing responsiveness to poor or less favorable environments.

There is evidence that the highly heterozygous PSD-4x clones may be superior to extensively evaluated cultivars for yield. DeJong et al. (1981) were able to identify 4x clones from 4x × 2x crosses (where the 2x parent was a Phureja-haploid Tuberosum hybrid with 2n pollen) which equalled or exceeded one of the highest yielding cultivars in Canada (Kennebec) for both marketable yield and yield stability. They noted that the 4x-2x hybrid clones were selected with little evaluation from a small population of about 10 000 seedlings, and that the 2x parents had been subject to little or no selection for yield or stability.

A general relationship betwen heterozygosity and stability has been reported in other crops. Lerner (1954) found that a more heterozygous genotype is more effective than

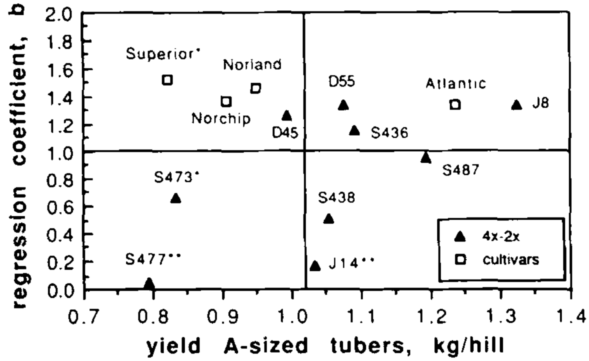

Fig. 1. Relationship between individual mean genotype yield and regression coefficient (b) for each genotype. Horizontal and vertical lines mark grand genotype means for b and yield, respectively. *, ** indicate significant deviations from regression mean squares at 5 and 1 percent levels, respectively.

a homozygote in resisting the unstabilizing effect of climatic variation. In maize, Adams & Shank (1959) indicated that increasing levels of heterozygosity in groups of lines and hybrids was positively related to increased homeostasis in the groups.

The PSD-4x clones exhibited similar stability and equal or higher yield of A-sized tubers than the four commercial cultivars. The results are particularly significant when it is noted that the PSD-4x clones were selected from a population of hundreds, with little or no prior evaluation. In contrast, a commercial potato cultivar is often selected from a population of 80 000–150 000 seedlings (DeJong et al., 1981) and undergoes many years of testing over a range of locations. To obtain high yielding, stable genotypes with so little selection pressure or breeding effort suggests that the 4x × 2x (FDR) breeding method may have greater potential for selection gains than conventional breeding methods.

Mass density. In evaluating mass density (correlated to total solids), the desired response in a clone is homeostasis, or nonresponsiveness over environments. The mean, s^2_d and b for each clone is listed in Table 2. Most of the clones were stable for this trait, with the exception of the cultivar Norland, which had a highly significant deviation from regression mean square. Two PSD-4x clones S477 and S487, had deviations from regression mean square which were significant only at the 10 percent level. The cultivar Atlantic was used as a standard for high mass density; a desirable clone should equal or exceed cv. Atlantic for this trait as well as exhibit high stability over environments.

Four of the five PSD-4x clones with haploid Tuberosum-*S. tarijense* hybrids as 2x parents had mass density equal to or higher than Atlantic, as did two 4x clones from with Phureja parentage, D45 and D55 (Figure 2). J8 and J14 (also with Phureja) had mass density significantly less than Atlantic. The PSD-4x clones D45, S438 and S487 were similar to cv. Atlantic for mean mass density and stability of mass density (responsiveness to high, or favorable environments). D55 and S473 had high mass density, high stability and were equally responsive to favorable and unfavorable environments.

The clone with the highest mean mass density (1.091) was S477. It had significantly

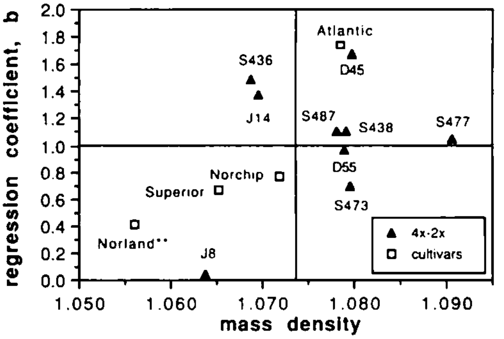

Fig. 2. Relationship between individual mean genotype mass density and regression coefficient (b) for each genotype. Horizontal and vertical lines mark grand genotype means for b and mass density, respectively. ** indicates significant deviation from regression mean square at 1 percent level of significance.

higher mass density than all other clones. Although the deviation from regression mean square was significant at the 10 percent level, S477 had mass density greater than 1.080 in each environment.

Chip color. Chip color is another quality trait which, ideally, should not vary greatly over environments. Mean chip color, s^2_d and b are listed in Table 2 for each clone. For chips to be acceptably light in color, they must have a chip color rating ≤ 4.0, on a scale of 1 = light, 10 = dark.

