

## **Analysis of an incomplete diallel cross among three *ssp. tuberosum* varieties and seven long-day adapted *ssp. andigena* clones of the potato (*Solanum tuberosum* L.)**

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### **Summary**

The main aim of the experiment was to study the behaviour of seven long-day adapted clones of *Solanum tuberosum* ssp. *andigena* (A) and three varieties of *S. tuberosum* ssp. *tuberosum* (T) in an incomplete diallel cross. The four groups of crosses, T × T, T × A, A × T and A × A, held 2, 12, 20 and 21 populations, respectively. Eleven of the intersubspecific crosses were exact reciprocals. Thirty random clones per population were grown as second clonal generation in an incomplete block design with four replications in plots of two plants per clone in 1980, the parents included in many plots. Data were recorded on ten characters.

The results showed that group T × A gave the highest tuber yield and A × T the second highest. The F-values indicated highly significant genotypic effects for all characters in all populations. The mean genotypic coefficients of variation (GCV), were the highest for group A × A for all characters. The ANOVA, based on population means showed significant mean squares for general combining abilities (GCA) and for differences of reciprocals for all characters; the specific combining ability (SCA) mean squares were significant only for date of emergence, plant height and haulm type. Almost all GCA effects of the parents were significant positive or negative. Several populations showed also significant SCA effects. The correlations between the GCA effects and the parental values were of about the same magnitude as the heritabilities; those between the population means and the midparental values were slightly lower.

Compared to the midparental values, most populations showed significant positive heterosis for date of emergence, haulm type, number of tubers and under water weight; all populations had significant negative heterosis for mean tuber weight and nearly all for plant height and general impression. All populations from groups T × T and A × A had significant negative heterosis for tuber yield and so had 13 out of the 20 populations from group A × T, while seven of the 12 from group T × A showed significant positive and four significant negative heterosis. The average heterosis for tuber yield of group T × T was –11%, of T × A 3.4%, of A × T –9% and of A × A –18%. The highest mean tuber yields were obtained from crosses with a very high yielding A-parent as female, while the heterosis was negative. Though significant differences between the 11 reciprocals occurred for all characters, consistent differences occurred only for tuber yield. Averaged over the 11 crosses the T × A populations outyielded their exact reciprocals by 10.7%. For the highest tuber yields in A–T crosses, therefore, the *tuberosum* cytoplasm seems to be preferable. By contrast for a high male fertility the *andigena* cytoplasm is preferable.

## Introduction

The potato of the northern temperate latitudes, *Solanum tuberosum* ssp. *tuberosum*, hereafter designated as *tuberosum* or T, was derived by semi-natural and artificial selection for adaptation to long-day conditions from *Solanum tuberosum* ssp. *andigena*, further designated as *andigena* or A, indigenous to South America. Historical evidence indicates that the initial number of introductions into Europe was very limited (Hawkes, 1967). This suggests that these introductions represented only a small part of the total genetic variation of *andigena*. Moreover, the selection for adaptation and the late blight epidemic of the mid-19th century probably eliminated much of the already limited variation (Simmonds, 1962). Therefore, it seems safe to conclude that the modern *tuberosum* varieties have a relatively narrow genetic base.

In 1959 Simmonds (1969) started a long-term selection experiment at the John Innes Institute, Hertford, UK, to produce long-day adapted *andigena* parents for incorporation in potato breeding programmes and at the same time to test the idea that *tuberosum* evolved by selection from *andigena*. From 1966/67 the experiment was carried on by Glendinning (1975a) of the Scottish Crop Research Institute at Pentlandsfield. Comparable programmes were initiated by Plaisted (1972) at Ithaca, New York, USA, in 1964, by the present author at Wageningen, the Netherlands, in 1967, and by Tarn (Tarn & Tai, 1973, 1977) at Fredericton, NB, Canada, in the late sixties. The main objective that these programmes have in common is: the integration of long-day adapted *andigena* clones, obtained by phenotypic recurrent selection within this subspecies, into *tuberosum*, to broaden the genetic base of the latter. A wider genetic base means more perspectives for the improvement of the potato by breeding.

Results show that already after four to five cycles of recurrent selection the better *andigena* clones are comparable with *tuberosum* clones for time of tuber initiation, maturity and yielding capacity (Simmonds, 1969; Glendinning, 1975b; Rasco et al., 1980; unpublished own data).

Howard (1963) reported that from A × T hy-

brids, selected for tolerance to long days, very high-yielding seedlings can be obtained in the first and second backcrosses to *tuberosum*. A further backcross led to material with yields no higher than those found in existing varieties. The heterosis, observed by Howard, has been confirmed more or less by the results from several other experiments. Paxman, working at the John Innes Institute (1966), found in a diallel cross of four *tuberosum* varieties and four fairly well long-day adapted *andigena* clones that the A × T seedling families outyielded the T × T families by 52%, while T selfed, A selfed and A × A yielded 49, 54 and 30% less, respectively, than T × T. Glendinning (1969) comparing 18 A × T families with four T × T families in 1967, noted a 13% higher tuber yield for the A × T families. In experiments at Ithaca a T × A hybrid population outyielded a T × T population by 15% in 1972 and by 17% in 1973 (Cubillos & Plaisted, 1976). In both populations the T-parents were the same; the A-parents had undergone five cycles of phenotypic recurrent selection for adaptation to long days. Tuber yield of the A × A population was 37% less in 1972 and 25% less in 1973 than that of the T × T population. In a field experiment by Tarn & Tai (1983) in New Brunswick, Canada, in 1979, mean tuber yield from eight-hill plots of 14 T × A families was 17% higher than that of eight T × T families. The latter were generally less vigorous and earlier in maturity and had fewer but heavier tubers than the T × A families. In earlier experiments Tarn & Tai (1977) intercrossed five T-clones and five long-day adapted A-clones, and produced four populations, viz. T × T, A × A, T × A and A × T. These were grown as spaced plants in the field in 1972 and 1973. A × T outyielded T × T by 29% in 1972 and 9% in 1973; T × A yielded 33% more than T × T in 1972 and 15% in 1973. Tuber yield of A × A was 33% higher in 1972 and 10% lower in 1973 than that of T × T in the respective years. There was also considerable positive heterosis of A × T and T × A over T × T for plant vigour and tuber number and negative heterosis for mean tuber weight in both years. The somewhat higher tuber yield of the T × A population as compared with that of the reciprocal A × T population was not significant in either

year. Highly significant differences for tuber yield between  $T \times A$  and  $A \times T$  hybrids, however, were reported by Hoopes et al. (1980) from five field experiments at Ithaca, NY, in different years. The  $T \times A$  outyielded their reciprocal  $A \times T$  hybrids by 12 to 33%. Both more tubers per plant and larger tubers contributed to the yield advantage of the  $T \times A$  hybrids. In an experiment at Riverhead, Long Island, NY, and at two locations in Peru the  $T \times A$  hybrids produced also higher tuber yields, but the differences from the  $A \times T$  hybrids were not significant. The percent of plants with berries was much higher in the  $A \times T$  hybrids than in the  $T \times A$  hybrids both at Ithaca and at the two Peruvian locations. Earlier Grun (1974) reported reciprocal differences for male fertility in crosses between *tuberosum* and *andigena*, the  $T \times A$  families having a high proportion of male sterile individuals, while their  $A \times T$  reciprocals were largely male fertile. Sanford & Hanneman (1982a) tested exact reciprocals among two early maturing *tuberosum* varieties and two late maturing *andigena* clones. In field experiments at Hancock, Wis., the hybrid families with *tuberosum* cytoplasm ( $T \times A$ ) outyielded their exact reciprocals ( $A \times T$ ) by 25 to 115%. There were no significant reciprocal differences in vine maturity or in flowering score. In all these experiments the higher-yielding (early) T-parent produced the higher-yielding progeny when used as the maternal parent. It was concluded that the occurrence of large reciprocal differences seemed to depend more upon having parents of opposite maturity than on the taxonomic origin of the parent's cytoplasm. Staub et al. (1982) produced, from initial crosses of three *tuberosum* cultivars with three long-day adapted *andigena* clones, four and two sets of exact reciprocal F1 and BC1 families, respectively. The results from field and greenhouse experiments showed that cytoplasmic factors did not influence morphological characters consistently, except those relating directly to fertility. No consistent differences between reciprocals occurred in tuber yield, tuber number and mean tuber weight and those differences which arose seemed to reflect a maternal rather than a cytoplasmic influence. F1 and BC1 families containing the sterility-resistant factors of *andigena* had higher

fertility than their respective reciprocals with cytoplasm of *tuberosum*.

The results from the above experiments are generally in agreement with one another as far as heterosis for tuber yield of  $T \times A$  and  $A \times T$  families over  $T \times T$  and  $A \times A$  families and reciprocal differences in male fertility between  $T \times A$  and  $A \times T$  families are concerned. The reciprocal differences for yield and other characters, however, did not always show similar tendencies in all experiments.

The aim of the present study was to get information for several agronomic characters of populations from crosses involving own long-day adapted *andigena* clones and *tuberosum* cultivars.

