

CROSSABILITY RELATIONSHIPS OF ANDEAN POTATO VARIETIES OF THREE PLOIDY LEVELS

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Solanum tuberosum, potato, ploidy, gene-flow, 'triploid block', crossability.

SUMMARY

The formation of triploids in $4x \times 2x$ crosses was studied in primitive potato varieties from the Andes of Peru and Bolivia. Triploid frequencies were as high as 80-100% in some crosses, although the actual number of seeds was low. The 'triploid block' varied according to the tetraploid parent, and was never entirely absent. The likelihood of triploid formation was studied in $4x \times 2x$ crosses where pollen from both tetraploids and diploids of known genotype was used. Even though the diploids were chosen for their non-production of $2n$ gametes, as detected in pollen grain size, 66% of the hybrids were tetraploid. The amount and probability of gene-flow between the tetraploid and diploid gene-pools, either directly through $2n$ gametes or through 'triploid bridges' was examined. Most of the 20 cultivars of *S. × chaucha* produced seed in crosses with tetraploids and diploids, although the fertility of the latter crosses was four times higher. The female fertility of some of the triploids thus allows them to exchange genes with the tetraploids and diploids, although gene-flow occurs more rapidly through direct transfer from diploids to tetraploids via $2n$ gametes.

INTRODUCTION

The presence of triploids in association with tetraploids and diploids is often taken as an indication of gene-flow between the diploid and tetraploid gene-pools. The potato fields of the Quechua Indians of the Andes of Peru normally contain many varieties, and all three ploidy levels can be found growing together (JACKSON et al., 1977a). Under such a situation, gene-exchange between diploids and tetraploids is theoretically possible. In fact, hybridisation between tetraploids and diploids has occurred in nature, for triploids do exist. The question to be examined in this paper is whether triploids actually represent a significant intermediate step in gene-flow between the tetraploids and diploids.

The formation of triploids in experimental crosses utilizing cultivated material is very low, generally not more than 7% (HANNEMAN & PELOQUIN, 1968). The low frequency of triploids in $4x \times 2x$ crosses has been attributed to the 'triploid block' (MARKS, 1966a), the post-fertilisation breakdown of endosperm in association with the triploid embryo (VON WANGENHEIM et al., 1960). A review of $4x \times 2x$ crossability, and the formation of triploids is given by KESSEL & ROWE (1975).

The variation in *Solanum × chaucha* JUZ. et BUK. ($2n = 36$) was reported by

MARKS (1966b) to be extensive, in apparent contradiction to expectations if triploids are produced as infrequently as in experimental $4x \times 2x$ crosses. JACKSON et al. (1977b) have shown that there are probably no more than about 25 cultivars within the species, and that the relatively high frequency with which triploids could be found in cultivated fields was due to the fact that a number of the cultivars were extremely widespread.

Much of the experimental material used in $4x \times 2x$ crosses has been based on *S. tuberosum* L. ($2n = 48$) cultivars, often crossed with *S. phureja* JUZ. et BUK. ($2n = 24$). These highly selected diploid clones were developed for their ability to induce high frequencies of dihaploids in $4x \times 2x$ crosses. Consequently, the formation of triploids was low. Certain diploid clones are known to produce a high frequency of $2n$ gametes (MOK & PELOQUIN, 1975) and in crosses with tetraploids, produced almost all tetraploid progeny. Thus the conclusions drawn from $4x \times 2x$ crosses in which specially selected parents were used may not be representative of what has happened in nature.

MATERIALS AND METHODS

Diploid, triploid and tetraploid primitive cultivars were taken from the potato collection maintained by the International Potato Center (CIP). The material was grown mainly at Huancayo (3380 m) in the Central Andes of Peru, although some material was grown on the coast at La Molina (238 m) during the cooler season, July to October. The diploids belonged to the species *S. stenotomum* JUZ. et BUK. ssp. *stenotomum* and ssp. *goniocalyx* (JUZ. et BUK.) HAWKES, and *S. phureja*; the tetraploids were *S. tuberosum* L. ssp. *andigena* (JUZ. et BUK.) HAWKES.

