BREEDING METHODS FOR PRODUCTION OF POTATOES FROM TRUE SEED

by

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ABSTRACT

BREEDING METHODS FOR PRODUCTION OF POTATOES FROM TRUE SEED

BY

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Under the supervision of Professor Stanley J. Peloquin

The traditional production of potatoes through vegetative propagation by means of tubers increases the chance of transfer of diseases and viruses from generation to generation and is wasteful of potential food. In addition, it requires costly storage and transport facilities commonly lacking in developing countries.

The use of true potato seed (TPS) for potato production has been proposed as an alternative practice since it minimizes the possibility of transfer of viruses and other pathogens. TPS also makes the total crop available for consumption by eliminating the use of tubers, and allows subsistence farmers to grow potatoes at a relatively low cost. To further develop this technique, research was needed to identify breeding methods which would generate high yielding and uniform families, and to determine factors involved in potato hybrid seed production using natural pollinators.

Fifty-seven families obtained through different breeding methods and categorized as hybrids, first and second generation open-pollinated (I OP and II OP) and self-pollinated, were evaluated for tuber yield, vegetative vigor and haulm uniformity of seedling transplants at two locations. The diplandrous tetraploid families from 4x x 2x crosses were obtained by using 2x hybrids which produced 2n pollen by parallel spindles (ps) at Anaphase II (FDR with crossing over) or by a combination of a synaptic mutant (sy3) with parallel spindles (FDR without crossing over). Seedlings from each family were transplanted to the field in a randomized complete block design with two replications.

Highly significant differences for tuber yield among families were found. Differences in mean tuber yields between the two locations (295 vs. 173 cwt/acre) were observed. For both locations, tuber yields of the hybrid families were significantly higher than those of I OP, II OP and self-pollinated families. All families obtained from 4x x 2x FDR with or without crossing over out yielded all other hybrid families and were also predominant among the higher yielding families at both locations. Non-significant differences in tuber yields were found between I OP and II OP families. Tuber yields of some I OP families approached those of the hybrids at one location. Self-pollinated families consistently had the lowest tuber yields at both locations. All hybrid families regardless of their genetic background also had better vigor and haulm uniformity than any of the I OP, II OP, or self-pollinated families.

These results indicate that the 4x x 2x FDR with or without crossing over breeding method is the most efficient in the production of high yielding and uniform TPS families for production of potatoes from true seed. Open-pollinated families also provide subsistence farmers with an alternative source of seeds for TPS production when large amounts of hybrid seeds are not available. Families produced from self-pollination were found to lack the yield, vigor and uniformity potential observed in hybrid families.

Practical and economical large scale controlled intermatings of tuber-bearing Solanums by bumblebees are required in order to obtain the desired tetraploid hybrids for production of potatoes from true seed. Moreover, knowledge of the means of attraction establishing an effective flower-pollinator relationship is required in order to apply it in potato hybrid seed production.

One hundred and eighty potato clones, representing cultivars and advanced selections involved in a yield trial at Rhinelander, were utilized as plant materials to study the relative efficiency of different potato clones for production of open-pollinated seeds and to obtain initial information about the behavior of bumblebees when intermating potato.

Data on amount of flowering, percent stainable pollen, fruits per plant and seeds per fruit were obtained in an attempt to determine the relationship between these variables in the production of TPS using natural pollinators. Bumblebee behavior in a potato field was observed following a bee during a foraging flight.

An effective foraging activity of bumblebees between different rows of potato clones was observed. Relatively large amounts of fruit and seed set were obtained from clones regardless of the amount of flowering or the presence or absence of flower odor. Seeds per fruit averaged 88.1 when the percent stainable pollen was 5% and below. Eight relatively male sterile clones were found that produced an average of 115 fruits for two plants and 152 seeds per fruit. A

modest linear positive correlation (r = 0.479) was found only for fruit set and percent stainable pollen. The existence of effective means of insect attraction originating from the potato flower other than those herein investigated, accounted for most of the variability observed in seed set.

The amounts of seed set obtained with values of percent pollen stainability below 5%, indicate that bumblebees do sometimes visit male sterile flowers. Effective outcrossing most likely takes place. Selection of relatively male sterile clones producing significant amounts of seed set for utilization in production of potato hybrid seed using bumblebees, appears as a good approach to reduce cost of hybrid seed production.

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CHAPTER I

AGRONOMIC EVALUATION OF TRANSPLANTED TRUE POTATO SEED FAMILIES

INTRODUCTION

Commercial production of potatoes has been done traditionally through vegetative propagation by means of tubers. Such vegetative propagation, however, increases the chances of transfer of diseases and viruses from generation to generation. It is also wasteful of potential food, since approximately two tons of tubers are needed to plant one hectare. Moreoever, storage facilities and transport requirements increase the total cost of production turning this conventional practice into a major limiting factor in potato production, especially in developing countries where production losses are usually greater due to poor quality tubers.

The use of true potato seed (TPS) for potato production offers several advantages: (1) It can minimize the possibility of transfer of diseases and viruses except for potato spindle tuber viroid (PSTV) and Andean potato leaf-roll virus (APLV) which can be transmitted through true seed; (2) Makes the total crop available for consumption; and (3) Of utmost importance by eliminating the use of tubers, reduces the total cost of production by 50-70% enabling the subsistence farmers to successfully grow a potato crop.

The use of TPS has been mainly limited to potato breeding programs for growing the first tuber generation. However, TPS is commonly used by subsistence farmers in Cuzco, Peru and in the People's Republic of China as a method to produce tuber seed potatoes (Franco 1979, personal communication; Li 1982) indicating the practicability of the technique. Since November 1977, the International Potato Center has concentrated research efforts towards the utilization of TPS for potato production. Although production technology has been developed, the need for further research regarding breeding methods to produce high yielding progenies suitable for agronomic production and hybrid seed production under field conditions has been emphasized (Mendoza 1979, Peloquin 1979, 1982).