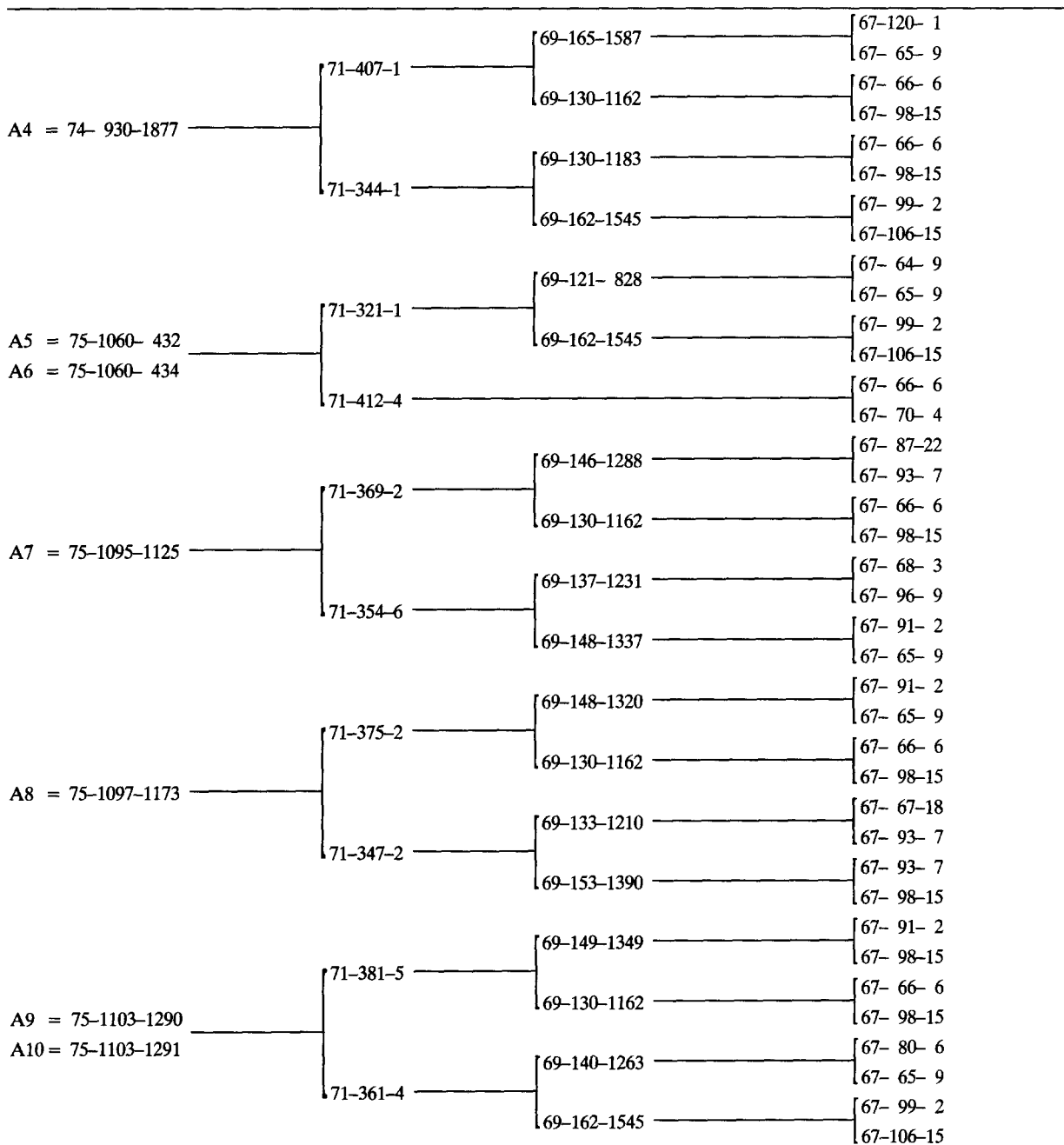
### Materials and methods

The starting material for the *andigena* long-day adaptation programme was kindly provided by the Potato Introduction Station at Sturgeon Bay, Wis., U.S.A. It consisted of lots of 50 true seeds from 59 accessions of *andigena*. The attempt to produce a composite cross in the sense of Harlan et al. (1940) in combination with phenotypic recurrent selection for long-day adaptation, was not very successful as already during the first cycle some 30 accessions got lost, due to non-tubering, non-flowering and male sterility. Nevertheless, the composite cross principle has been followed as far as possible by applying hand pollination of selected individual clones with one another.

The A-parents (A4–A10) used in the present study resulted from the fourth cycle of phenotypic recurrent selection (Table 1). From the pedigrees it is apparent that there occurred some inbreeding in A4, A8, A9 and A10, while there is a fairly close relationship between the parents; A5 and A6 are even full sibs and so are A9 and A10.

The seven fairly well long-day adapted A-clones and three *tuberosum* cultivars, viz. Humalda (T1), Oberarnbacher Frühe (T2) and Profijt (T3) were mated in 1977. This resulted in the incomplete diallel cross as indicated in Table 2. Except the combination of T1 with T3 it is a half diallel without selfings, though not all combinations are on the

**Table 1.** Pedigrees of the *andigena* clones. In each cross the upper parent is the female. Each clone number consists of three parts. The first part indicates the year in which the genotype was raised from true seed; the second part is the population number and the third part is the number of the individual clone in the population concerned. Below the pedigrees the PI numbers have been given from which the 1967 populations were grown. For PI numbers see Ross & Rowe (1965)



**Population numbers with corresponding PI numbers**

64 = PI WRF 1286  
 65 = PI 161695  
 66 = PI 161716  
 67 = PI 161771  
 68 = PI 184903

70 = PI 186180  
 80 = PI 225629  
 87 = PI 232046  
 91 = PI 232842  
 93 = PI 233984

96 = PI 233993  
 98 = PI 233997  
 99 = PI 234002  
 106 = PI 243382  
 120 = PI 258879

same side of the diagonal; only 11 of the  $3 \times 7 = 21$  possible intersubspecific exact reciprocals were included. The total number of combinations, therefore, is  $(10 \times 9) : 2 - 1 + 11 = 55$ .

As an extensive description of the methods used has been given by Maris (1986), they are only described here briefly. In March 1978, 100 seeds from each of the 55 crosses were sown in seed pans. After about five weeks from each population 60 random seedlings were transplanted into 10 cm clay pots. The numbered seedlings were grown until harvest at about maturity in July in a greenhouse.

In 1979, from each of the first 40 of the 60 clones per population one plant was grown to maturity on a sandy soil at Wageningen and two plants on a clay soil in the Flevopolder for early harvest in order to obtain healthy seed tubers for the second clonal generation.

The first 30 of the 40 clones of each population were grown in an incomplete block design with four replications and in plots of two plants per clone on a clay soil in the Flevopolder in 1980, the parental cultivars and clones being included in many plots of two plants. Seed tubers of clones and parents were of comparable size. Observations per plant were recorded on: date of emergence; number of main stems; plant height at the beginning of main flowering; maturity; general impression of the underground plant parts, mainly tuber appearance at harvest between 22 September and 10 October, after mechanical destruction of the haulms

shortly before lifting; number of tubers; tuber yield; mean tuber weight and under water weight. In addition, data per plot of two plants were recorded on haulm type, flowering and spontaneous fruit set.

For the statistical analysis of the data of the second clonal generation in 1980, the method for the incomplete diallel cross, described by Garretsen & Keuls (1973), was applied.

From the analysis of variance per population the mean was obtained for each character. Furthermore mean squares (MS) for the genotypes, replications and the error were calculated as well as F-values. For each character the phenotypic (PCV) and genotypic coefficients of variation (GCV) were determined according to the formulae:  $PCV = 100\sqrt{\sigma_p^2}/\bar{X}$  and  $GCV = 100\sqrt{\sigma_g^2}/\bar{X}$ , where  $\sigma_p^2 =$  genotypes MS/number of replications,  $\sigma_g^2 =$  (genotypes MS-error MS)/number of replications and  $\bar{X} =$  population mean. From the outcome the averages for each of the four groups of crosses,  $T \times T$ ,  $T \times A$ ,  $A \times T$  and  $A \times A$ , were computed.

For the analysis of variance for general (GCA) and specific combining abilities (SCA) and reciprocal effects the means per population across four replications were used. From the variance components  $\hat{\sigma}_{GCA}^2$  and  $\hat{\sigma}_{SCA}^2$  the ratio  $\hat{\sigma}_{GCA}^2/(\hat{\sigma}_{GCA}^2 + \hat{\sigma}_{SCA}^2)$  was computed for each character to assess the relative importance of the GCA genetic variance to the total genotypic variance. When this ratio is  $>0.5$  GCA is more important than SCA in the inheritance of the character concerned, while the reverse is true when this ratio is  $<0.5$ .

The narrow sense heritability was computed according to the formulae  $4\hat{\sigma}_{GCA}^2/(4\hat{\sigma}_{GCA}^2 + 4\hat{\sigma}_{SCA}^2 + \hat{\sigma}_{Rec}^2 + \hat{\sigma}_e^2)$ , where  $\hat{\sigma}_{GCA}^2$ ,  $\hat{\sigma}_{SCA}^2$ ,  $\hat{\sigma}_{Rec}^2$  and  $\hat{\sigma}_e^2$  are the estimates of the variance components for GCA, SCA, reciprocal differences and the error, respectively.