Pollinations were carried out in insect-proof screenhouse or cages, using the cut-stem technique (MCLEAN & STEVENSON, 1952). Although a number of crosses were made between individual tetraploid and diploid clones, most pollinations were made using a bulk sample of pollen that was produced by mixing the pollen collected from five flowers from different clones. The fruits were collected one month after pollination, and left to ripen for a further month, before the seeds were extracted by hand. Only plump seeds were counted.

Chromosome counts were obtained from root-tips, which were pretreated in water at $\pm 0^\circ\text{C}$ for 24 hours, followed by fixation in Jacobsen's solution (99 parts 30% ethanol: 1 part 85% lactic acid) for 24 hours or longer (TARN, 1967). Hydrolysis was carried out in 1N HCl at 60°C for 10 min, followed by staining in 45% lacto-propionic orcein for a minimum of 3 hours.

The formation of $2n$ pollen was determined in the diploid clones on the basis of size differences between n and $2n$ pollen grains. Following the method of QUINN et al. (1974) pollen grains were stained with aceto-carmin or iodine, and the frequency of $2n$ pollen was estimated in an incremental scale at 5% intervals. A minimum level of 5% $2n$ pollen was considered as sufficient to have a significant effect on seed set in $4x \times 2x$ crosses.

Triploid formation in $4x \times 2x$ crosses was also assessed using mixtures of $2n$ and n pollen, from tetraploids and diploids respectively, in approximately equal proportions. The tetraploids had white flowers, and were known to produce only white-

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flowered progeny after selfing. The diploids had self-coloured purple flowers and the genotypes for flower colour were known.

RESULTS

Triploid formation. A total of 357 preliminary pollinations were made between tetraploid females and diploid males in 1973 to investigate the experimental formation of triploids (Table 1). The lower fruit set of the February 1973 pollinations made at La Molina was due to the higher temperatures at that location, even though the crosses were identical to those made in Huancayo. However, the seed formation per fruit was higher at La Molina. Fruit and seed set were low for both locations, but the fact that only triploid progeny were produced was a significant finding. The $4x \times 2x$ crosses of August 1973 yielded 45 seeds, 81% of which were triploid. Three dihaploid and one tetraploid plants were also produced.

In February and August 1973, 234 $2x \times 4x$ pollinations were made. The February pollinations gave 32% fruit set, all of which were parthenocarpic. In August, two crosses produced one seed each. One plant was unthrifty and no chromosome count was made; the other was tetraploid.

More extensive crosses were made to examine the crossability relationships of the cultivated tetraploids and diploids in January 1974 (Table 2). All pollinations were made in Huancayo. Tetraploid clones from the same geographical area were grouped prior to pollination with the idea that they would probably be from the same gene-pool. Each group of tetraploids was pollinated with a bulk of pollen from diploid clones from the same geographical area. Overall, triploids were formed at a frequency of 14%, although two groups produced 87% triploids, and a third, 73% triploids. The fruit set was consistent for all groups, although the percentage of parthenocarpic fruits varied considerably. Generally, the highest triploid frequencies were obtained when the seed/fruit were low.

The high seed set of the Cusco (Canas and Canchis) Group 8 was due to pollen contamination from a tetraploid. One of the pollinators had been misclassified, and was tetraploid. One aspect of the $4x \times 2x$ crosses was the high frequency of aborted seeds, which could be seen as empty seed coats in the fruits. Five dihaploid seedlings were obtained in four of the groups, but their occurrence was irrespective of a high or low frequency of tetraploids in the progeny.

There was variation within and between groups, both for seed set and triploid formation. Twenty-two tetraploids produced triploids in these crosses. Three clones,

Table 1. Seed production from $4x \times 2x$ crosses in La Molina and Huancayo.

Date	Location	Pollina- tions	Fruit	F/P	Seed	S/F	Germinated seeds			% 3x
							2x	3x	4x	
Feb. 1973	Huancayo	119	48	0.4	8	0.2	0	2	0	(100)
Feb. 1973	La Molina	76	9	0.1	5	0.6	0	1	0	(100)
Aug. 1973	La Molina	162	39	0.2	45	1.1	3	17	1	81

F/P = Fruit/pollination; S/F = Seed/fruit.

Table 2. Seed production from 4x × 2x crosses in which female clones were grouped according to geographic origin and pollinated with a bulk sample of pollen from diploid clones.