Breeding procedures proposed for TPS although somewhat different, all aim to the production of highly heterozygous and uniform TPS progenies. Hermsen (1979) also proposed autonomous apomixis as a Utopian approach to achieve the breeding goals for TPS progenies. Peloquin (1979) discussed the possibility of utilizing selected diploid parents producing 2n gametes by first division restitution in 2x x 2x or 4x x 2x crosses for obtaining maximum uniformity and heterozygosity in the 4x progeny. In the study reported here, the objective is to identify the breeding method that provides the optimum type of progeny for further utilization in production of potatoes from true seed. The choice will depend upon the tuber yields obtained with a particular breeding scheme, and the practicability of the method per se.

LITERATURE REVIEW

Inbreeding depression in polysomic polyploids is similar to the theoretical rate at which first order interactions are lost from tri- and tetra-allelic loci (Busbice and Wilsie 1966; Bingham 1980) thus, maximizing the number of tetra-allelic loci is of utmost importance to the full expression of heterosis in polysomic polyploids. In the case of potato, a tetrasomic polyploid, the importance of maximizing heterozygosity has been demonstrated by the increased vegetative vigor, tuber yield and uniformity of 4x progenies obtained from 4x x 2x crosses (Hanneman and Peloquin 1969; Mendiburu and Peloquin 1971; Mendiburu, Peloquin and Mok 1974; De Jong and Tai 1977). Conversely, by the severe inbreeding depression resulting from selfing (Rowe 1967a, 1967b; De Jong and Rowe 1971). Both results suggest that genetic interactions from tri- and tetra-allelic loci are important determinants of yield and vigor. The larger number of alleles per locus possible in the tetraploid materials increases the number of possible intra- and inter-locus interactions, as compared to diploids, and since non-additive gene effects are of major importance for tuber yield, tetraploids appear to have a greater yield potential than diploids (Mendiburu et al. 1974; Mendoza and Haynes 1976; Dodds 1965). Chase (1963) proposed an analytical breeding scheme for potatoes based on intermating haploids with the diploid tuber-bearing Solanum species followed by selection and chromosome doubling. The efficiency of this proposed technique was investigated by Rowe (1967a) using diploid clones which were also doubled with colchicine to produce tetraploid counterparts. Data presented on yield performance, indicated no advantage of colchicine doubled 4x clones over 2x hybrid clones.

Mendiburu, Peloquin and Mok (1974) proposed a breeding scheme ideally suited to maximize heterozygosity by making use of 2n gametes. It was indicated that the amount of heterozygosity in the progeny would depend on the mode of 2n gamete formation and consequently on the mode of polyploidization. The uniqueness of 2n pollen formed by parallel spindles at Anaphase II, a first division restitution (FDR) mechanism, to pass onto the progeny a great portion of non-addition effects in a largely intact array provides FDR gametes with a superior breeding value when using this scheme to produce 4x hybrids from 4x-2x crosses (Mendiburu 1971; Mok and Peloquin 1975b).

Highly heterozygous and uniform tetraploid progenies are in this way generated, providing also a means to incorporate germplasm from cultivated and wild 2x selections via FDR 2n gametes into more adapted Group Tuberosum 4x genotypes and broadening the genetic base at the 4x level. These characteristics make the breeding scheme a very attractive approach to obtain progenies with adequate uniformity and vigor which are required for successful utilization of TPS. Selected highly heterozygous Phureja-haploid Tuberosum 2x hybrids producing FDR 2n gametes can be used in this breeding scheme to synthesize tetraploid progenies with desirable degree of heterozygosity and uniformity (Hanneman and Peloquin 1968, 1969).

Positive results using this 4x x 2x breeding method have been obtained by Quinn and Peloquin (1973); Mendiburu and Peloquin (1977a); Mok and Peloquin (1975b); De Jong and Tai (1977); and De Jong et al. (1981). They found that the mean tuber yields of unselected tetraploids from 4x x 2x FDR crosses were higher than their selected tetraploid parents or than the check varieties utilized in the experiments. This clearly shows that the high yields and uniformity of the 4x hybrids resulted from the large amount of heterozygosity and epistasis transferred from the 2x parent to the tetraploid progeny.

These large heterotic effects observed for tuber yield are also observed in the male gametophyte formed by FDR. Gametophyte heterosis due to the ability of FDR gametes to retain more epistasis and heterozygosity has been proposed to account for this phenomena (Simon and Peloquin 1976). Preliminary experiments involving reciprocal crosses between tetraploid Tuberosum cultivars and Phureja-haploid Tuberosum 2x hybrids showed reciprocal cross differences for tuber yield in progenies of 4x x 2x vs. 2x x 4x crosses. These differences were explained in terms of the FDR mode of 2n pollen formation which maximized heterozygosity in the 4x x 2x crosses rather than the superiority of one cytoplasm over the other (Kidane-Mariam and Peloquin 1974).

In terms of marketable yield, 4x x 2x crosses exhibit lower yields than the 4x parents, and further they resembled the tuber appearance of the 2x parent (De Jong and Tai 1977). The overall tuber type is considered to be less attractive by the highly selective consumer in developed countries and has been one of the main problems in the utilization of this breeding scheme for TPS production. Exploiting the full potential of these 4x hybrids from 4x x 2x crosses therefore requires that heterosis for total yield be directed into a more marketable form through the development of improved 2x parents with better horticultural characteristics (De Jong et al. 1981).

In this regard, improved materials having better tuber types for utilization in the 4x x 2x breeding method have been reported by Okwuagwu (1981). These are represented by a group of 2x FDR clones with a meiotic modification characterized by lack of chiasmata which will normally lead to complete sterility, but when combined with the parallel spindle mechanism, it offers a unique opportunity to transfer 100% of the heterozygosity and epistasis of the 2x parent to the progeny in 4x x 2x crosses. Using a few of these clones, some 4x progenies from 4x x 2x crosses were obtained that had good tuber type particularly for eye depth, and were comparable to standard varieties in appearance (Schroeder 1982).