Seven of the thirteen clonal entries had a mean chip color rating ≤ 4.0 over the six environments (Figure 3). The two standard chipping cultivars, Atlantic and Norchip, were in this class. The PSD-4x clones with good chip color ratings including S438, S436, D45, D55 and J14. Of these clones, S438 had significantly better chip color than the best cultivar, Norchip, and the rest were not significantly different from cvs Norchip or Atlantic (Table 2).

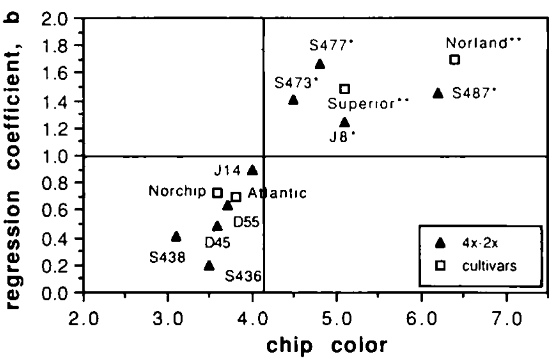

Fig. 3. Relationship between individual mean genotype chip color rating and regression coefficient (b) for each genotype. Horizontal and vertical lines mark grand genotype mean for b and chip color rating, respecitvely. *, ** indicate significant deviations from regression mean squares at 5 and 1 percent levels, respectively.

Only the unacceptable clones for chipping, (chip color rating >4.0) had significant lack of stability over environments. They also all had b>1.0, indicating responsiveness to favorable environments for chip color; under some environmental conditions, these clones could be expected to have lower chip color ratings than in other environments (Figure 3), while the clones with the best mean chip color ratings could be expected to be relatively consistent over environments.

Conclusions

The 4x clones from 4x-2x crosses had mass density and chip color which was equal or superior to the cultivars. The PSD-4x clones with haploid Tuberosum-*S. tarijense* hybrids as 2x parents and the PSD-4x clones with Phureja-haploid Tuberosum hybrid grandparents [4x × (4x × 2x)] had the best tuber quality traits. These results differ from those reported by DeJong et al. (1981) where, while some PSD-4x clones with Phureja gave higher total and marketable yields than check cultivars, quality traits such as mass density and general tuber appearance were not acceptable. The negative traits from Phureja (deep eyes, raised internodes, late maturity, short tuber dormancy, etc.) may be somewhat alleviated by crossing again to 4x Tuberosum (as with D45 and D55), or avoided by utilizing wild relatives of potato in the 4x × 2x breeding method after such germplasm has been assessed for contributions to tuber quality traits such as mass density and general tuber appearance.

It appears that the 4x-2x breeding method may be useful not only for the generation of high yielding cultivars, but also for production of phenotypically stable, widely adapted clones which possess the quality attributes which are essential for commercial acceptability. Of particular interest are clones such as S487, which has high marketable yield and adaptation to both favorable and unfavorable environments; or J8, S436 and

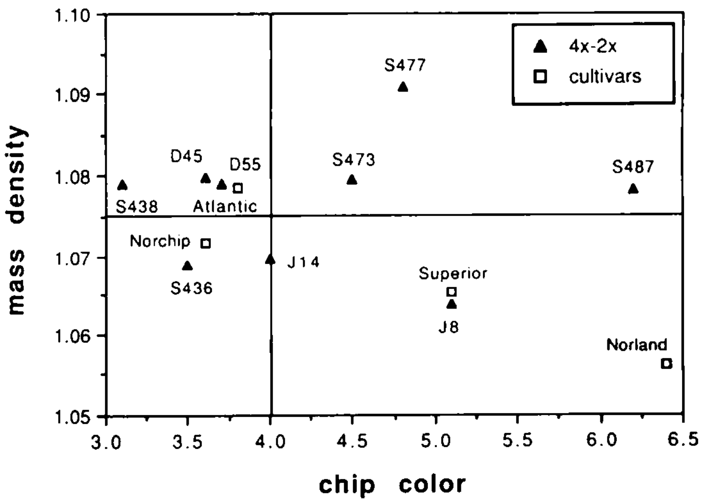

Fig. 4. Chip color vs. mass density for 13 clones evaluated over six environments. Chip color ≤4.0 acceptable, and mass density ≥1.075 acceptable. Clones in upper left quadrant have both acceptable chip color and mass density, and are the most desirable.

D55, which are similar to elite cultivars such as Atlantic in being high yielding, stable and adapted to favorable environments. Also of interest are the clones which combine the quality traits of high mass density and low chip color rating which are required in a chipping cultivar (Figure 4). The clones S438, D45 and D55 were similar to cv. Atlantic for chip color and mass density; the clones S436 and J14 were similar to cv. Norchip for those qualities.

The potential of the 4x × 2x breeding method is demonstrated by the superiority of this group of previously unselected 4x clones from 4x-2x crosses. The ability to obtain clones which are equal or superior to commercial cultivars from such small initial populations indicates that the 4x × 2x method may increase the efficiency of cultivar development when incorporated into conventional potato breeding programs.

Acknowledgements

Paper No. 3048 from the Laboratory of Genetics. Research supported by College of Agricultural and Life Sciences; International Potato Center; USDA CGRO 84-CRCR-1-1389; and Frito Lay, Inc.

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