Geographical group (number of clones)	Pollinations	Fruit	F/P	Seed	S/F	Germinated seeds			% 3x
						2x	3x	4x	
1. Cajamarca/La Libertad (13)	313	107	0.3	123	1.1	2	34	3	87
2. Huanuco (7)	180	60	0.3	171	2.8	1	2	24	7
3. Pasco/Junin (10)	253	101	0.4	41	0.4	1	13	1	87
4. Huancavelica (9)	237	91	0.4	239	2.6	0	5	79	6
5. Ayacucho (13)	354	98	0.3	58	0.6	0	4	13	23
6. Apurimac (10)	226	77	0.3	242	3.1	0	2	113	2
7. Cusco (Paucartambo) (9)	217	71	0.3	31	0.4	0	8	3	73
8. Cusco (Canas and Canchis) (17)	368	147	0.4	1459	9.9	1	1	116	1
9. Puno (13)	213	50	0.2	279	5.6	0	0	49	0
10. Bolivia (3)	53	21	0.4	1	0.05	0	0	0	0

F/P = Fruit/pollination; S/F = Seed/fruit.

Table 3. The production of triploid and tetraploid progeny following 4x × 2x crosses.

Tetraploid clone (Geographical group)	Progeny			
	3x	Tr. p.p. ¹	4x	Te.p.p. ²
701344 (1)	17	0.63	1	0.04
701243 (1)	2	0.5	0	0
701392 (1)	13	0.46	0	0
701628 (7)	5	0.19	2	0.07
701659 (3)	5	0.18	0	0
701685 (4)	4	0.15	26	0.96
701655 (3)	3	0.13	0	0
701646 (3)	3	0.13	1	0.04
701717 (5)	3	0.11	11	0.39
701095 (1)	2	0.07	0	0
701535 (3)	1	0.05	0	0
701620 (7)	1	0.05	0	0
701622 (7)	1	0.04	0	0
701626 (7)	1	0.04	1	0.04
701748 (5)	1	0.04	1	0.04
701920 (2)	1	0.04	2	0.08
702122 (8)	1	0.04	3	0.14
701849 (2)	1	0.04	11	0.44
701565 (6)	1	0.04	15	0.56
701666 (4)	1	0.04	21	0.84
701591 (6)	1	0.04	54	2.08
701658 (3)	1	0.03	0	0

¹ Triploids per pollination.² Tetraploids per pollination.

CIP 701344, CIP 701243 and CIP 701392 (all Cajamarca/La Libertad Group) were the most successful with respect to triploid formation, with 0.63, 0.5 and 0.46 triploids per pollination respectively. The other 19 tetraploids formed triploids at a frequency of 0.03 to 0.19 triploids per pollination. Of the 22 clones, only 12 produced triploids at a greater frequency than tetraploids (Table 3). With the exception of one clone, CIP 702122 (Group 8), these data demonstrate that the tetraploids varied with respect to the strength of the 'triploid block'.

Pollen competition. The results of $4x \times 2x$, mixed pollen crosses, i.e. $4x \times (4x + 2x)$, tetraploid self-pollinations and the diploid crosses are given in Table 4. In the $4x \times 2x$ crosses, clone CIP 701582 was the most successful tetraploid to produce seed, with an average of 0.7 seed/fruit. When the mixed pollen was used, seed set was considerably reduced as compared with the self-pollinations (reductions of 38%, 49% and 79% for clones CIP 701617, CIP 701582 and CIP 702858, respectively).

The seed production of the diploids was variable. In the cross CIP 702953 \times CIP 701114, seed production was as low as the tetraploid self-pollinations. The other cross, CIP 702953 \times CIP 701207, was considerably more fertile, with an average of 260 seed/fruit.

The three plants from the $4x \times 2x$ crosses had self-coloured flowers; one was tetraploid (from a $2n$ gamete) and two were triploid (Table 4). Within two of the families where mixed pollen was used, hybrids were recognisable by their self-coloured flowers. Their frequency was very much lower than the white-flowered phenotypes. In the family CIP 701582, one hybrid was triploid and four were tetraploid, whereas the other 51 white-flowered tetraploids were selfed progeny. In the family CIP 702858, two hybrids were triploid and two were tetraploid. It was not possible phenotypically to detect hybrids in the third family, CIP 701617, as the diploid pollinator, CIP 701114, produced male gametes for both white and self-coloured flowers.