Improvement of the 2x hybrid parent should take into consideration the magnitude of general and specific combining abilities and the degree of parent-offspring correlation for yield. Results about the importance of GCA and SCA for tuber yield have been reported. Quinn and Peloquin (1973) using fifteen progenies from a six by six diallel among diplandrous tetraploids found that both general and specific combining ability were highly significant for tuber yield. Mok and Peloquin (1975b) based on studies with 4x x 2x FDR, 4x x 2x SDR and 4x-4x crosses generated by using 4FDR, 4SDR (SDR: Second Division Restitution mechanism for 2n pollen production) 2x parents and nine tetraploid cultivars reported that when families of all three categories were analyzed together, both general and specific combining ability were significant for tuber yield. These results are in agreement with the fact that functioning FDR 2n gametes have the ability to transmit considerable amounts of non-additive genetic effects. De Jong and Tai (1977) using also 4x x 2x crosses with two 2x parents and 12 cultivars reported that SCA was not important for tuber yield. The different result obtained in this work appears to be due to the utilization of only two 2x parents.

Significant GCA among 4x and 2x parents for total and marketable yield have been reported (De Jong and Tai 1977; McHale and Lauer 1981b) suggesting that when selecting parental materials for 4x x 2x crosses in TPS production, the best general combiners for total and marketable yield among 4x cultivars and 2x hybrids materials could be used as parents. This, however, implies the requirement of using suitable testers to assess the potential of the breeding materials to maximize genetic gain (McHale and Lauer 1981a; 1981b).

High parent-offspring correlations would be also desirable if an adequate level of predictability for tuber yield of 4x x 2x crosses is to be obtained from yield performance of the 2x parent. Unfortunately, it appears that this correlation for tuber yield is not strong (McHale and Lauer 1981b), and only high parent-offspring correlations for maturity and tuber appearance have been reported (Schroeder 1982).

Parent-offspring correlations in 4x progenies from 4x x 2x crosses appear to be affected by the fact that at the tetraploid level the most important fraction of the genetic variance seems to be non-additive genetic variance (Mendoza 1979; Vargas and Mendoza 1980; Thompson 1980), whereas at the diploid level results indicate that additive genetic variance is the most important component (Landeo and

Hanneman 1982a, 1982b). Due to this difference in genetic variance components affecting tuber yield at the 4x and 2x level, parent-offspring correlations could not be expected and reasonable extrapolations from the 2x parent to the 4x progenies do not appear to be feasible.

The idea of maximizing heterozygosity to obtain higher yield responses in 4x x 2x crosses should also take into consideration the notion of the optimal level of heterozygosity; that is, up to what extent will increasing levels of heterozygosity, translate into further yield gains. Sanford and Hanneman (1982) in a trial involving varying doses of different taxonomic groups created 1-way hybrids (Tuberosum x Tuberosum), 2-way hybrids (Tuberosum x Phureja-Tuberosum FDR), and 3-way hybrids (Andigena x Phureja-Tuberosum FDR). The latter were expected to be more heterozygous, since they combined the high yielding capacity of both Phureja-Tuberosum hybrids and Andigena-Tuberosum hybrids. Results presented indicated no significant superiority of 3-way hybrids over 2-way hybrids for tuber yield, suggesting the existence of a heterotic threshold in the cultivated potato beyond which point increases in heterozygosity will not result in higher yield responses. The higher efficiency of FDR 2n gametes in maximizing heterozygosity and uniformity through 4x x 2x crosses in potato breeding is, however, once more demonstrated.

Even though maximum productivity can be attained at the 4x level, breeding work is more desirable at the 2x level due to the simplicity that disomic inheritance provides to the genetic studies, and the ease by which specific dominant genes can be combined for potato improvement. Important consideration is also given to the fact that many of the most useful wild and cultivated species which are good sources of pest and disease resistance are diploids. Iwanaga (1980) based on the efficiency of FDR 2n gametes in transmitting heterozygosity and dominant genes, proposed the utilization of 4x x 2x crosses in order to obtain heterozygous uniform progenies with combined multiple pest and disease resistance. Selection for multiple resistance, agronomic traits and production of FDR 2n gametes is done at the 2x level and finally the selected 2x FDR materials with desirable characteristics are transferred to the 4x level via 4x x 2x crosses.

The 4x x 2x FDR breeding scheme, therefore, can be utilized for production of TPS progenies not only with higher overall tuber yield performances and uniformity, but also with acceptable levels of pest and disease resistance.

Synthesis of 4x progenies from 2x x 2x crosses of unrelated parents with FDR operating in both sexes (Bilateral Sexual Polyploidization) has been proposed as a mean to maximize heterozygosity and provide optimum levels of genetic diversity in tetraploid progenies (Mendiburu and Peloquin 1977b). The mating of unrelated diploids provides the opportunity to maximize heterozygosity through normal sexual reproduction by obtaining tetraploid progenies with a higher frequency of tri- and tetra-allelic loci.

In this regard, Rowe (1967a) showed that di-allelic duplex clones derived by doubling diploid hybrids, were lower yielding than comparable selected diploids. Mendiburu and Peloquin (1977b) presented results obtained from 2x x 2x crosses of diploids producing 2n pollen and 2n eggs. The tetraploid hybrids obtained were generally more vigorous with significantly higher tuber yields than their diploid full sibs. The feasibility of using the 2x x 2x breeding scheme is therefore shown through these results.

Although the utilization of the wild 24-chromosome species S. chacoense offers an opportunity to develop selected male fertile 2x haploid Tuberosum-S. chacoense hybrids with adaptability and 2n gametes for further use in 2x x 2x crosses (Leue and Peloquin 1980, 1981); the practicability of this method is hampered by the difficulty of screening for FDR 2n eggs and finding frequencies of 2n eggs high enough to produce the large number of seeds per fruit required for TPS production.

Open pollinated progenies provide a practical source of seed for the utilization of TPS in potato production especially if large amounts of seeds are not available from TPS hybrid seed production (Thompson 1980; Peloquin 1979; Accatino 1979). The yield response however will depend on the degree of heterozygosity of the maternal clone, its adaptability and the amount of outcrossing provided by the natural pollinators (Peloquin 1979). A high level of heterozygosity in the maternal clone is pointed out as the main condition to obtain an acceptable level of yield response from the open-pollinated progenies even in presence of some degree of selfing.

