Theor Appl Genet (1983) 66: 87–91

Tuberosum × Tuberosum and Tuberosum × Andigena potato hybrids: comparisons of families and parents, and breeding strategies for Andigena potatoes in long-day temperate environments

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Received March 3, 1981
Communicated by H. F. Linskens

Summary. Tuberosum × Tuberosum families and Tuberosum × long-day adapted Andigena families are compared with each other and with their parents using multivariate analyses. The Tuberosum × Tuberosum families, representative of those used in present-day breeding programs, have lower mean tuber weights, marketable yields and total yields than their parents, and a trend towards the Andigena clones which represent their putative ancestors. The Tuberosum × Andigena families are superior to the Tuberosum × Tuberosum families in total yield and tuber number, but have reduced tuber size, later maturity and more persistent stolons. The characteristics of the Andigena parents dominate the inter-Group hybrids. The multivariate analyses facilitate the identification of superior hybrid families and superior parents. The results are discussed in the context of further Andigena selection, cytoplasmic male sterility, and reciprocal differences in inter-Group hybrid families. Future breeding strategies are proposed.

Key words: *Solanum tuberosum* – Andigena – Multivariate analyses – Heterosis – Breeding strategies

Introduction

In recent years increasing attention has been directed to the use of primitive cultivated potatoes as a source of new variation for breeding programs in north temperate latitudes. The tetraploid material of *Solanum tuberosum* L. Group Andigena was first used by Simmonds (1969) and Plaisted (1972), and later in the Agriculture Canada potato breeding program. The potential of this material to increase yields is well established (John Innes Institute 1966; Glendinning 1969, 1975; Cubillos and Plaisted 1976; Tarn and Tai 1977), and at least one F_1 Tuberosum × Andigena hybrid has recently been released as a variety (Plaisted et al. 1981).

Adapted Andigena selections exert a strong influence in crosses with clones of *S. tuberosum* Group Tuberosum (Tai and Tarn 1980) and the high frequencies of late maturities, persistent stolons and small tubers occurring in even the better crosses remain problems for the breeder. Simmonds (1976) has recognized the distinctness of this material and emphasized the need to learn how best to utilize it. This paper extends the previous work of Tai and Tarn (1980) by applying multivariate analyses to both Tuberosum × Tuberosum and Tuberosum × Andigena families. The results add to our understanding of the performance of conventional Tuberosum × Tuberosum families, and enable conclusions to be drawn on the use of both Tuberosum and Andigena parents.

Materials and methods

The families studied, and their parentages, are given in Table 1. The Tuberosum parents were selected to represent a range of the types used as parents in intra-Tuberosum crosses in a cultivar development program. The Andigena parents were selected from a population of long-day adapted types on the basis of better maturity, tuber size and yield.

The families were first grown in the field in 1978 when 30 hills per family were harvested at random. The field was divided into three blocks for the 1979 experiment. Each block contained an 8-hill plot of each of ten clones of each of the 22 families as well as a plot of each of 22 parental clones. Two Tuberosum parents, F51043 and F60019, were not available. In each block the ten clones per family were planted adjacent to each other in a random section of the block and the parental clones were randomly ordered and planted adjacent to each other. Within-row spacing was 25 cm throughout. Between-row spacing was 91 cm. The experiment was planted on May 11, topkilled 118 days later and subsequently harvested and graded. Fertilizer was banded at planting at the rate of 1344 kg/ha of 10–20–10 plus 2 Mg, and normal management and pest control practices were carried out.

Ten traits were compared in the present study:

1. *Early vigour* scored at 27 days when most of the plants were emerged on a scale from 1 (no emergence) to 5 (largest plants).
2. *Midseason vigour* at 84 days on a scale from 1 (small) to 5 (large).
3. *Maturity* of the haulm at 110 days scored from 1 (early) to 5 (late).
4. *Die-back of stolons* scored at time of digging on a scale from 1 (completely dead) to 5 (still attaching tubers to plant remains).
5. *Appearance* of the tubers scored from 1 (excellent) to 5 (poor).
6. *Total tuber number* per plot.
7. *Mean tuber weight* in gms per tuber calculated by total yield per plot/total number of tubers per plot.
8. *Marketable yield* in kg per plot of tubers ≧ 55 mm diameter.
9. *Total yield* in kg per plot.
10. *Specific gravity* determined on a sample from each plot by the weight in air, weight in water method.