Both diploids were originally chosen because it was not possible to find $2n$ gametes in the pollen. However, in the progeny of the crosses using the diploid CIP 701207, six out of the nine hybrids from both families were tetraploid, not triploid. This demonstrates that even the very rare $2n$ gamete is more likely to produce seed than the n gamete when it forms a triploid. These results support the strength of the 'triploid block'.

Triploid fertility. In February 1973, 398 pollinations were made using triploid accessions of *S. \times chaucha* cv. Huayro (Table 5). The triploids were used as both males and females. The Huancayo pollinations were more successful than those at La Molina. Although seed set was always low when triploids were used as females (<1 seed/fruit), it was higher for the $3x \times 2x$ crosses than for the $3x \times 4x$ crosses. The fact that two of the triploid accessions, CIP 701408 and CIP 702498, produced seed when used as males in crosses with diploids was an interesting finding. A study of the pollen from these two accessions showed an extremely high percentage of deformed pollen, and only the occasional regular pollen grain.

Of the 32 seeds which were produced, chromosome numbers of the progeny ranged from $2n = 44-48$ for the $4x \times 3x$ and $3x \times 4x$ crosses, and from $2n = 25-27$ for the $3x \times 2x$ and $2x \times 3x$ crosses.

Table 4. The results from various crosses of diploids and tetraploids.

Cross	Pollinations	Fruit	F/P	Parthenocar- pic fruit (%)	Seed	S/F	% Germ- inated			4x
							white	self- coloured	3x	
<i>4x × 2x</i>										
701617 × 701114	12	6	0.50	5(83%)	1	0.2	0	0	0	0
701582 × 701207	11	7	0.64	3(43%)	5	0.7	20	0	1	0
702858 × 701207	12	7	0.58	5(71%)	2	0.3	100	0	2	1
<i>4x × (4x + 2x)¹</i>										
701617 × (701617 + 701114)	12	9	0.75	0	162	18.0	96	147	0	-
701582 × (701582 + 701207)	11	7	0.64	0	66	9.4	91	51	5	55
702858 × (702858 + 701207)	11	7	0.64	0	53	7.6	89	42	4	44
<i>4x self-pollinations</i>										
701617	10	8	0.80	0	262	32.7		100%	0%	
701582	11	6	0.55	0	130	21.7		100%	0%	
702858	12	7	0.58	0	258	36.9		100%	0%	
<i>2x test crosses</i>										
702953 × 701114	5	5	1.0	0	194	38.8		50%	50%	
702953 × 701207	7	7	1.0	0	1817	259.6		0%	100%	

¹ A mixture of pollen from the same tetraploid clone and a diploid clone.

F/P = Fruit/pollination; S/F = Seed/fruit.

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The crossability of triploids, as females only, with tetraploids and diploids was further studied in January and February, 1975, at Huancayo. One hundred and nine accessions of 20 cultivars of *S. × chaucha* were used, and 1650 bulk pollinations made, from which 7228 seeds were obtained (Table 6). The crossability of each cultivar was also compared with its fertility as measured by seed production after open-pollination in the field at Huancayo (Table 7). Although fruit set for each cross was more or less equal, the seed set of the 3x × 2x crosses was four times greater than that of the 3x × 4x crosses, and the percentage of parthenocarpic fruit was much lower, 7% compared with 29%.

The triploid cultivars showed a wide range of female fertility, although none failed to produce seed in either cross. Some of the cultivars had relatively high seed/fruit values in crosses with diploids, notably cv. Pishpita, which produced an average of 27 seed/fruit. With regard to cv. Huayro, the 1973 results for female fertility were confirmed, although seed set in 1975 was higher. The seed set from open-pollinated flowers was generally closer to the seed/fruit values of the 3x × 2x crosses, for the cultivars for which comparisons could be made.

A total of 409 self-pollinations were made, yielding 25 fruit. Most were parthenocarpic, and only one clone, cv. Hayaparara, produced two seeds, of which one germinated. The plant was unthrifty and died before a chromosome count could be made.

Table 5. Fruit and seed production when *S. × chaucha* cv. Huayro was used as male and female in crosses with diploids and tetraploids.