MATERIALS AND METHODS

Fifty-seven families obtained through different breeding methods and categorized as hybrids, first and second generation open-pollinated (IOP and IIOP respectively), and self-pollinated were evaluated for tuber yield, vigor and haulm uniformity of seedling transplants at Hancock and Rhinelander during the summer of 1982. The TPS families were further divided into groups according to the type of cross as indicated in Table 1. The diplandrous tetraploids from 4x x 2x crosses (unilateral sexual polyploidization) were obtained by using 2x hybrid pollen parents producing 2n pollen by parallel spindles (ps) at Anaphase II, genetically equivalent to first division restitution (FDR) mechanism (FDR with crossing over), which transmits about 80% of heterozygosity of the 2x parent to the 4x progeny (Mok and Peloquin 1975a) or, 2x parents producing 2n pollen by a combination of a synaptic mutant (sy3) with parallel spindles (FDR without crossing over) which provides a unique means of transferring 100% of the heterozygosity and epistasis of the 2x parent to the 4x progeny (Okwuagwu 1981). Open-pollinated families were included in this trial, since they are produced under field conditions by natural pollinators and could provide an alternative for the small farmer.

A. Field experiment

Seeds from each family, previously treated with 1500 ppm giberellic acid, were seeded in plastic trays containing Jiffy mix. Seedlings approximately three weeks old were then transplanted to 5 x 5 cm peat pots, and three weeks later transplanted to the field in a

Table 1. Groups of TPS families.

I. 4x clones x 2x hybrid

1. Butte x I(1)
2. W760 x I
3. W231 x I
4. W853 x I
5. W639 x I
6. Merr x I
7. Merr x C-59(3)
8. W853 x C-59
9. Merr x C-39(4)
10. W639 x C-166(3)
11. Merr x C-166
12. [W639 x (Platte x J)] x C-39(2)
13. [W639 x (W643 x J)] x C-166
14. [W639 x (W643 x J)] x C-77(3)
15. [W639 x (Platte x J)] x C-166
16. [W639 x (Platte x J)] x C-59
17. [W639 x (W643 x J)] x C-39

II. 4x clone x 4x clone

1. W853 x W231
2. W853 x W744
3. W853 x W639
4. Merr x W231
5. Merr x W853

III. [4x x (2x x 4x)] x 4x clone = tetraploid-diploid-tetraploid (TDT) x 4x clone

1. [W582 x (W5293.3 x Kenn)] x W231(5)
2. [W582 x (W5293.3 x Kenn)] x W853

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(1) I = 2x Phureja 243462– haploid-Tuberosm W-1 (Katahdin) hybrid, parallel spindle mutant.

(2) J = 2x Phureja 225696 – haploid-Tuberosum W-42 (Chippewa) hybrid, parallel spindle mutant.

(3) Synaptic-parallel spindle mutant obtained among I x J hybrids.

(4) Parallel spindle mutant obtained among I x J hybrids.

(5) W5293.3 = 2x Phureja 225710 – haploid–Tuberosum W-1 (Katahdin) hybrid. W series = Wisconsin advanced breeding selections.

Table 1 (continued):

IV. (4x clone x I) I OP(6)

1. (W760 x I) I OP
2. (W639 x I) I OP
3. (W726 x I) I OP
4. (W231 x I) I OP

V. (4x clone x 4x clone) I OP

1. (W639 x Merr) I OP
2. (W231 x W639) I OP

VI. [4x x (4x-2x)] I OP

1. [W639 x (W231 x I)] I OP
2. [W639 x (W643 x J)] I OP
3. [W639 x (W643 x J)] I OP
4. [W639 x (W643 x J)] I OP

VII. (4x clone) I OP

1. (W744) I OP
2. (W760) I OP
3. (W231) I OP
4. (W639) I OP
5. (W853) I OP
6. (Merr) I OP
7. (T-874) I OP

VIII. [4x x (4x x 2x)] II OP

1. [W639 x (W643 x J)] II OP

IX. (4x clone) II OP

1. Platte II OP
2. W744 II OP
3. W760 II OP
4. W639 II OP

X. [4x x (4x-2x)] selfed

1. [W639 x (Platte x J)] selfed
2. [W582 x (W5293.3 x Kenn)] selfed
3. [W639 x (W643 x J)] selfed
4. [W639 x (W643 x J)] selfed
5. [W639 x (W643 x J)] selfed
6. [W639 x (W643 x J)] selfed

---

(6) I = clone I = W5295.7

Table 1 (continued):

XI. [4x clone] selfed

1. Merr. selfed
2. W639 selfed
3. W853 selfed
4. W744 selfed
5. W231 selfed

randomized complete block design with two replications.—Each family consisted of 14 hills and 20 hills per row in Hancock and Rhinelander, respectively. Distance between hills was 0.45 m at Hancock and 0.30 m at Rhinelander. Distance between rows was 0.90 m. Three transplants were placed in each hill initially and later thinned out to two.

1. Vegetative vigor, haulm uniformity and haulm maturity

Data on vigor and haulm uniformity were obtained during the growing period in the field using the following scales:

Vigor:
1 = good
2 = medium
3 = poor

Haulm uniformity:
1 = non-uniform (0-30% uniformity)
2 = semi-uniform (31 to 60% uniformity)
3 = uniform (61 to 90% uniformity)
4 = clonal uniformity (91 to 100% uniformity).

The measurement of haulm maturity was made at Hancock and Rhinelander at the time of harvest. Families were rated on the scale of 1 to 3, where:

1 = early
2 = medium
3 = late.

2. Tuber yields

The tuber yield of each family in each replication was weighed to the closest 1/4 lb, at harvest. Days to harvest were computed as the number of days from transplanting to harvest. Trials were harvested at 137 days at Hancock and 110 days at Rhinelander.

3. Statistical analysis

Two-way analysis of variance was performed for each location and combined over the two locations. Single degree of freedom comparisons were used to evaluate the differences in tuber yields between groups of progenies combined over the two locations.