The percentage of heterosis of the population means over their mid-parents was calculated from the formula  $H\% = \{(M - \bar{P})/\bar{P}\} \times 100$ , where  $H =$  heterosis,  $M =$  population mean and  $\bar{P} =$  mid-parent.

Table 2. Mating design of the incomplete diallel. T1 = Humalda, T2 = Oberarnbacher Frühe, T3 = Profijt; for A4–A10 see Table 1

♀	♂	T1	T2	T3	A4	A5	A6	A7	A8	A9	A10
T1											
T2		×		×	×		×	×	×	×	×
T3					×		×	×	×	×	×
A4		×	×	×							
A5		×	×	×	×		×	×	×	×	×
A6		×		×	×						
A7		×	×	×	×		×				
A8		×	×	×	×		×	×			
A9		×	×	×	×		×	×	×		
A10		×	×	×	×		×	×	×	×	

## Results

**Parental mean performances.** The parents were very different for all characters except plant height (Table 3). Generally, the differences between the A-parents were greater than between the T-parents. Most of the extreme values, then, occurred among the A-parents, viz. for: date of emergence (A5 and A6), number of main stems (A9 and A4), haulm type (A4 and A5 or A9), maturity (A7 and A5), number of tubers (A6 and A5) and tuber yield (A4 and A5). The very high tuber yield of A5 was directly due to a large number of tubers and a medium high mean tuber weight; the early emergence and late maturity have probably had a favourable indirect effect on tuber yield of this clone. The full sibs A9 and A10 and particularly A4 and A5 were also very different from each other in several respects.

**Phenotypic and genotypic coefficients of variation.** The F-values obtained from the analysis of variance per population showed highly significant differences among the genotypes for all characters. For most of the characters the differences between the mean performances of the four groups of populations were very small and in some cases even nil (Table 4). A × A, however, had the latest emer-

gence, earliest maturity, poorest general impression, largest number of tubers, lowest tuber yield and lowest mean tuber weight. T × T had the smallest number of main stems, best general impression, smallest number of tubers, highest mean tuber weight and lowest under water weight. The differences in means between T × A and A × T were negligible except those for number of tubers and tuber yield; the higher tuber yield of T × A was almost entirely due to a larger number of tubers per plant.

The differences between the mean PCV's and the mean GCV's within the groups of populations were very small for all characters (Table 4). This leads to the conclusion that the variation was largely due to genetic differences within the populations rather than to non-genetic effects (cf. Maris, 1986, p. 473). It should be borne in mind, however, that the 1980 experiment was done in only one environment. Consequently the variance from genotype × environment interaction ( $\sigma_{gE}^2$ ) could not be separated from genotypic variance ( $\sigma_g^2$ ). The latter, then, may be overestimated.

A × A showed the highest mean GCV's for all characters; they were the lowest for T × T for date of emergence, number of tubers, tuber yield and under water weight. Except for date of emergence and to a lesser extent for number of tubers and

Table 3. Mean performance of each parent in 1980 for ten characters, viz.: date of emergence (days in May), number of main stems (per plant), plant height (scores from 1 = short to 5 = tall), haulm type (scores from 1 = poor to 4 = attractive), maturity (in days after 31 July), general impression (scores from 3 = very poor to 9 = very good), number of tubers (per plant), tuber yield (in g per plant), mean tuber weight (in g per tuber), and under water weight (in g per 5 kg). Two plants per plot

Parents*	Number of plots	Date of emergence	Number of main stems	Plant height	Haulm type	Maturity	General impression	Number of tubers	Tuber yield	Mean tuber weight	Under water weight
T1	31	11.8	2.7	4.5	3.9	62.3	7.2	12.5	2588	207	312
T2	53	12.8	3.7	5.0	3.4	61.6	7.0	12.6	2401	191	343
T3	54	11.8	4.7	5.0	3.9	77.4	5.9	18.6	2761	149	412
A4	44	11.9	7.6	4.8	3.0	62.0	5.9	22.9	1842	80	362
A5	38	9.5	5.6	5.0	4.0	87.6	6.1	36.2	4738	131	393
A6	38	15.1	3.0	4.9	3.1	69.7	5.8	11.3	1859	165	376
A7	35	10.7	4.3	5.0	3.3	45.8	6.8	21.1	2450	116	326
A8	32	12.4	3.1	5.0	3.1	62.1	5.4	18.3	2104	115	310
A9	36	12.2	2.4	4.9	4.0	76.5	5.6	16.9	2102	124	412
A10	41	11.3	4.7	5.0	3.7	49.3	4.9	25.2	2286	91	364

\* See Tables 1 and 2.

**Table 4.** Mean performance and mean and range of phenotypic (PCV) and genotypic (GCV) coefficients of variation (calculated per population) per group of crosses for characters studied on the second clonal generation in 1980. T = *tuberosum*; A = *andigena*. For dimension of characters see heading of Table 3

Group of crosses	Number of populations	Group mean	PCV %		GCV %	
			mean	range	mean	range
date of emergence						
T × T	2	12.9	13.3	11.4–15.3	12.4	10.3–14.4
T × A	12	12.6	16.6	13.2–22.6	16.0	12.4–22.1
A × T	20	12.7	18.0	10.7–45.5	17.2	10.0–45.2
A × A	21	13.2	21.8	11.3–59.5	21.2	10.5–59.2
number of main stems						
T × T	2	3.5	33.8	25.1–42.5	30.9	21.9–39.9
T × A	12	4.2	33.9	24.6–49.4	30.9	21.5–46.9
A × T	20	4.1	31.9	22.3–50.8	29.2	18.5–49.3
A × A	21	4.1	38.4	24.5–52.7	35.4	20.9–50.8
plant height						
T × T	2	4.6	10.6	7.3–14.0	10.0	6.3–13.8
T × A	12	4.8	8.7	2.7–12.4	8.3	2.3–12.0
A × T	20	4.7	10.1	3.4–20.9	9.6	2.8–20.6
A × A	21	4.6	13.2	3.0–23.8	12.8	2.3–23.5
maturity						
T × T	2	67.0	27.0	26.9–27.2	26.4	26.4–26.5
T × A	12	69.6	25.3	16.0–34.9	24.6	15.6–34.1
A × T	20	68.9	25.8	19.6–37.6	25.3	19.2–37.2
A × A	21	64.9	29.6	16.8–45.5	29.1	16.2–45.3
general impression						
T × T	2	5.9	13.9	12.2–15.6	13.1	11.2–15.1
T × A	12	5.5	13.6	10.5–18.0	12.6	9.3–16.7
A × T	20	5.6	15.0	11.1–19.5	14.2	10.3–18.9
A × A	21	5.1	16.2	10.0–24.2	15.5	8.9–23.6
number of tubers						
T × T	2	15.4	29.7	29.5–30.0	27.0	26.7–27.3
T × A	12	24.2	37.0	30.1–45.8	34.9	26.9–44.0
A × T	20	21.5	35.4	22.7–44.8	33.5	20.0–43.3
A × A	21	25.4	42.8	30.9–53.4	41.0	28.6–51.5
tuber yield						
T × T	2	2256	32.8	32.2–33.4	31.6	31.2–31.9
T × A	12	2418	33.3	25.2–44.5	32.1	23.8–43.6
A × T	20	2284	35.1	25.7–50.6	34.0	23.9–50.0
A × A	21	2003	40.2	27.9–54.2	39.2	26.2–53.3
mean tuber weight						
T × T	2	149	40.3	38.5–42.1	38.3	36.8–39.8
T × A	12	100	39.1	30.9–46.4	36.5	28.8–44.9
A × T	20	106	39.4	27.3–48.9	37.5	24.4–46.6
A × A	21	79	40.5	26.6–51.6	38.9	24.5–50.0
under water weight						
T × T	2	347	11.7	11.3–12.1	11.4	11.1–11.7
T × A	12	375	12.5	10.0–15.3	12.3	9.8–15.1
A × T	20	368	12.4	9.0–14.8	12.2	8.7–14.6
A × A	21	370	12.6	10.5–16.3	12.3	10.0–16.0

plant height, however, the differences in mean GCV within characters between the four groups were not really great. This does not alter the fact that on the average the within-population genotypic variation was greatest in group A × A and least in group T × T.

The ranges in GCV were quite narrow for all characters in group T × T, except for number of main stems and plant height, but this group consisted of only two populations. By contrast, in group A × A the ranges in GCV were wide for all characters, in particular for date of emergence and plant height; the same applied to T × A and A × T, though mostly to a lesser extent.

*Analysis of variance for combining abilities and reciprocals.* The means across the 30 clones and over the four replications for each of the 55 separate populations, used for this analysis and ordered according to the above four groups, are given in Table 5. Mean squares due to GCA and SCA and to differences of reciprocals are shown in Table 6.

The GCA mean squares appeared to be highly significant for all characters, except plant height for which it was significant; the SCA mean squares were highly significant only for plant height and haulm type and significant for emergence. All characters showed highly significant differences of reciprocals, except general impression for which the mean square was significant.