An analysis of variance was carried out for each of the ten traits within each of the two populations (i.e., the Tuberosum × Tuberosum families and the Tuberosum × Andigena families). The family means for each trait within each population were compared by Duncan's multiple range test. Standard deviations of population means were calculated from the means of families within each population. The means and standard deviations of the Tuberosum and Andigena parental groups are based on all the clones used as parents and tested in the experiment. It should be noted that the Tuberosum clones used as parents of the Tuberosum × Tuberosum families and those used as parents of the Tuberosum × Andigena families are combined in the Tuberosum parent mean.

Canonical analyses were performed according to Seal (1965) and used as described by Tai and Tarn (1980). All traits except yield and midseason vigour were included in the analyses. The two-dimensional canonical diagrams were drawn using the first two significant canonical variates for the means of the families and the Tuberosum and Andigena parents.

Results

Table 1 shows the performance of five traits for the 22 families used in the experiment. When families were compared within populations, significant differences were obtained for all traits in both populations. A mean ranking, which provides a subjective evaluation of the merit of a family within a population, is given in column 4 of Table 1. It is calculated as the average of the ranking of desirable maturity, mean tuber weight

Table 1. Parentages of Tuberosum × Tuberosum and Tuberosum × Andigena families, their-ranking based on maturity, mean tuber weight and marketable yield, and the means for selected traits

Cross no.	Parentage		Mean rank	Maturity	Tuber no.	Mean tuber wt (g)	Marketable yield (kg)	Total yield (kg)
	Female	Male						
	Tuberosum × Tuberosum							
1	F62008	Katahdin	7	3.1 abc*	62.7 b	113 cd	4.16 b	6.82 ab
2	F64073	F59045	6	2.7 cde	61.2 b	122 bcd	4.71 ab	6.86 ab
3	F66041	F59103	3	2.6 de	44.9 c	154 a	4.78 ab	6.47 b
4	F62008	F47024	4	3.5 a	47.8 c	154 a	5.01 ab	6.92 ab
5	96-56	F60019	1	2.5 e	54.2 bc	151 ab	6.15 a	7.90 a
6	Jemseg	F51043	2	2.4 e	54.1 bc	138 abc	5.12 ab	7.11 ab
7	BL61-74-167	F66011	8	3.4 ab	76.5 a	99 d	4.11 b	7.15 ab
8	F56047	F66011	5	3.0 bcd	55.1 bc	128 abcd	4.81 ab	6.82 ab
	Tuberosum × Andigena							
9	F47024	A665	3	3.5 abc*	72.4 de	134 a	6.69 a	9.11 a
10	F66011	A213	11	3.0 cde	108.2 ab	87 efg	3.65 cd	8.57 a
11	Jemseg	A213	7	2.5 def	85.9 cd	96 def	4.08 bcd	7.82 abc
12	Jemseg	A319	1	2.3 f	63.5 e	111 bc	4.22 bcd	6.81 c
13	Kennebec	A665	1	3.1 bcd	66.3 e	126 ab	5.40 b	8.01 abc
14	F55070	A522	5	3.0 bcde	85.5 cd	104 cd	4.56 bcd	8.46 ab
15	F59045	A522	10	3.4 abc	73.2 de	104 cd	3.85 cd	7.09 bc
16	F59045	A669	13	3.6 ab	103.1 ab	88 efg	3.91 cd	8.46 ab
17	F62008	A522	4	3.2 bc	77.8 de	116 bc	4.83 bc	8.36 ab
18	F62008	A669	8	3.6 ab	83.8 cd	102 cde	4.96 bc	8.26 ab
19	F66011	A473	12	3.9 a	101.7 ab	86 fg	4.12 bcd	8.41 ab
20	Jemseg	A677	9	2.6 def	95.1 bc	93 defg	3.83 cd	8.37 ab
21	Kennebec	A677	14	3.2 bc	112.5 a	78 g	3.20 d	8.54 a
22	Sable	A677	6	2.5 ef	95.6 bc	90 defg	4.17 bcd	8.40 ab

* Within each group of families in each column means followed by the same letter are not significantly different at the 0.05 level of probability using Duncan's Multiple Range test

Table 2. Means and SD for 15 Tuberosum and seven Andigena parents, and for eight Tuberosum × Tuberosum and 14 Tuberosum × Andigena families