RESULTS

A. Analysis of variance

Results from analyses of variance for tuber yield at Hancock and Rhinelander, and combined over the two locations are presented in Tables 2, 3 and 4, respectively. The analysis of variance combined over locations indicates that in terms of tuber yield, differences among families were highly significant. The same was found for locations, and for the interaction of families x locations. Non-significant differences were obtained for replications within locations.

The mean tuber yield, standard deviation and coefficient of variability for both Hancock and Rhinelander are listed in Table 5. Differences in mean tuber yields between the two locations were found, indicating a location effect on yield response which was expected, since more favorable environmental conditions for potato cultivation are present at Hancock compared to Rhinelander.

B. Tuber yields of TPS families

Mean tuber yields of the different groups of TPS families for Hancock and Rhinelander are presented in Table 6. For both locations, tuber yields of the groups of hybrids (groups I, II and III) were significantly higher than the groups of first and second generation open pollinated (groups IV through IX), and also the groups of selfed pollinated families (groups X and XI). The results of

Table 2. Analysis of variance for tuber yield of families at Hancock

Source	df	SS	MS	F
Total	113	696,534.70		
Replications	1	206,28	206.28	0.73
Families	56	680,464.85	12,151.16	42.89**
Error	56	15,863.57	283.28	

**Significant at the 0.01 level.

Table 3. Analysis of variance for tuber yield of families at Rhinelander

Source	df	SS	MS	F
Total	113	509,890.98		
Replications	1	902.86	902.86	4.27
Families	56	497,158.76	8,877.84	42.03**
Error	56	11,829.36	211.24	

**Significant at the 0.01 level.

Table 4. Analysis of variance for tuber yield of families combined over the two locations

Source	df	SS	MS	F
Total	227	2,055,219.99		
Families	56	1,047,917.49	18,712.80	75.68**
Locations	1	848,794.31	848,794.31	3,432.82**
Fam x Loc	56	129,706.12	2,316.18	9.37**
Rep (loc)	2	1,109.14	554.57	2.24
Error	112	27,692.93	247.26	

**Significant at the 0.01 level.

Table 5. Statistics for tuber yield of families at Hancock and Rhinelander

Location	Tuber yield mean (cwt/acre)	Standard deviation	c.v. (%)
Hancock	295.9	16.8	5.7
Rhinelander	173.9	14.5	8.4

Table 6. Mean tuber yields (cwt/acre) and horticultural traits for 11 groups of TPS families at Hancock and Rhinelander

		Mean yield	Range	Vigor	Haulm uniformity	Haulm maturity
I.	4x clone x 2x hybrid(1)					
	Hancock	390*	277-471	1.1*	2.5*	1.9*
	Rhinelander	256	173-343	1.4	2.1	2.2
II.	4x clone x 4x clone					
	Hancock	320	258-360	1.0	2.1	2.4
	Rhinelander	177	143-213	1.7	2.2	2.9
III.	[4x x (2x x 4x)] x 4x clone(2) (TDT x 4x clone)					
	Hancock	282	275-288	1.0	2.5	1.5
	Rhinelander	222	217-228	1.8	2	2
IV.	(4x clone x I) I OP(3)					
	Hancock	304	273-330	1.5	1.6	1.9
	Rhinelander	156	140-184	1.8	2	2.6
V.	(4x clone x 4x clone) I OP					
	Hancock	268	230-306	1.5	2	3
	Rhinelander	143	138-147	2	2	3
VI.	[4x x (4x x 2x)] I OP(4)					
	Hancock	263	243-287	2	1.8	1.5
	Rhinelander	149	131-159	1.8	1.7	2.8
VII.	(4x clone) I OP					
	Hancock	249	206-295	1.9	1.9	2
	Rhinelander	134	84-179	2.3	2	2.5
VIII.	[4x x (4x x 2x)]II OP(5)					
	Hancock	231		2	2	3
	Rhinelander	170		1.5	2	3

---

*Value is overall mean of families within the group.

(1) 2x hybrid includes: -clone I = W5295.7 a parallel spindle mutant clone
-synaptic-parallel spindle mutant clones.

(2) 2x = W5293.3

(3) I = clone I = W5295.7

(4) 2x includes: = clone I = W5295.7; -clone J = W5337.3

(5) 2x = clone J = W 5337.3

Table 6 (continued):

		Mean yield	Range	Vigor	Haulm uniformity	Haulm maturity
IX.	(4x clone) II OP					
	Hancock	240	222-265	1.8	2	2.3
	Rhinelander	134	111-169	2	1.8	2.5
X.	[4x x (4x x 2x)] selfed(6)					
	Hancock	208	178-233	1.8	1.6	1.8
	Rhinelander	106	92-121	1.8	1.7	2.6
XI.	(4x clone) selfed					
	Hancock	217	181-241	1.8	2.1	1.8
	Rhinelander	88	77-96	1.9	1.8	2.4

(6) 2x includes: -clone J = W5337.3; -W5293.3

comparisons between groups combined over the two locations are listed in Table 7.

Tuber yields of TPS families within groups are listed in Appendix A-1. The tuber yields of the best 20 families at each location are given in Table 8. Significant differences in tuber yield among families within group I occurred as tabulated in Table 8.

The diplandrous tetraploid families obtained from matings between 4x clones and 2x Phureja-haploid Tuberosum hybrids that form 2n pollen by FDR with or without crossing over (group I) had significantly higher tuber yields when compared to both 4x x 4x (group II) and TDT x 4x (group III) as indicated in Table 7. These families were also predominant amongst the higher yielding families for both locations (Table 8). Non-significant differences in tuber yields were found between 4x x 4x families (group II) and TDT x 4x families (group III) as indicated in Table 7.

With regard to the open-pollinated families, tuber yields of families from (4x x I) IOP (Group IV) were significantly higher yielding than all the other groups of first generation open pollinated families and approached the yields of hybrids at Hancock. Non-significant differences in tuber yields were found between groups of IOP (groups IV through VII) and IIOP (groups VIII and IX). Tuber yields from self-pollinated families (groups X and XI) were found to be the lowest amongst all groups as indicated in Table 7.