Table 5. Population means for the characters studied on the second clonal generation in 1980. For T1–T3 and A4–A10 see Tables 1 and 2. For dimension of characters see heading of Table 3

Crosses	Date of emergence	Number of main stems	Plant height	Haulm type	Matu- rity	General impres- sion	Number of tubers	Tuber yield	Mean tuber weight	Under water weight
T2 × T1	12.9	3.0	4.5	3.5	65.0	6.1	13.7	2219	162	327
T2 × T3	12.9	3.9	4.6	3.8	69.0	5.7	17.0	2293	135	366
T2 × A4	12.6	5.4	4.8	3.7	68.1	5.7	29.6	2556	86	348
T2 × A6	13.2	3.6	4.9	3.7	73.3	5.9	18.8	2508	133	346
T2 × A7	11.6	4.9	4.8	3.7	56.8	5.7	25.0	2522	101	344
T2 × A8	12.4	3.6	4.8	3.4	61.9	5.4	24.0	2476	103	324
T2 × A9	13.3	3.3	4.5	3.7	68.8	5.5	23.4	2407	103	386
T2 × A10	12.7	4.2	4.7	3.7	63.5	5.4	27.4	2612	95	369
T3 × A4	12.5	5.2	4.8	3.9	80.1	5.6	28.0	2253	81	415
T3 × A6	13.5	3.2	4.8	3.7	77.2	5.4	18.3	2127	116	396
T3 × A7	13.3	4.5	4.7	3.8	65.8	6.0	21.5	2423	113	382
T3 × A8	11.7	3.7	5.0	3.7	70.9	5.3	24.5	2594	106	365
T3 × A9	12.1	3.7	4.6	3.9	76.6	5.3	23.1	2282	99	420
T3 × A10	12.0	4.6	4.8	3.8	71.8	5.2	26.4	2256	85	408
A4 × T1	12.5	5.0	4.6	3.6	65.7	5.6	26.5	2245	85	364
A5 × T1	11.6	4.0	4.9	3.7	71.8	6.6	17.9	2808	157	352
A6 × T1	14.0	3.3	4.7	3.6	71.0	5.8	15.5	2232	144	344
A7 × T1	12.9	3.2	4.5	3.6	66.0	5.9	17.8	2317	130	328
A8 × T1	12.6	2.7	4.6	3.7	62.8	5.8	17.9	2357	132	318
A9 × T1	13.0	3.4	4.5	3.7	67.1	5.7	21.4	2336	109	359
A10 × T1	13.0	3.9	4.5	3.7	61.7	5.4	21.7	2329	107	355
A4 × T2	11.7	5.1	4.9	3.7	74.4	5.7	24.4	2150	88	371
A5 × T2	11.6	3.9	4.8	3.8	68.3	6.0	23.2	2719	117	359
A7 × T2	12.6	4.4	4.8	3.8	65.9	6.2	19.8	2403	122	366
A8 × T2	11.4	3.9	4.9	3.4	54.6	5.6	18.6	2087	113	338
A9 × T2	12.7	4.2	4.7	3.8	66.5	5.4	23.2	2056	88	365
A10 × T2	13.1	4.1	4.9	3.8	68.9	5.3	26.6	2416	91	372
A4 × T3	12.4	5.9	4.8	3.6	74.4	5.5	25.0	2192	88	412



Table 5. Continued.

Crosses	Date of emergence	Number of main stems	Plant height	Haulm type	Maturity	General impression	Number of tubers	Tuber yield	Mean tuber weight	Under water weight
A5 × T3	14.6	4.1	4.4	3.7	76.9	5.7	19.2	2392	125	378
A6 × T3	13.0	3.6	4.9	3.7	73.2	5.3	17.8	1983	112	394
A7 × T3	13.8	4.0	4.5	3.8	66.6	5.6	21.0	2088	100	379
A8 × T3	11.8	4.3	4.8	3.7	72.1	5.3	22.5	2273	101	367
A9 × T3	13.2	4.1	4.6	3.8	81.1	5.1	24.8	1927	78	435
A10 × T3	12.7	4.2	4.8	3.8	68.3	5.3	24.4	2363	97	404
A5 × A4	11.8	5.6	4.5	3.2	61.0	5.1	31.3	2219	71	362
A5 × A6	12.1	3.8	4.9	3.6	73.5	5.7	22.7	2537	112	360
A5 × A7	11.4	4.5	4.9	3.7	62.5	5.8	27.4	2676	97	363
A5 × A8	12.9	4.1	4.6	3.6	69.5	5.0	28.3	2556	90	348
A5 × A9	11.2	4.2	4.8	3.7	81.0	5.5	23.4	2284	98	385
A5 × A10	11.1	4.7	4.8	3.7	64.1	5.1	31.8	2502	79	372
A6 × A4	13.8	4.4	4.6	2.9	63.5	5.1	20.5	1604	78	357
A7 × A4	14.2	5.4	3.9	3.3	59.2	5.4	25.2	1685	67	389
A7 × A6	14.2	3.6	4.7	3.5	61.4	5.5	20.9	2040	98	358
A8 × A4	12.4	4.8	4.3	3.0	58.6	4.8	29.5	1769	60	341
A8 × A6	13.1	3.0	4.5	3.5	58.7	4.8	20.2	1745	86	336
A8 × A7	14.1	3.2	4.6	3.6	59.2	5.3	20.6	1956	95	346
A9 × A4	13.8	4.8	4.4	3.5	75.2	4.8	32.7	1805	55	405
A9 × A6	13.8	3.1	4.8	3.5	78.5	4.9	17.5	1645	94	392
A9 × A7	15.2	2.7	3.9	3.3	62.8	5.1	23.9	1867	78	376
A9 × A8	14.0	3.0	4.6	3.5	66.8	4.8	23.3	1850	79	360
A10 × A4	13.8	5.0	4.5	3.5	58.8	4.5	32.3	1712	53	384
A10 × A6	14.6	3.7	4.5	3.6	66.2	4.9	21.7	1910	88	380
A10 × A7	14.0	4.3	4.5	3.6	57.0	5.2	24.6	1901	77	367
A10 × A8	12.9	4.1	4.7	3.5	55.9	5.0	25.6	1965	77	380
A10 × A9	13.6	4.1	4.3	3.6	69.4	4.7	28.8	1806	63	400
Mean	12.9	4.1	4.6	3.6	67.4	5.4	23.3	2204	95	369
LSD 5%	0.4	0.2	0.1	0.1	2.5	0.2	1.2	92	5	7
LSD 1%	0.5	0.3	0.1	0.1	3.3	0.3	1.5	121	6	9

Table 6. Mean squares for general (GCA) and specific combining abilities (SCA) and for differences of reciprocals (Diff. of Rec.), estimates of variance components ( $\hat{\sigma}_{GCA}^2$ ,  $\hat{\sigma}_{SCA}^2$ ,  $\hat{\sigma}_{Rec}^2$  and  $\hat{\sigma}_e^2$ ), variance ratios, and heritabilities in the narrow sense ( $h_n^2$ ), based on the population means of characters studied on the second clonal generation in 1980. For dimension of characters see heading of Table 3

Source of variation	D.F.	Date of emergence	Number of main stems	Plant height	Haulm type	Maturity	General impression	Number of tubers	Tuber yield	Mean tuber weight	Under water weight
GCA	9	2.43**	2.72**	0.121*	0.138**	192.16**	0.844**	90.28**	381593**	4211.1**	3387.7**
SCA	34	0.73*	0.12	0.045**	0.026**	16.59	0.036	5.13	29440	87.1	104.5
Diff. of Rec.	11	0.25**	0.12**	0.008**	0.004**	13.33**	0.025*	4.74**	39471**	77.5**	87.5**
Error	162	0.032	0.019	0.0003	0.0015	1.59	0.0128	0.35	2192	8.3	13.2
$\hat{\sigma}_{GCA}^2$		0.17	0.27	0.01	0.01	18.04	0.08	8.76	36355	424.5	337.9
$\hat{\sigma}_{SCA}^2$		0.39	-0.00	0.03	0.02	2.67	0.01	0.32	-8209 <sup>a)</sup>	7.9	13.9
$\hat{\sigma}_{Rec}^2$		0.22	0.11	0.01	0.00	11.74	0.01	4.39	37279	69.2	74.3
$\hat{\sigma}_e^2$		0.03	0.02	0.00	0.00	1.59	0.01	0.35	2192	8.3	13.2
$\hat{\sigma}_{GCA}^2/(\hat{\sigma}_{GCA}^2 + \hat{\sigma}_{SCA}^2)^{b)}$		0.30	1.00	0.25	0.33	0.87	0.89	0.96	1.29	0.98	0.96
$h_n^2$		0.27	0.91	0.19	0.37	0.75	0.85	0.85	0.96	0.94	0.90

\* = P<0.05; \*\* = P<0.01; <sup>a)</sup> due to negative value variance ratio>1.00; <sup>b)</sup> variance ratio.

The GCA to SCA variance ratios, computed from the variance components  $\sigma_{GCA}^2$  and  $\sigma_{SCA}^2$ , indicated that in the inheritance of characters SCA was the most important for date of emergence, plant height and haulm type, while GCA was by far the most important for all other characters.

The heritability in narrow sense was low for date of emergence, haulm type and in particular plant height and ranged from fairly high to high for all remaining characters. As expected, this appeared to be largely in accordance with the above variance ratios.