Location	Cross	Pollinations	Fruit	F/P	Seed	S/F
Huancayo	3x × 4x	75	43	0.6	1	0.02
La Molina		74	12	0.2	0	0
Huancayo	3x × 2x	36	24	0.7	16	0.7
La Molina		35	10	0.3	7	0.7
Huancayo	4x × 3x	70	20	0.3	3	0.2
La Molina		42	6	0.1	1	0.2
Huancayo	2x × 3x	29	15	0.5	0	0
La Molina		37	5	0.1	4	0.8

F/P = Fruit/pollination; S/F = Seed/fruit.

Table 6. Total seed production from 3x × 4x and 3x × 2x crosses in Huancayo, 1975.

Cross	Pollinations	Fruit	F/P	Seed	S/F
3x × 4x	825	613	0.74	1232	2.0
3x × 2x	825	677	0.82	5996	8.9

F/P = Fruit/pollination; S/F = Seed/fruit.

Table 7. Seed production of triploid cultivars following $3x \times 4x$ and $3x \times 2x$ crosses.

Cultivar	$3x \times 4x$ seed/fruit	% Partheno- carpic fruit	$3x \times 2x$ seed/fruit	% Partheno- carpic fruit	Open-pollinated seed/fruit
Huayro	2.0	23.5	8.7	2.3	8.2
Duraznillo	2.4	21.1	3.4	18.7	7.6
Garhuash shuito	0.8	52.0	10.3	8.9	8.9
Puca shuito	1.2	43.4	9.4	9.9	9.0
Yana shuito	1.3	25.8	9.4	0	13.0
Pishpita	3.1	4.9	27.1	0	25.4
Rucunag	3.2	10.0	2.1	8.3	7.5
Piña	3.7	5.6	2.5	13.3	6.2
Komar ñahuichi	4.1	0	5.3	0	—
Surimana	1.3	50.0	7.0	0	1.4
Collo	1.0	40.0	4.3	0	6.0
Manzana	7.5	0	7.5	0	5.0
Ccusi	4.2	0	—	—	—
Tarmeña	0	100.0	1.7	0	8.0
Yuracc incalo	4.0	25.0	12.7	0	—
Colquepata	2.7	0	2.7	—	—
Rodeñas	4.7	0	0	0	—
Morhuarma	3.2	20.0	0	—	12.2
Hayaparara	0	100.0	6.0	0	13.2
Rancas	0.4	57.1	3.0	0	—

DISCUSSION

The results have provided further insight into the amount and probability of gene-flow between diploid, triploid and tetraploid Andean potato varieties. The contacts between the three gene-pools are dependent upon a number of crossability factors, namely the likelihood of triploid formation and the role of $2n$ gametes from the diploids.

Post-fertilisation breakdown is common in $4x \times 2x$ crosses, and consequently the number of seeds produced is very low compared to what might reasonably be expected in intra-tetraploid crosses. Most of the progeny are tetraploid, resulting from the union of reduced and $2n$ gametes from the tetraploids and diploids, respectively, even though the formation of $2n$ gametes in the diploids is at a relatively low frequency. The formation of triploids at high frequencies following $4x \times 2x$ crosses, when certain tetraploids were used was unexpected. In absolute terms, however, the actual number of triploids was low. The 'triploid block' varied amongst the tetraploids, and was never entirely absent. If it were absent, then high seed set would be expected and all progeny triploid. This is apparently the situation in crosses of *S. polytrichon* RYDB. \times *S. phureja*, in which only triploid F_1 -progeny were found (RAMANNA & ABDALLA, 1970).

The number of triploid progeny formed following the use of mixed pollen ($n + 2n$) was also low in comparison with the formation of tetraploids by the union of normal reduced gametes from the tetraploid. The strength of the 'triploid block' is supported by these results. Yet the fact that two of the tetraploids used in these mixed

pollen crosses, CIP 701582 and CIP 702858, produced triploids is interesting, as earlier $4x \times 2x$ crosses failed. In crosses such as these, a few triploid seeds are formed along with a relatively large number of normally-developing tetraploid seeds. The triploid seeds grow to maturity in a medium, i.e. the fruit, which is itself developing normally. Thus a few triploids may well be 'carried along' although in the absence of tetraploids the failure of fruit growth would generally preclude their survival.