C. Vegetative vigor, haulm uniformity, and maturity

Results from visual observations of vegetative vigor and haulm

Table 7. Results of tuber yield comparisons between groups of TPS families combined over the two locations

-4x clone x 2x hybrid(1) vs. Rest	**
-4x clone x 2x hybrid vs. 4x clone x 4x clone	**
-4x clone x 2x hybrid vs. TDT x 4x clone	**
-4x clone x 4x clone vs. TDT x 4x clone	N.S.
-(4x clone x I)(2) I OP vs. [4x x (4x x 2x)] I OP(3)	**
-(4x clone x I) I OP vs. (4x clone x 4x clone) I OP	**
-[4x x (4x x 2x)] I OP vs. [4x x (4x x 2x)] II OP(4)	N.S.
-(4x clone) I OP vs. (4x clone) selfed	**
-[4x x (4x x 2x)] I OP vs. [4x x (4x-2x)] selfed(5)	**
-[4x x (4x x 2x)] II OP vs. [4x x (4x-2x)] selfed	**

**Significant at the 0.01 level.

N.S. = non-significant

(1) 2x hybrid includes: -clone I = W5295.7, a parallel spindle mutant clone; -synaptic-parallel spindle mutant clones.

(2) I = clone I = W5295.7.

(3) 2x includes: -clone I = W5295.7; -clone J = W5337.3.

(4) 2x = clone J = W5337.3.

(5) 2x includes: -clone J = W5337.3; -W5293.3.

Table 8. Mean yields (cwt/acre) of best 20 families.

	HANCOCK				RHINELANDER			
Rank	Parentage	Group	Mean yield(1)		Parentage	Group	Mean yield	
1	[W639x(PlattexJ)]xC-166(2)	I	471	a*	[W639x(W643xJ)]xC-166	I	343	a*
2	W639xI(3)	I	467	a	W639xC-166	I	312	b
3	Merr x C-39(4)	I	443	ab	[W639x(PlattexJ)]xC-39	I	291	bc
4	Merr x C-59(2)	I	438	ab	[W639x(W643xJ)]xC-77(2)	I	282	bc
5	Merr x I	I	424	b	[W639x(PlattexJ)]xC-59	I	280	c
6	[W639x(PlattexJ)]xC-39	I	419	b	Butte x I	I	276	c
7	W639 x C-166	I	377	c	Merr x C-59	I	270	c
8	W760 x I	I	375	c	Merr x C-39	I	267	c
9	W231 x I	I	374	c	[W639x(PlattexJ)]xC-166	I	257	cd
10	W853xW744	II	360	cd	Merr x I	I	249	cd
11	W853 x I	II	359	cd	[W639x(W643xJ)]xC-39	I	247	cd
12	W853xW639	II	352	cd	W853 x C-59	I	232	d
13	[W639x(W643xJ)]xC-39	I	349	cd	W639 x I	I	229	d
14	Butte x I	I	336	d	[W582x(W5293.3xKenn)]xW231	III	228	d
15	(W639xI) I OP	IV	330	d	Merr x C-166	I	221	d
16	Merr x W231	II	322	de	W853 x I	I	218	de
17	(W726xI) I OP	IV	321	de	[W582x(W5293.3xKenn)]xW853(5)	III	217	de
18	(W231xI) I OP	IV	292	e	W853 x W639	II	213	de
19	(W760xI) I OP	IV	273	e	W760 x I	I	209	de
20	(W760) II OP	IX	265	e	Merr x W853	II	188	e

*Means followed by the same letter are not significantly different at the 0.05 level.

(1) Value is mean of two replications.

(2) Synaptic-parallel spindle mutant clone obtained from I x J hybrids, where J = W5337.3.

(3) I = clone I = 2x Phureja-haploid Tuberosum hybrid, parallel spindle mutant clone.

(4) Parallel spindle mutant clone obtained from I x J hybrids.

(5) W5293.3 = 2x Phureja-haploid Tuberosum hybrid. W series = Wisconsin advanced breeding selections.

uniformity for all groups of TPS progenies at both locations are summarized in Table 6. Average values for these horticultural traits indicate that the hybrids (group I, II and III), regardless of their genetic background, had better vigor and haulm uniformity than any of the groups of either open pollinated (groups IV through IX) or self pollinated families (groups X and XI). The latter were consistently rated lowest for these horticultural characteristics at both locations.

The distribution in percent of families for classes of vigor and haulm uniformity for the groups of hybrids (groups I, II and III) combined over the two locations are presented in Tables 9 and 10, respectively. Sixty-four percent of the group I families and 50% of group II and III had good vigor at both locations. Similar distribution for the different classes of vigor were observed in the three groups of hybrids.

Families of groups I and II had similar distribution for the different classes of haulm uniformity. Seventy-seven percent of group I families, 80% of group II and 100% of group III occurred among the medium classes of this horticultural characteristic. Fifteen percent of group I families and 10% of group II were uniform. None of group III families were uniform.

The distribution in percent of families for classes of haulm maturity at Hancock and Rhinelander are listed in Table 11. Nineteen percent and 10% of the families at Hancock and Rhinelander, respectively, had early maturity. A higher frequency (56%) of late maturing families

Table 9. Distribution of families (%) in classes of vegetative vigor* among three groups of hybrids combined over the two locations.

	Group		
	I	II	III
Class	percent of families		
1	64	50	50
1.5	15	30	25
2.0	18	20	25
2.5	3	--	--
3.0	--	--	--

*Scale: 1 = good; 2 = medium; 3 = poor.

Table 10. Distribution of families (%) in classes of haulm uniformity* among three groups of hybrids combined over the two locations.

	Group		
	I	II	III
Class	percent of families		
1	--	--	--
1.5	8	10	--
2.0	65	60	80
2.5	12	20	20
3.0	15	10	--
4.0	--	--	--

*Scale: 1 = non-uniform (0 to 30% uniformity); 2 = semi-uniform (31 to 60% uniformity); 3 = uniform (61 to 90% uniformity); 4 = clonal uniformity (91 to 100% uniformity).

Table 11. Distribution of haulm maturity classes at Hancock and Rhinelander.