*General combining ability effects.* Almost all GCA effects of the parents were highly significant or significant positive or negative (Table 7). Good general combiners for tuber yield were A5 and the three *tuberosum* cultivars; these four parents also affected mean tuber weight, haulm type and general impression positively. For most of the characters there was at the least a fairly close relationship between the means of the parents (Table 3) and the GCA effects, in that the higher mean performances of the parents corresponded with the positive GCA effects and the lower mean performances with the negative ones. This holds good for haulm type, maturity, tuber yield and under water weight and in particular for number of main stems, general impression and mean tuber weight, but less so for

plant height and date of emergence (cf. Table 13, column b).

*Specific combining ability effects.* Although the SCA mean squares for most characters were non-significant (Table 6), several populations did relatively better or worse than expected on the basis of the GCA of the parents involved, i.e. significant positive as well as negative SCA occurred (Table 8). With one exception even all SCA effects of the two T  $\times$  T crosses were significant, but, except for date of emergence and for mean tuber weight of T2  $\times$  T3, negative. This means that these within *tuberosum* crosses did worse among other things for tuber yield than expected on the above criterion. Most of the significant SCA effects of A  $\times$  A were also negative; for tuber yield 10 out of 15. Of the six crosses with A5, however, three had a significant positive and only one a significant negative SCA for tuber yield. The T  $\times$  A and the A  $\times$  T crosses showed more significant positive than significant negative SCA effects; for tuber yield nine out of 13.

Generally, the T  $\times$  A and A  $\times$  T crosses did better than expected and the T  $\times$  T and A  $\times$  A crosses did worse. Many crosses of all groups had significant SCA effects for plant height, date of emergence, tuber yield, mean tuber weight, number of tubers and under water weight and, except those of

Table 7. General combining ability effects of the parents for characters studied on the second clonal generation in 1980. For T1-T3 and A4-A10 see Tables 1 and 2. For dimension of characters see heading of Table 3

Parents	Date of emergence	Number of main stems	Plant height	Haulm type	Maturity	General impression	Number of tubers	Tuber yield	Mean tuber weight	Under water weight
T1	-0.13*	-0.51**	-0.02**	0.08**	0.08	0.54**	-5.01**	193**	39.2**	-23.5**
T2	-0.54**	0.03	0.16**	0.10**	-0.31	0.37**	-1.59**	255**	22.5**	-13.7**
T3	-0.23**	0.15**	0.12**	0.22**	7.16**	0.17**	-1.76**	134**	14.0**	26.3**
A4	0.04	1.20**	-0.11**	-0.19**	-0.70*	-0.22**	5.29**	-243**	37.5**	9.6**
A5	-0.97**	0.32**	0.11**	0.05**	2.97**	0.20**	2.03**	358**	3.2**	-3.3*
A6	0.72**	-0.57**	0.09**	-0.09**	1.92**	-0.10**	-4.05**	-264**	12.3**	-4.0**
A7	0.62**	0.01	-0.14**	-0.03**	-6.28**	0.13**	-0.43*	-74**	-5.0**	-5.4**
A8	-0.17**	-0.41**	0.01*	-0.14**	-0.30**	-0.30**	0.29	-99**	-5.8**	-22.9**
A9	0.48**	-0.39**	-0.15**	0.02	4.77**	-0.33**	1.34**	-236**	18.3**	23.1**
A10	0.24**	0.23**	-0.02**	0.03*	-4.04**	-0.40**	3.92**	-85**	-24.5**	13.9**

\* =  $P < 0.05$ ; \*\* =  $P < 0.01$ .

Table 8. Specific combining abilities of the crosses calculated from the population means and the general combining abilities for characters studied on the second clonal generation in 1980. For population means see Table 5. For dimension of characters see heading of Table 3

Crosses	Date of emergence	Number of main stems	Plant height	Haulm type	Maturity	General impression	Number of tubers	Tuber yield	Mean tuber weight	Under water weight
T2 × T1	0.68**	-0.53**	-0.26**	-0.28**	-1.97**	-0.17*	-2.89**	-433**	-8.1**	3.0
T2 × T3	0.79**	-0.30**	-0.31**	-0.09**	-5.04**	-0.23*	-2.84**	-299**	10.0**	-13.8**
T2 × A4	-0.23*	-0.00	0.17**	0.19**	5.07**	0.13	0.09	138**	2.3	-3.6
T2 × A6	0.12	0.12	0.01	0.13**	4.49**	0.24*	1.23*	254**	9.0**	-3.5
T2 × A7	-0.86**	0.58**	0.15**	0.08**	0.75	-0.00	1.22**	78**	-2.6	6.9**
T2 × A8	-0.26**	0.11	0.04**	-0.16**	-3.12**	0.01	-0.60*	-77**	-0.5	0.4
T2 × A9	0.17	0.09	-0.03**	0.03	-4.00**	-0.00	0.34	9	-3.9*	-1.1
T2 × A10	0.31**	-0.13*	0.03**	-0.00	3.36**	-0.01	1.46**	141**	-5.9**	3.1
T3 × A4	-0.23**	0.17*	0.17**	0.14**	3.60**	0.23**	-0.24	129**	4.1*	10.4**
T3 × A6	-0.12	-0.19**	0.01	0.00	-1.07	-0.14*	0.66*	-78**	-1.7	5.4**
T3 × A7	0.28**	0.06	0.00	-0.00	-1.86**	0.06	0.23	-7	-2.3	-7.6**
T3 × A8	-0.71**	0.24**	0.14**	0.01	2.65**	0.03	1.75**	196**	0.6	-4.6*
T3 × A9	-0.47**	0.12	0.01	0.01	-0.27	-0.04	1.15**	3	-6.8**	10.9**
T3 × A10	-0.53**	-0.00	0.08**	-0.01	-0.25	0.07	0.02	58*	0.2	-1.4
A4 × T1	-0.29*	0.29*	0.11**	0.09**	-0.87	-0.07	3.00**	92*	-22.8**	10.7**
A5 × T1	-0.18	0.17	0.18**	0.02	1.54	0.43**	-2.32**	53	19.0**	11.6**
A6 × T1	0.51**	0.37**	0.00	0.02	1.79	-0.01	1.36**	39	13.4**	4.2
A7 × T1	-0.47**	-0.31**	0.04**	0.00	5.00**	-0.22**	0.03	-5	5.9*	-10.3**
A8 × T1	0.02	-0.38**	-0.01	0.14**	1.02	0.19*	-0.59	60	-0.5	-2.8
A9 × T1	-0.23	0.29*	0.05**	0.03	-4.95**	0.07	1.85**	175**	-13.9**	-7.8*
A10 × T1	0.00	0.16	-0.07**	-0.00	-1.53	-0.16	-0.42	18	-9.2**	-2.6
A5 × T2	0.22	-0.47**	-0.10**	0.03	-1.55	-0.02	-0.44	-98*	-5.8*	8.8**
A5 × T3	2.92**	-0.39**	-0.45**	-0.15**	-0.42	-0.13	-4.27**	-303**	1.9	-12.3**
A5 × A4	0.15	0.04	-0.12**	-0.20**	-8.45**	-0.31**	0.76	-100*	-4.7*	-11.5**
A5 × A6	-0.54**	0.02	0.07**	0.09**	1.41	0.20*	1.51**	179**	-5.2*	0.0
A5 × A7	-1.13**	0.13	0.30**	0.04	-1.37	0.00	2.59**	189**	-5.8*	4.5
A5 × A8	1.16**	0.16	-0.15**	0.12**	4.84**	-0.28**	2.76**	95*	-7.4**	7.0*
A5 × A9	-1.19**	0.24*	0.21**	0.08	6.06**	-0.22*	-3.18**	-42	14.2**	-2.0
A5 × A10	-1.05**	0.11	0.08**	-0.00	-2.01*	-0.06	2.63**	26	-6.1*	-5.8*
A6 × A4	0.14	-0.25**	-0.00	-0.43**	-4.90**	0.05	-3.94**	-152**	-0.1	-15.8**
A7 × A4	0.64**	0.15	-0.46**	-0.02	-0.99	0.06	-2.87**	-200**	4.5*	17.6**
A7 × A6	-0.03	0.13	0.12**	0.00	-1.42	0.07	2.18**	115**	-5.2*	0.2
A8 × A4	-0.35*	-0.01	-0.22**	-0.27**	-2.37**	-0.11	0.69	-91*	-6.0*	-12.9**
A8 × A6	-0.33*	-0.03	-0.23**	0.17**	-4.90**	-0.17*	0.75	-155**	-12.7**	-4.3
A8 × A7	0.76**	-0.42**	0.10**	0.18**	3.80**	0.05	-2.47**	-73*	7.1**	7.1*
A9 × A4	0.38*	-0.03	0.04**	0.10**	3.94**	-0.02	2.84**	81*	7.2**	5.1
A9 × A6	-0.29*	0.04	0.23**	0.00	4.61**	-0.09	-2.99**	-119**	3.1	5.7*
A9 × A7	1.20**	-0.94**	-0.42**	-0.31**	-2.87**	-0.08	-0.22	-26	-1.2	-8.9**
A9 × A8	0.80**	-0.21*	0.11**	0.01	0.34	-0.00	-1.55**	-18	9.8**	-7.4*
A10 × A4	0.62**	-0.46**	0.01	0.11**	-3.63**	-0.26**	-0.13	-163**	9.2**	-6.7*
A10 × A6	0.74**	0.01	-0.19**	0.02	1.13	0.02	-1.37**	-5	1.2	2.9
A10 × A7	0.24	0.02	0.04**	-0.01	0.14	0.05	-2.10**	-143**	4.5*	-8.7**
A10 × A8	-0.05	0.25*	0.08**	-0.00	-1.73	0.29**	-1.83**	-54	9.6*	21.8**
A10 × A9	-0.01	0.23*	-0.14**	0.00	1.48	0.05	0.31	-76*	2.2	-4.2

\* = P<0.05; \*\* = P<0.01.

group T × T, few crosses had such effects for general impression. Besides additive types of gene action, therefore, non-additive types of gene action were probably important in the expression of all characters, though to a different extent.