Triploid formation is inhibited by yet another factor, namely the frequency at which the cross between the tetraploids and the diploids actually occurs. On account of their sympatric distribution in native fields throughout Peru and Bolivia, the two gene-pools have the potential for hybridisation and gene-exchange. In the Andean region, the self- and cross-fertility of the tetraploids is extremely high, as cut-stem pollinations made with the tetraploids have shown (JACKSON, 1975). GLENDINNING (1976) estimated that 80% of the progeny from fruits collected from *andigena* tetraploids in the field in Scotland were the result of selfing, even though bees were observed visiting the plants. Undoubtedly hybridisation between the cultivated tetraploids and diploids does take place, as evidenced by the presence of triploids, but the cross may occur only infrequently. Thus, although the 'triploid block' is weaker in some tetraploid clones, the common formation of triploids is probably rarely achieved in nature. It is unlikely that triploids were formed from $2x \times 4x$ crosses.

On account of their ability to set seed in crosses with diploids and tetraploids, the potential exists for gene-flow through triploid 'bridges'. Most progeny formed from $3x \times 4x$ or $3x \times 2x$ crosses are aneuploid, whose fertility is generally much lower than the euploid parents. Each season, however, a few seeds may be formed in nature which have the exact or nearly exact euploid number following $3x \times 4x$ or $3x \times 2x$ hybridisation. If gene-flow occurs through triploid 'bridges', it requires twice as many steps as directly through $2n$ gametes from diploids. The direction of gene-flow through triploids seems more likely from the tetraploid gene-pool into the diploid, rather than in the other direction. Gene-flow of this type has probably played a minor role in the extension of the gene-pools at the two ploidy levels. Crossability relationships are summarised in Fig. 1.

Of more evolutionary significance is the extension of the tetraploid gene-pool through direct introgression from the diploids via $2n$ gametes. The role of $2n$ gametes

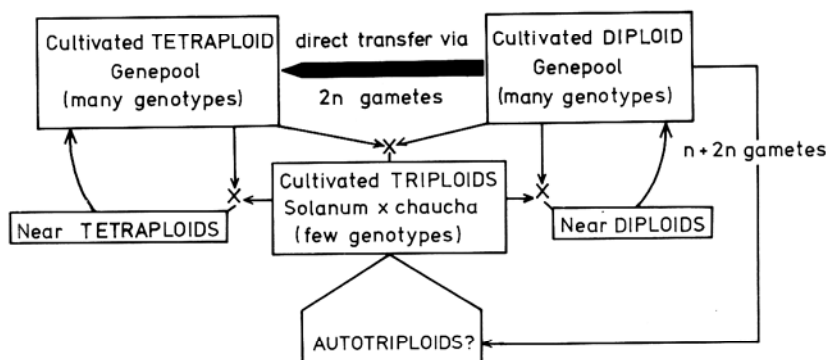


Fig. 1. Crossability relationships of the cultivated diploids, triploids and tetraploids of the Andes.

needs no emphasis, and their presence in the Andean diploids appears to be fairly widespread (QUINN et al., 1974) and consequently $4x \times 2x$ crosses in which they are present are functional $4x \times 4x$ crosses. They provide a direct method of transfer of diploid germplasm into the tetraploids (MENDIBIRU & PELOQUIN, 1971) with a consequent increase of variability at the tetraploid level. On the other hand, it has not been possible to demonstrate experimentally the formation of autotriploids from within the diploid gene-pool, although some self-compatible diploids have been identified in the CIP collection (JACKSON, 1975). The selective advantage of $2n$ gametes *vis-à-vis* n gametes in $4x \times 2x$ crosses is obvious, and the extremely vigorous nature of the tetraploid progeny has been demonstrated (MENDIBIRU & PELOQUIN, 1971; QUINN & PELOQUIN, 1973).

The 'triploid block' is weaker in certain clones of *S. tuberosum* ssp. *andigena* than reported in *S. tuberosum* ssp. *tuberosum*. A 'triploid block' in the wild tetraploid species *S. acaule*, *S. polytrichon* and *S. stoloniferum* SCHLECHTD. et BCHÉ. is apparently absent. Further cytological research is needed to compare triploid formation in the cultivated and wild potatoes, and the effect of environment on $2n$ gamete production in diploids.

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