Trait	Parents		Hybrid families	
	Tuberosum	Andigena	Tuberosum × Tuberosum	Tuberosum × Andigena
Early vigour	2.48 ± 0.79	2.62 ± 0.68	1.76 ± 0.18	2.26 ± 0.37
Midseason vigour	2.62 ± 0.47	3.24 ± 0.37	2.94 ± 0.44	3.12 ± 0.44
Maturity	2.07 ± 0.54	3.29 ± 0.36	2.90 ± 0.42	3.11 ± 0.49
Die-back of stolons	1.62 ± 0.57	3.38 ± 1.24	2.67 ± 0.62	3.23 ± 0.83
Total tuber no.	50.36 ± 9.09	89.24 ± 34.96	57.08 ± 9.87	87.46 ± 15.75
Total yield (kg)	7.17 ± 1.45	6.57 ± 1.52	7.01 ± 0.42	8.20 ± 0.60
Mean tuber wt (g)	144.37 ± 21.52	79.45 ± 24.88	132.23 ± 20.08	101.18 ± 17.21
Marketable yield (kg)	5.70 ± 1.55	2.62 ± 1.67	4.87 ± 0.64	4.39 ± 0.87
Specific gravity	1.076 ± 0.007	1.080 ± 0.008	1.078 ± 0.004	1.079 ± 0.004
Appearance	3.14 ± 0.99	3.57 ± 0.46	2.79 ± 0.31	2.72 ± 0.46

and marketable yield. Families 3, 5 and 6 of the Tuberosum × Tuberosum population and families 12, 13, 9 and 17 of the Tuberosum × Andigena population are considered to be superior families because of their high ranks.

Characteristics of the two groups of parents and the two populations of F_1 hybrids are presented in Table 2. The 15 Tuberosum parents provide the standard against which the rest of the material can be compared: they have moderate vigour, earliest maturity, least persistent stolons, low tuber number, largest mean tuber weight, and marketable yield. The Tuberosum × Tuberosum population has reduced early vigour, greater midseason vigour, later maturity and more persistent stolons when compared with its parental group. Tuber number increased in the hybrids, but mean tuber weight, total yield and marketable yield decreased.

The seven Andigena parents have characteristically high early and mid-season vigours, late maturity and very persistent stolons. This group has the highest tuber number and smallest tuber size: total yield is low, and only 40% of this is marketable.

The Tuberosum × Andigena population exceeds the performance of the Andigena parents for all traits except vigour. However, the performance of this population is inferior to its Tuberosum parents for most characteristics, the exceptions being tuber number and a 14.4% increase in total yield. The scores for mid-season vigour, maturity, stolons, tuber number and mean tuber weight are closer to the Andigena parents, whereas early vigour and marketable yield are closer to the Tuberosum parent. Total yield is the only character that is not intermediate to the two parents. Compared with the Tuberosum × Tuberosum families the Tuberosum × Andigena families have later maturity, more persistent stolons, and a larger number of smaller tubers for a 17% increase in total yield and a 10% decrease in marketable yield.

Multivariate analysis of variance indicated significant differences between mean vectors of the families ($\chi^2 = 212.65$, df = 168). All eight canonical variates were significant at the 1% level and the first five accounted for 40.3, 18.7, 15.5, 8.7 and 7.7% of the total variation, respectively. The canonical diagram based on the first and second canonical variates utilized 59.0% of the variation (Fig. 1). It separates the two parental groups – with the exception of one "Tuberosum" parent, a Dutch leafroll resistant breeding line which has a species background, that appears towards the top of the Andigena distribution area – and shows distinct areas for