*Heterosis.* From the results presented in Table 9 it is apparent that positive as well as negative heterosis occurred. Negative heterosis is not always a disadvantage, e.g. the occasionally negative heterosis for date of emergence means that the average emergence of the populations concerned was earlier than that of their mid-parent and, generally, an early emergence is favourable. For several other characters, viz. number of stems, plant height, maturity, number of tubers, mean tuber weight and under water weight, at one time negative heterosis, at another time positive heterosis may be desirable. Positive heterosis is always desired for haulm type, general impression and tuber yield.

The majority of the populations showed significant heterosis for all characters. The magnitude of the mean heterosis, however, varied very much across the characters, and within some characters also between the four groups of crosses. Most populations showed significant positive heterosis for date of emergence, haulm type, number of tubers and under water weight. Of these characters the heterotic effect was generally large for number of tubers and with some populations, particularly of groups A × T and A × A, for date of emergence, whereas it was small for haulm type and especially for under water weight. All populations had highly

significant negative heterosis for mean tuber weight and almost all populations for plant height and general impression. The heterotic effect was large for mean tuber weight, small for plant height and intermediate for general impression. The two populations of group T × T and most of those of group A × A had significant negative heterosis for number of stems, while of group T × A and A × T as many populations showed significant positive as significant negative heterosis for this character. The heterotic effect varied from medium negative to largely positive. For maturity there were more populations with significant positive than with significant negative heterosis, the latter occurring exclusively among groups A × T and A × A. With a few exceptions, mainly among group A × T, the heterotic effect was not large. All populations of groups T × T and A × A showed significant negative heterosis for tuber yield and so did 13 out of the 20 populations of group A × T, while none of these was significant positive. However, the six populations from the intersubspecific crosses with T2 as the female parent all had significant positive heterosis for tuber yield and so had one out of the six populations with T3 as female (T3 × A8), whereas four of these were significant negative. The positive heterotic effect for tuber yield can probably be attributed to the very large positive heterotic effect for number of tubers of the populations concerned. None of the exact reciprocals, neither with T2 nor with T3 as the male parent showed significant positive heterosis for yield, on the contrary, two with T2 and all six with T3 were significant negative.

Table 9. Heterosis (in %) of population means over their mid-parents for ten characters studied on the second clonal generation in 1980. For means of the parents and the populations see Tables 3 and 5, respectively. For dimension of characters see heading of Table 3

Crosses	Date of emergence	Number of main stems	Plant height	Haulm type	Maturity	General impression	Number of tubers	Tuber yield	Mean tuber weight	Under water weight
T2 × T1	5**	-6*	-5**	-4**	5**	-14**	9	-11**	-19**	-0
T2 × T3	5**	-7*	-8**	4**	-1	-12**	9*	-11**	-21**	-3**
T2 × A4	2	-4*	-2**	16**	10**	-12**	67**	20**	-36**	-1
T2 × A6	-5**	7*	-1**	14**	11**	-8**	57**	18**	-25**	-4**
T2 × A7	-1	23**	-4**	10**	6*	-17**	48**	4*	-34**	3*
T2 × A8	-2	6*	-4**	5**	0	-13**	55**	10**	-33**	-1
T2 × A9	6**	8*	-9**	0	-1	-13**	59**	7**	-34**	2*
T2 × A10	5**	0	-6**	4**	15**	-9**	45**	11**	-33**	4**

Table 9. Continued

Crosses	Date of emergence	Number of main stems	Plant height	Haulm type	Matu- rity	General impres- sion	Number of tubers	Tuber yield	Mean tuber weight	Under water weight
T3 × A4	5**	-15**	-2**	13**	15**	-5**	35**	-2	-30**	7**
T3 × A6	0	-17**	-3**	6**	5**	-8**	22**	-10**	-26**	1
T3 × A7	18**	0	-6**	6**	7**	-6**	8**	-7**	-15**	4**
T3 × A8	-3*	-5*	0	6**	2	-6**	33**	7**	-20**	1
T3 × A9	1	4	-7**	-1	0	-8**	30**	-6**	-27**	2*
T3 × A10	4*	-2	-4**	0	14**	-4	21**	-11**	-29**	5**
A4 × T1	5**	-3	-1**	4**	6**	-15**	50**	1	-41**	8**
A5 × T1	9**	-4	3**	-6**	-4*	-1	-26**	-23**	-7**	-0
A6 × T1	4**	16**	0	3**	8**	-11**	30**	0	-23**	0
A7 × T1	15**	-9**	-5**	0	22**	-16**	6	-8**	-19**	3*
A8 × T1	4**	-7*	-3**	6**	2	-8**	16**	0	-18**	2
A9 × T1	8**	33**	-4**	-6**	-4*	-11**	46**	-0	-34**	1
A10 × T1	13**	5*	-5**	-3**	12**	-11**	15**	-4*	-28**	5**
A4 × T2	-5**	-10**	0	16**	19**	-12**	37**	1	-35**	5**
A5 × T2	4*	-16**	-4**	3**	-9**	-8**	-5*	-24**	-27**	-2*
A7 × T2	7**	11**	-4**	13**	22**	-10**	18**	-1	-21**	9**
A8 × T2	-10**	15**	-2**	5**	-11**	-10**	20**	-7**	-26**	3**
A9 × T2	2	38**	-5**	3**	-4*	-14**	57**	-9**	-44**	-3**
A10 × T2	9**	-2	-2**	7**	24**	-11**	41**	3	-36**	5**
A4 × T3	5**	-4*	-2**	4**	6**	-7**	20**	-5*	-23**	6**
A5 × T3	37**	-20**	-12**	-6**	-7**	-5**	-30**	-36**	-11**	-6**
A6 × T3	-3*	-6*	-1**	6**	-1	-9**	19**	-14**	-29**	0
A7 × T3	23**	-11**	-10**	6**	9**	-12**	6	-20**	-25**	3**
A8 × T3	-2	10**	-4**	6**	4	-6**	22**	-7**	-23**	2
A9 × T3	11**	15**	-7**	-4**	5**	-11**	40**	-21**	-43**	6**
A10 × T3	10**	-11**	-4**	0	9**	-2	11**	-6**	-19**	4**
A5 × A4	10**	-15**	-8**	-9**	-19**	-15**	6**	-33**	-33**	-4**
A5 × A6	-2	-12**	-1**	1	-6**	-4*	-4	-23**	-24**	-6**
A5 × A7	13**	-9**	-2**	1	-6**	-10**	-4*	-26**	-21**	1
A5 × A8	18**	-7**	-8**	1	-7**	-13**	4	-25**	-26**	-1
A5 × A9	3	5*	-3**	-7**	-2	-6**	-12**	-33**	-23**	-4**
A5 × A10	7**	-9**	-4**	-4**	-7**	-7**	4	-29**	-29**	-2
A6 × A4	2	-17**	-5**	-5**	-3	-13**	20**	-13**	-36**	-3**
A7 × A4	26**	-9*	-20**	5**	9**	-15**	15**	-21**	-32**	13**
A7 × A6	10**	-1	-5**	9**	5*	-13**	29**	-5*	-31**	2*
A8 × A4	2	-10**	-12**	-2	-5*	-15**	43**	-10**	-39**	1
A8 × A6	-5**	-2	-9**	13**	-11**	-14**	36**	-12**	-38**	-2
A8 × A7	22**	-14**	-8**	13**	9**	-13**	5	-14**	-18**	9**
A9 × A4	15**	-4*	-9**	0	7**	-17**	64**	-8**	-46**	5**
A9 × A6	1	15**	-2**	-1	7**	-14**	23**	-17**	-35**	-1
A9 × A7	33**	-19**	-21**	-10**	2	-18**	26**	-18**	-35**	2
A9 × A8	14**	9**	-7**	-1	-4*	-13**	32**	-12**	-34**	-0
A10 × A4	19**	-19**	-8**	4**	6*	-17**	34**	-17**	-38**	6**
A10 × A6	11**	-4	-9**	6**	11**	-8**	19**	-8**	-31**	2*
A10 × A7	27**	-4*	-10**	3**	20**	-11**	6*	-20**	-25**	6**
A10 × A8	9**	5*	-6**	3**	1	-3	18**	-10**	-26**	13**
A10 × A9	-6**	15**	-13**	-6**	10**	-10**	37**	-18**	-42**	3**

\* = P&lt;0.05; \*\* = P&lt;0.01.

The average heterosis for tuber yield of group T × T was -11%, of T × A 3.4%, of A × T -9% and of A × A -18%. Although the mean positive heterosis of group T × A in itself is small, it makes quite a difference in comparison with the mean heterosis of groups (T × T) + (A × A), being -17%.