	Hancock		Rhinelander	
Class	No. of families	%	No. of families	%
Early	11	19	6	10
Medium	32	57	19	34
Late	14	24	32	56

was observed at Rhinelander as compared to Hancock (24%). Only groups V (4x x 4x) I OP and VIII [4x x (4x x 2x)] II OP were consistently late maturing at both locations. Variation in maturity classes was present among families within a group as indicated in Appendix A-1.

DISCUSSION

Results at both locations indicate that the 4x x 2x breeding method is the most efficient in the production of high yielding TPS families. In addition to higher tuber yields, the 4x progenies from 4x x 2x FDR with or without crossing over also had an outstanding degree of vegetative vigor, and higher values for haulm uniformity when compared to all other groups of TPS families. The large yields obtained were expected, since the 4x x 2x breeding scheme is suited to broaden the genetic base and maximize heterozygosity in the 4x progenies as result of the transmission of 80-100% of the heterozygosity and epistasis of the 2x hybrid parent to the 4x progeny via 2n pollen. Mok and Peloquin (1975b) when comparing tuber yields of 4x x 2x FDR, 4x x 2x SDR and 4x x 4x crosses, reported that the tuber yields of 4x x 2x FDR families were significantly higher than either 4x x 2x SDR or 4x x 4x matings. The study herein reported although not involving 4x x 2x SDR families, is in complete agreement with those results.

The 4x x 2x breeding method also appears to have a high level of practicality for TPS production. First of all, screening for 2n pollen production can be done easily and subsequently the 2n pollen producing 2x hybrids can be identified by their cytological mechanism of 2n pollen formation. Another consideration is the level of seed set following 4x x 2x crosses which is high at higher frequencies of 2n pollen. This could impose a restriction on the 2x hybrid parent in relation to the frequency of 2n pollen formation. Fortunately, this does not seem to represent a constraint, since considerable amounts of seeds per fruit are obtained even with frequencies of 2n pollen as low at 10% (Schroeder and Peloquin 1983).

Although data on total tuber yield from 4x x 2x crosses is encouraging, lower marketable yields compared to cultivars have been reported by De Jong and Tai (1977). This evaluation was based on the tuber appearance of the 4x progeny resembling 2x hybrid parents which have rough tubers. Hybrid 2x parents with improved horticultural traits are desirable for a broader utilization of this breeding method, but tuber appearance should not be regarded as a disadvantage, since the nutritional benefits that this scheme can provide to developing countries with generally insufficient diets when producing potatoes from true seed, by far surpass the arguments of less attractiveness of the tubers. Also in this regard, Schroeder (1982) has reported some 4x x 2x families with very satisfactory tuber type comparable to standard varieties in appearance. Thus, the full acceptability of this breeding method in developed countries with highly selective consumers does not seem far from being obtained.

When selecting 2x parents for further utilization in 4x x 2x crosses, segregating generations of 2x hybrid populations should be considered, since these will most likely be a good source for selecting materials with more favorable gene combinations. However, final selection should take into account the correlations between the performance of 2x parents and that of the 4x progeny.

Selection of the 4x seed parent should be based on good adaptability and on the number of fruits per plant and seed set obtained i.e. 4x cultivars with higher fruit and seed set are to be selected. Male sterility is also desirable, since this will largely increase the efficiency of the scheme by avoiding self-seed production. Recent results presented in Chapter II of this thesis, indicate that eight relatively male sterile clones producing an average of 152 open-pollinated seeds per fruit were found. This suggests the possibility that effective outcrossing might have taken place. Large scale production of 4x hybrids from 4x x 2x crosses at low cost using these clones could be achieved through the use of natural pollinators, the bumblebees.

Significant general combining ability among parents for total and marketable yield has been reported (McHale and Lauer 1981b, De Jong and Tai 1977), indicating that superior 4x progenies will be obtained from 4x x 2x crosses between parents with the highest average performance. Therefore, high general combining ability of the 4x seed parent appears to be desirable. This will also allow for further utilization of these materials in the future, as new selected 2x hybrid pollen parents are released. However, specific combining ability with certain 2x hybrid clones is also important, since this will provide elite combinations that could be rapidly adopted for TPS production.

Also, high yielding 4x hybrids can be selected and easily fixed by asexual propagation.

The overall vegetative vigor and haulm uniformity of the groups of open-pollinated TPS families I OP and II OP were lower than those observed in the hybrids similar to the results obtained for mean tuber yields. No control of pollen parent in the production of open-pollinated seeds exist, therefore I OP and II OP have the same probability of having been generated by either 2n pollen from a 2x hybrid or a normally reduced gamete of a 4x clone, depending on the type of materials surrounding the seed parents. If this constitutes a valid assumption, it could have accounted for the non-significant differences observed between I OP and II OP, since the latter are expected to exhibit less heterozygosity due to a higher probability of an increased degree of selfing. Also, the fact that the tuber yields of the (4x x 2x) I OP families approached those of the hybrids at Hancock, could be an indication that this OP seeds were produced mainly with 2n pollen, thus increasing the mean tuber yields above expectations.

In order to assure the highest degree of outcrossing in open-pollinated seed production, 4x cultivars with low male fertility and high seed set would be desirable. This would also contribute to increased tuber yields in OP TPS families.

The fact that self-pollinated progenies had the lowest tuber yields among all groups of TPS families, and also had lowest values for vegetative vigor and haulm uniformity, indicates that inbreeding rather than producing vigorous progenies had deleterious effects reflected on yield, vigor and uniformity. Busbice and Wilsie (1966) observed that in polysomic polyploids, inbreeding is greater in the early generations than would be predicted on the basis of the inbreeding coefficient in a two allele model. Mendiburu et al. (1974) indicated that in potato, inbreeding depression was explained as a consequence of the loss of inter- and intralocus interactions. Results herein presented from only one generation of selfing do agree with the theoretical explanations given.

As long as the screening for FDR 2n eggs will continue to involve difficult and time-consuming cytological work, the commercial production of TPS from 2x x 2x crosses with FDR gametes in both sexes, will still be far from having a practical application, although, maximum heterozygosity in the 4x progeny is achieved with this breeding scheme.