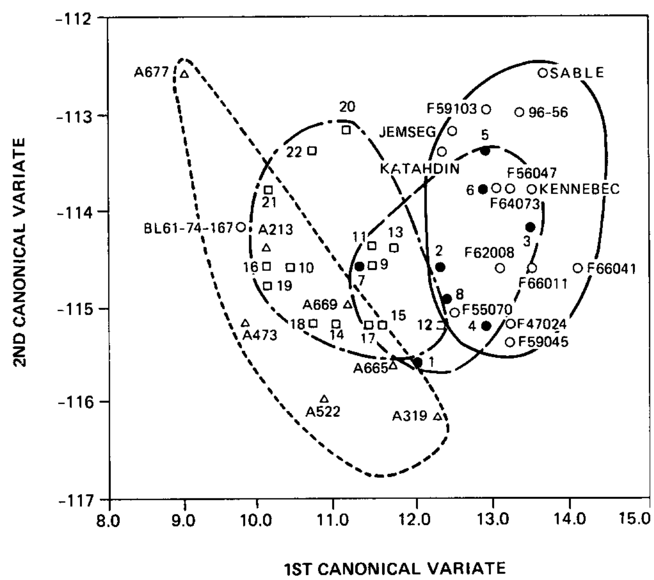

Fig. 1. Canonical diagram for the Tuberosum parents (○), the Tuberosum × Tuberosum crosses (●), the Andigena parents (△), and the Tuberosum × Andigena crosses (□)

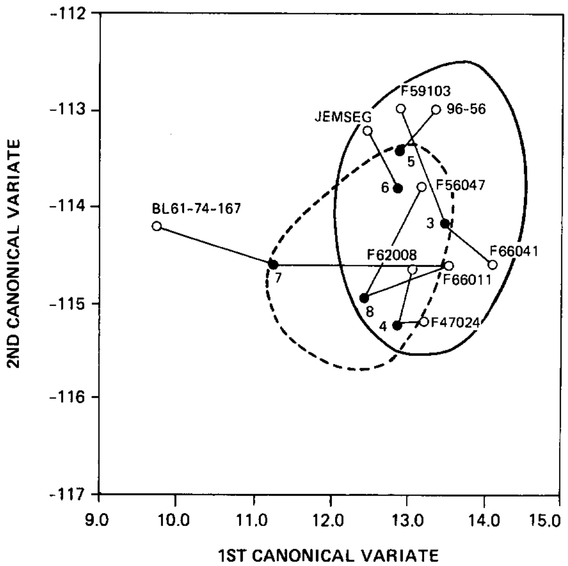

Fig. 2. Canonical diagram for selected Tuberosum × Tuberosum crosses (●) and some of their parents (○)

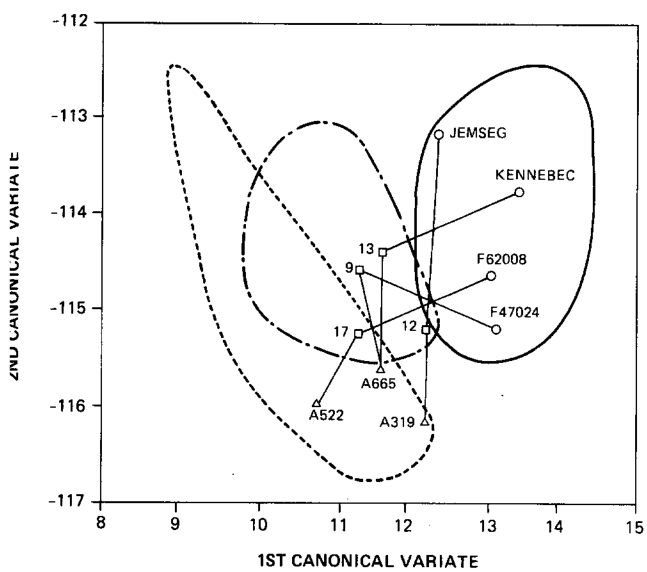

Fig. 3. Canonical diagram for the better Tuberosum × Andigena crosses (□) and their Tuberosum (○) and Andigena (△) parents

both the Tuberosum × Tuberosum families and the Tuberosum × Andigena families.

The Tuberosum × Tuberosum families show a trend towards the Andigena group for most traits, and lower yields than their parents (Table 2). This behaviour is reflected in the canonical diagram (Fig. 2) by the positions of families to the left and below the mid-parent points. The families that have the highest mean ranks (Table 1) are located in the center of the Tuberosum area, while the lower ranking families are on the lower left closer to the area of the Andigena parents. The axis of the Tuberosum × Tuberosum family cluster thus parallels the axis of poor to good cross performance.

The Tuberosum × Andigena family cluster occupies an area between the parental groups and overlaps the Andigena group (Fig. 3). The majority of the hybrid families are closer to their Andigena parent than to their Tuberosum parent. Also, the long axis of this cluster approximately parallels the axis of the Andigena parental cluster. Both characteristics indicate the dominant influence of Andigena parents. The family points are above and to the left of the mid-parent points. The Tuberosum × Andigena families with high mean ranks (Table 2) are mostly in the lower right area.