*Differences between reciprocal crosses.* Among the 11 intersubspecific, exact reciprocal crosses, of which five with T2 and six with T3, significant differences between their population means occurred for all characters (Table 10). For haulm type and general impression only one and two differences, respectively, were significant. About as many differences were significant positive as significant negative within the characters date of emergence, number of main stems, plant height, general impression and mean tuber weight. A positive difference indicates that the population mean of T × A is larger than that of its exact reciprocal A × T. For under water weight only one of the five significant differences was positive. For number of tubers, however, six of the seven significant and all non-significant differences were positive, while for tuber yield even all eight significant differences

were positive and only one of the non-significant differences was negative.

The significant higher tuber yields of the eight combinations T × A over their exact reciprocals were in three cases due to a larger number of tubers, in three cases to a higher mean tuber weight and in two cases to both a non-significant larger number of tubers and a non-significant higher mean tuber weight. The, indeed, non-significant lower tuber yield of T3 × T10 was due to a significant lower mean tuber weight.

From the data on tuber yield (Table 5) it has been computed that the five T2 × A crosses and the six T3 × A crosses outyielded their reciprocals by 13.1% and 8.6%, respectively; averaged over the 11 crosses T × A yielded 10.7% higher than A × T.

There was no consistent relationship between the difference in maturity of the parents and the differences in tuber yield of exact reciprocals. T2 is later maturing than A10 and earlier than A9 (Table 3), but both T2 × A9 and T2 × A10 outyielded their exact reciprocals. Although T3 matures much later than A7, T3 × A7 outyielded A7 × T3 significantly.

Table 10. Differences between population means of reciprocal crosses for characters studied on the second clonal generation in 1980. For means of the populations concerned see Table 5. For dimension of characters see heading of Table 3

Parents	(T × A) - (A × T) for									
	date of emergence	number of main stems	plant height	haulm type	maturity	general impression	number of tubers	tuber yield	mean tuber weight	under water weight
T2, A4	0.9**	0.3	-0.1	-0.0	-6.3**	-0.0	5.2**	406**	-2	-23**
T2, A7	-1.0**	0.5*	0.0	-0.1	-9.1**	-0.5**	5.2**	120	-21**	-22**
T2, A8	1.0**	-0.3	-0.1	0.0	7.3**	-0.2	5.4**	389**	-10*	-14**
T2, A9	0.6*	-0.9**	-0.2**	-0.1	2.3	0.1	0.2	351**	15**	21**
T2, A10	-0.4	0.1	-0.2**	-0.1	-5.4**	0.2	0.8	196**	4	-3
T3, A4	0.1	-0.7**	0.0	0.3**	5.7**	0.1	3.0**	61	-7	3
T3, A6	0.5	-0.4*	-0.1	0.0	4.0*	0.1	0.5	144*	4	2
T3, A7	-0.5	0.5*	0.2**	0.0	-0.8	0.4*	0.5	335**	13*	3
T3, A8	-0.1	-0.6**	0.2**	0.0	-1.2	0.1	2.0*	321**	5	-2
T3, A9	-1.1**	-0.4*	0.0	0.1	-4.5*	0.2	-1.7*	355**	21**	-15**
T3, A10	-0.7**	0.4*	0.0	0.0	3.5	-0.1	2.0*	-107	-12*	4

\* = P < 0.05; \*\* = P < 0.01.

**Flowering and fruiting.** The data on flowering and spontaneous fruitset in the field have been given per group of crosses in Table 11. As A5 was the only male sterile one of the ten parents, the results with this parent have been mentioned apart from the other A × T and A × A crosses.

All groups of crosses showed an about equally high proportion of flowering clones except the A5 × A crosses. Only 30% of the clones of the

latter group produced flowers, which was highly significant different from the other groups.

Except between groups A × T and A × A, which had about equally high percentages of fruiting clones, the differences in fruiting between these and the other groups were quite great, in particular between the intersubspecific groups T × A and A × T, while group T × T was intermediate. Noteworthy is that only one of the 54 flowering clones of

**Table 11.** Number and percentage of clones with flowers and with fruits of total per group of crosses, recorded on the second clonal generation in 1980. T = *tuberosum*, A = *andigena*

Group of crosses	Number of populations	Number of clones				
		total	with flowers	(%)	with fruits	(%)
T × T	2	60	54	(90)	34	(57)
T × A	12	360	314	(87)	82	(23)
A × T	17	510	484	(95)	440	(86)
A5 × T	3	90	71	(88)	8	(9)
A5 × A	6	180	54	(30)	1	(1)
A × A	15	450	435	(97)	400	(89)
Total	55	1650	1412	(86)	965	(58)

**Table 12.** Number and percentage of clones with flowers and with fruits of total number of clones for each of 11 populations T × A and their exact reciprocals A × T, recorded on the second clonal generation in 1980. For the parents see Tables 1 and 2

Parents	T × A					A × T				
	Number of clones									
	total	with flowers	(%)	with fruits	(%)	total	with flowers	(%)	with fruits	(%)
T2, A4	30	30	(100)	12	(40)	30	30	(100)	30	(100)
T2, A7	30	29	(97)	1	(3)	30	30	(100)	29	(97)
T2, A8	30	24	(80)	2	(7)	30	30	(100)	28	(93)
T2, A9	30	29	(97)	6	(20)	30	28	(93)	27	(90)
T2, A10	30	29	(97)	9	(30)	30	30	(100)	30	(100)
Total	150	141	(94)	30	(20)	150	148	(99)	144	(96)
T3, A4	30	28	(93)	8	(27)	30	25	(83)	22	(73)
T3, A6	30	28	(93)	5	(17)	30	30	(100)	30	(100)
T3, A7	30	22	(73)	9	(30)	30	27	(90)	19	(63)
T3, A8	30	23	(77)	3	(10)	30	30	(100)	28	(93)
T3, A9	30	19	(63)	7	(23)	30	27	(90)	24	(80)
T3, A10	30	24	(80)	15	(50)	30	29	(97)	27	(90)
Total	180	144	(80)	47	(26)	180	168	(93)	150	(83)
Grand total	330	285	(86)	77	(23)	330	316	(96)	294	(89)

group  $A5 \times A$  and no more than eight of the 71 flowering clones of group  $A5 \times T$  bore fruits.

For the 11  $T \times A$  crosses and their exact reciprocals the data on flowering and fruiting of each individual population are presented in Table 12. In all populations with T2 the number of flowering clones was larger than in the comparable populations with T3 and this number was larger in almost all populations  $A \times T$  than in the exact reciprocals  $T \times A$ . Nevertheless, the proportion of flowering clones was large in nearly all cases and the differences between reciprocals were generally small. However, large differences in number and percentage of fruiting clones occurred in all cases between  $T \times A$  and  $A \times T$ . The percentages of fruiting clones ranged from 3 to 50 within the populations  $T \times A$  and from 63 to 100 within  $A \times T$ .

## Discussion

The main objective of adaptation programmes is to increase the genetic variation of *tuberosum* by crossing long-day adapted clones, in the present case of *andigena*, to *tuberosum* cultivars.

The GCV's obtained, showed that the mean genotypic variation was greatest for all characters in group  $A \times A$  and least for most characters in group  $T \times T$  (Table 4). Except for date of emergence, number of tubers and under water weight, the mean GCV's of groups  $T \times A$  and  $A \times T$  were closer to those of  $T \times T$  than to those of  $A \times A$ . This does not alter the fact that for most characters the differences in mean GCV's between the four groups were small, which suggests that for the increase of the genetic variation no special group deserves special attention. However, the magnitude of the ranges within characters between groups was very different. The ranges were narrowest for all characters in group  $T \times T$  and widest in group  $A \times A$ , while the magnitude of the ranges of group  $T \times A$  and particularly of  $A \times T$  for most characters was much closer to that of group  $A \times A$  than of  $T \times T$ . Although the mean genotypic variations were greatest in group  $A \times A$ , depending upon the combination, the within-population genotypic variation in groups  $A \times A$ ,  $T \times A$  and

$A \times T$  varied from lower to far higher than in group  $T \times T$ .

The mean GCV's of the different groups showed virtually the same tendencies as the variances of the comparable groups reported by Cubillos & Plaisted (1976) and Tarn & Tai (1977), except for mean tuber weight and under water weight (specific gravity). Nevertheless, the differences in genotypic variation between groups are somewhat disappointing at first sight. The question, however, arises whether it is realistic to expect much higher within population genotypic variations of  $T \times A$  or  $A \times T$  crosses than of  $T \times T$  crosses. Generally *tuberosum* varieties are considered to be highly heterozygous (Simmonds, 1969, p. 31), as can be concluded from the wide diversity that occurs after selfing. Since in tetraploids four alleles are available per locus, in the case of multiple alleles no more than four different alleles per locus can be present in one genotype. By crossing such a tetra-allelic genotype, whether to an *andigena* clone or to another *tuberosum* variety, the heterozygosity of the hybrid for that locus cannot increase, but different alleles may give rise to a different expression of the hybrid. Within a population the maximum number of different alleles per locus is eight, four from the female and the male parent each. If for a character more than one to many loci with multiple alleles are involved, the within-population genotypic variation for that character may range from low to high depending on the total number of different alleles and the effect of each individual allele, i.e. the more identical alleles occur the lower and the more different alleles there are the higher the genotypic variation will be. From this it is understandable that the effect of the long-day adapted *andigena* clones on the genotypic variation of the intersub-specific hybrids is generally not great, which does not mean that no different alleles from *andigena* may be introduced. It is rather obvious, however, that several identical alleles occur in both subspecies, so that the number of different alleles introduced in one population will be limited. This subject has also been studied and discussed by Sanford & Hanneman (1982b).