Discussion

The poor performance of the Tuberosum × Tuberosum families in relation to their parents has also been noted by Maris (1969) and Tai (1974). The results of Maris (1969) and the present results show that families are later than their parents, whereas Tai (1974) found them to be similar. In all three cases, the families have lower mean tuber weights, marketable yields and total yields than their parents while tuber numbers are higher in the families than in their parents. This situation is also apparent in the canonical diagram (Fig. 1) which shows that poorer Tuberosum × Tuberosum families are closer to the Andigena clones (representative of their putative ancestors) than to their Tuberosum parents. These results are consistent with the difficulties breeders have experienced obtaining selections with improved performance in traits such as yield from relatively homozygous Tuberosum × Tuberosum families as noted, for example, by Simmonds (1969, 1976) and Mendoza and Haynes (1974).

The Tuberosum × Andigena families behave similarly to the different set of families studied earlier (Tai and Tarn 1980). In the present experiment the three Andigena parents involved in the five top-ranking Tuberosum × Andigena families are clustered together at the bottom right of the Andigena area and two of these, A665 and A319, are very close to the Tuberosum area. The other parent, A522, was identified as a superior parent in earlier work (Tai and Tarn 1980). Thus, canonical analysis applied to these experiments has facilitated the identification of superior Tuberosum × Andigena families and superior Andigena parents. It has been less successful in identifying superior Tuberosum parents. Both experiments also emphasize the importance of non-additive genic interactions because families are not located at the midpoints of straight lines between their parents. On the other hand, there is evidence of general combining ability for some of the Andigena parents as shown by the clustering of families 20, 21 and 22 with A677 in common, and families 14, 15, 17 with A522 in common. This effect was also noted by Tai and De Jong (1980) for two Phureja × haploid Tuberosum clones.

Good Tuberosum × Tuberosum families can combine good maturity, tuber size and marketable yield (e.g., 96–56 × F60019), but this does not occur readily in the Tuberosum × Andigena families evaluated so far. Considering the top Tuberosum × Andigena families in the present experiment, Jemseg × A319 ranks first for maturity and sixth for a marketable yield 63% of that of the highest family, while Kennebec × A665 ranks fifth for maturity (later than all but two of the Tuberosum × Tuberosum families) and second for marketable yield. A similar situation was noted by Tai and Tarn (1980). Some segregates from the better crosses have more acceptable overall performance, but the use of first generation hybrids between these two Groups is not considered as the best present use of the adapted Andigena material.

It is interesting to note that subjective mean ranking of families within each of the two populations based on three important traits gives a reasonably good indication of superior families. However, there were families whose mean ranking did not match their positions in the canonical diagram because an exceptional rank of a single trait may dominate the result when only a few traits are considered. Further, ranking does not take into consideration the correlation between traits.

The combination of cross evaluation and canonical analysis used here and by Tai and Tarn (1980) provides a means of identifying superior Andigena parents. These clones can now be used as standards to select more similar or better clones from within Andigena populations. Once such a pool of superior Andigena parents is available, it should be possible to select clones that perform considerably better than the best presently available. This selection is expected to maintain the distinctness of the Andigena material that in Tuberosum × Andigena hybrids leads to the multiplicative interaction of yield components that contributes to the heterosis (Tarn and Tai 1977).

An alternative approach is to backcross selected hybrid clones to Tuberosum. In this case, it may be desirable to make the initial cross in the direction Andigena × Tuberosum to avoid the cytoplasmic male sterilities frequently found in the Tuberosum × Andigena progenies (Grun 1974; Hoopes et al. 1980; Tarn and Miller, unpublished). Also, the reciprocal differences in yield in favour of Tuberosum cytoplasm, reported by Hoopes et al. (1980), become a consideration. Such a backcross strategy has the potential to improve the problem traits of maturity, the related dieback of stolons, and mean tuber weight, and its impact on heterosis is being studied in a new set of experiments.

Acknowledgements. The technical assistance of Miss S. M. Miller is gratefully acknowledged. Appreciation is expressed to Drs. H. De Jong and D. A. Young for a critical review of the manuscript.

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