The present GCV's for plant height, tuber yield, number of tubers, mean tuber weight and under



water weight are of about the same magnitude as the CV's and GCV's reported by Kaminski (1977) and Yildirim & Çalışkan (1985), respectively; their values for maturity were much lower.

The idea of multi-allelic loci for polygenically inherited characters in the autotetraploid potato fits well in with the observation that additive gene effects were important for all characters studied, as appeared from the significant GCA mean squares, whereas most SCA mean squares were non-significant (Table 6).

Besides in the interpretation of the genetic base of the expression for important characters such as yield (Mendoza & Haynes, 1974), combining ability analysis may also be helpful in the selection of parents. The literature on combining abilities in potatoes is not extensive. Plaisted et al. (1962) concluded from the results of a large but incomplete NC experiment II design, grown at three sites in the USA, that SCA was much more important than GCA in the inheritance of yield. Mullin and Lauer (1966) found about equal values for the GCA and SCA components of variance for tuber yield, but for tuber appearance the GCA component of variance was about eight times larger than the SCA component. In a  $10 \times 10$  half-diallel cross to investigate after-cooking darkening, Dalianis et al. (1966) showed GCA to be important. Tai (1976) observed highly significant SCA differences for total and marketable yields and number of tubers in a partial diallel cross of 12 *tuberosum* varieties; the GCAs were highly significant for average tuber weight, average weight of marketable tubers and specific gravity, whereas the SCA of specific gravity was also highly significant. From the results of a  $6 \times 6$  half-diallel cross Killick (1977) concluded that GCA was responsible for differences in maturity. For among other things yield and after cooking-blackening only SCA differences were found to be significant and for mean tuber weight both the variance components for GCA and SCA were significant. Veilleux & Lauer (1981) studied three hybrid potato populations and obtained in both pollen and stylar parents significant GCA mean squares for yield, tuber set, marketable yield, number of marketable tubers and hollow heart in all three populations; SCA mean squares were signif-

icant only for yield and hollow heart. In an experiment with a population of *andigena* in Peru, Thompson et al. (1983) observed only non-additive variance for yield, but additive variance estimates were relatively high for tuber number and size. In a different experiment, also in Peru, Thompson & Mendoza (1984) found relatively high additive variances for yield as well as for tuber number and size.

From this selected literature survey it is apparent that the answer to the question whether GCA or SCA is the most important in the same quantitatively inherited characters was not always the same. This may depend on e.g. kind of the material, experimental design and/or environmental conditions.

A wide ratio between the estimated GCA and SCA variance components, however, was always associated with a high and a narrow ratio with a low heritability (Table 6). High heritabilities based on population means, as was the case in this study, provide the possibility for an efficient selection of parents for the characters involved, i.e. the selection of parents with the best GCA. They also enable an efficient selection to be made among populations. Generally heritabilities based on population means are considerably greater than those based on individual seedlings. This was observed by Tai & Young (1984). They, however, also found that the advantage of higher heritabilities based on population means was more than undone by the lower variation among population means so that the response to individual clone selection was still higher than that to population selection for the characters studied.

Of importance for the selection of parents is that the correlations between the GCA effects of the parents (Table 7) and their mean performances (Table 3) were of about the same magnitude as the heritabilities for all characters, except haulm type for which the correlation was much higher. The correlations between the population means (Table 5) and the midparental values (computed from the mean performances in Table 3) were from somewhat to considerably lower than the heritabilities for most characters (Table 13).

The great advantage of high correlations between GCA values and the mean performances of

the parents as well as between population means and midparental values is that the most promising parents can be selected directly on their per se performance, so without laborious and expensive test crosses in diallels or other designs. This confirms the results earlier obtained and discussed by Maris (1969).

In some cases positive GCA effects are largely undone by negative SCA effects. For instance both T1 and T2 had a positive GCA for tuber yield (Table 7), but their SCA was negative (Table 8). Thus the actual mean tuber yield for T2 × T1 amounted to: 2204 (experimental mean, Table 5) + 193 + 255 (GCA for T1 and T2) - 433 (SCA of T2 × T1) = 2219 g per plant. The population mean for yield of T2 × T1 was 11% below the midparental value (Table 9).

Negative heterotic effects for yield and other characters are rather common for within ssp. *tuberosum* crosses (Maris, 1969; Tai, 1974; Tarn & Tai, 1983). This is attributed to the relatively narrow genetic base of this subspecies (Mendoza & Haynes, 1974); most *tuberosum* varieties, then, are more or less closely related to each other. The same holds good for the *andigena* parents used in the present study, as can be derived from the pedigrees of these parents (Table 1). All A × A populations, then, showed negative heterosis for yield (Table 9).

Table 13. Heritabilities (a), correlations between GCA values of the parents and their mean performances (b) and correlations between population means and midparental values (c) for characters studied on the second clonal generation in 1980. For dimension of characters see heading of Table 3

Character	a	b (df = 8)	c (df = 53)
Date of emergence	0.27	0.30	0.16
Number of main stems	0.91	0.97**	0.85**
Plant height	0.19	0.26	0.21
Haulm type	0.37	0.77*	0.55**
Maturity	0.75	0.84**	0.72**
General impression	0.85	0.97**	0.72**
Number of tubers	0.85	0.69*	0.59**
Tuber yield	0.96	0.78**	0.51**
Mean tuber weight	0.94	0.96**	0.78**
Under water weight	0.90	0.85**	0.81**

\* = P < 0.05; \*\* = P < 0.01.

By contrast several T × A crosses showed significant positive heterosis for yield, while most of the negative heterotic effects of the T × A and A × T crosses were smaller than those of the T × T and A × A crosses. From these results it is concluded that intersubspecific crosses affect yield favourably; in some cases positive heterosis can be obtained, particularly with the T-parent as the female. However, as positive heterosis may be lost in continued crosses, it is more important that high mean yields can occur independently of positive heterosis. The highest and the second highest yielding crosses, A5 × T1 and A5 × T2 (Table 5), respectively, even showed negative heterosis of 23% and 24% (Table 9). These very high mean yields and at the same time negative heterosis have to be ascribed to the extremely high yield of A5 (Table 3). Therefore, it seems more important to search for superior clones than for positive heterotic effects.

The assumption of Sanford & Hanneman (1982a) and Staub et al. (1982) that differences in tuber yield between exact reciprocals would be a maternal rather than a cytoplasmic effect is not confirmed by the results of the present study. All significant differences in tuber yield were positive, i.e. the T × A crosses outyielded their exact reciprocals, whatever the photoperiod response or the maturity of the parents (Table 10). Therefore, it is concluded that for high tuber yield in *andigena-tuberosum* crosses the *tuberosum* cytoplasm is preferable. For a high male fertility the reverse is true, as can also be concluded from the data in Tables 11 and 12. According to Grun & Staub (1979) subspecies *tuberosum* has cytoplasm that is sensitive to dominant genes of *andigena* (and probably of itself) that among other things condition male sterility, whereas the *andigena* cytoplasm is resistant to these dominant genes. The present results, however, suggest that not all *tuberosum* genotypes have sensitive cytoplasm and not all *andigena* genotypes have resistant cytoplasm, as part of the T × A progeny was male fertile, whereas the A5 × T and A5 × A crosses were largely male sterile. It is also obvious to assume that most *andigena* genotypes are heterozygous for the dominant genes. The latter might be the best explanation for the male

fertility of part of the T × A progeny.

The results from the present study indicate that long-day adapted *andigena* material is of importance for the improvement of the potato, particularly as far as tuber yield is concerned.

The adaptation to long-day conditions can be realized unexpectedly fast. However, long-day adapted *andigena*'s have a serious drawback, namely they are on average very highly susceptible to almost all kinds of potato diseases. This means that resistances to these diseases have to be introduced from *tuberosum* cultivars after the adaptation. Obviously this necessitates some consecutive crosses to combine the most important resistances in one population.

To avoid these consecutive crosses, an alternative could be to combine *andigena* with *tuberosum* before instead of after the adaptation. To this end for example eight highly male fertile and, where possible, unrelated *tuberosum* varieties, together resistant to the most common and important potato diseases, could be used as females in sets of eight *andigena* accessions. Each variety should be pollinated with a mixture of pollen from at least ten genotypes from one accession, thus variety 1 × accession 1, variety 2 × accession 2, and so on, resulting in eight *tuberosum-andigena* populations. Selected clones from each population need to be tested for resistances to diseases that can be expected to occur on the basis of the resistances present in the parent variety. Say three to five resistant clones from hybrid population 1 are individually crossed with three to five resistant clones from hybrid population 2. In this way the eight hybrid populations are used to produce a composite cross, which is completed after three cycles of recurrent selection. The resulting hybrid population can be expected to be completely long-day adapted and, moreover, to be resistant to the most important potato diseases.

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