Breeding methods usually attempt to maximize heterozygosity in the generation used for commercial field production. The 4x x 2x FDR with or without crossing over scheme, is the best breeding method to meet this goal for production of potatoes from true seed. However, the full potential of this method will be achieved when multiple pest and disease resistance are combined with 2n gamete production in superior 2x hybrid parents for full transmission into the 4x progeny. This represents an optimal combination for the subsistence farmer of the developing countries with very scarce economical resources for potato production and to whom all efforts to achieve full applicability of the production of potatoes from true seed should be directed.

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Appendix A-1. Yield and horticultural traits of TPS families.

	Yield[1] (cwt/acre)	Vigor[2]	Haulm uniformity[2]	Haulm maturity[2]
I. 4x clone x 2x hybrid				
1. Butte x I				
Hancock	336	2	2	3
Rhinelander	276	2.5	2	3
2. W760 x I				
Hancock	375	1	2	1.5 seg[3]
Rhinelander	209	1	2	2 seg
3. W231 x I				
Hancock	374	1.5	2	1.5 seg
Rhinelander	173	1	1.5	2 seg
4. W853 x I				
Hancock	359	2	2	1
Rhinelander	218	2	1.5	1
5. W639 x I				
Hancock	458	1	2	1
Rhinelander	229	1	2	1
6. Merr x I				
Hancock	425	1	2	1.5 seg
Rhinelander	249	1.5	2	2 seg
7. Merr x C-59				
Hancock	438	1	3	1.5 seg
Rhinelander	270	1	2.5	2 seg
8. W853 x C-59				
Hancock	312	1	2.5	1.5 seg
Rhinelander	232	1.5	3	1.5 seg
9. Merr x C-39				
Hancock	444	1	2	3
Rhinelander	267	1	2	3

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(1) Value is mean of two replications.

(2) Value is mean of family rate for two replications.

(3) Seg = segregation for haulm maturity.

Appendix A-1 (continued):

	Yield (cwt/acre)	Vigor	Haulm uniformity	Haulm maturity
10. W639 x C-166				
Hancock	377	1	2	2 seg
Rhinelander	312	2	2	3
11. Merr x C-166				
Hancock	375	1	3	2 seg
Rhinelander	221	1.5	2	3
12. [W639x(PlattexJ)]xC-39				
Hancock	420	1	2	3
Rhinelander	291	1	1.5	3
13. [W639x(W643xJ)]xC-166				
Hancock	416	1	2	2 seg
Rhinelander	343	1	2.5	2.5 seg
14. [W639x(W643xJ)]xC-77				
Hancock	277	1	3	1
Rhinelander	282	2	2	1.5 seg
15. [W639x(PlattexJ)]xC-166				
Hancock	471	1	3	3
Rhinelander	257	2	1.5	3
16. [W639x(PlattexJ)]xC-59				
Hancock	416	1	2	2 seg
Rhinelander	280	1	2	3
17. [W639x(W643xJ)]xC-39				
Hancock	349	1	2	1
Rhinelander	247	1.5	2	1
II. <u>4x clone x 4x clone</u>				
1. W853 x W231				
Hancock	307	1	2	1.5 seg
Rhinelander	144	1.5	1.5	2.5
2. W853 x W744				
Hancock	360	1	2	3
Rhinelander	154	2	2	3
3. W853 x W639				
Hancock	352	1	2	3
Rhinelander	213	2	3	3

Appendix A-1 (continued):

		Yield (cwt/acre)	Vigor	Haulm uniformity	Haulm maturity
	4. Merr x W231				
	Hancock	322	1	2	3
	Rhinelander	185	1.5	2.5	3
	5. Merr x W853				
	Hancock	258	1	2.5	1.5 seg
	Rhinelander	188	1.5	2	3
III.	[4x x (2x x 4x)] x 4x clone = TDT x 4x clone				
	1. [W582x(W5293.3xKenn)]xW231				
	Hancock	288	1	2.5	2 seg
	Rhinelander	228	2	2	2 seg
	2. [W582x(W5293.3xKenn)]xW853				
	Hancock	275	1	2	1
	Rhinelander	217	1.5	2	2 seg
IV.	(4x clone x I) I OP				
	1. (W760 x I) I OP				
	Hancock	273	2	2	2 seg
	Rhinelander	140	2	2	3
	2. (W639 x I) I OP				
	Hancock	330	1	2	2 seg
	Rhinelander	184	1.5	2	2 seg
	3. (W726 x I) I OP				
	Hancock	321	1	1.5	1.5 seg
	Rhinelander	145	2	2	3
	4. (W231 x I) I OP				
	Hancock	292	2	1	2 seg
	Rhinelander	154	1.5	2	2.5 seg
V.	(4x clone x 4x clone) I OP				
	1. (W639 x Merr) I OP				
	Hancock	230	2	2	3
	Rhinelander	138	2	2	3
	2. (W231 x W639) I OP				
	Hancock	306	1	2	3
	Rhinelander	147	2	2	3

Appendix A-1 (continued);

		Yield (cwt/acre)	Vigor	Haulm uniformity	Haulm maturity
VI.	[4x x (4x x 2x)] I OP				
	1. [W639x(W231xI)] I OP				
	Hancock	243	2.5	1.5	2.5 seg
	Rhinelander	159	2	2	3
	2. [W639x(W643xJ)] I OP				
	Hancock	287	2	1.5	1
	Rhinelander	131	2.5	2	2.5 seg
	3. [W639x(W643xJ)] I OP				
	Hancock	251	2	2	2.5
	Rhinelander	147	2	1.5	3
	4. [W639x(W643xJ)] I OP				
	Hancock	271	2	2	1
	Rhinelander	158	1	1.5	3
VII.	(4x clone) I OP				
	1. (W744) I OP				
	Hancock	233	2	1.5	3
	Rhinelander	140	3	2	3
	2. (W760) I OP				
	Hancock	295	1.5	2	2 seg
	Rhinelander	133	2.5	2	3
	3. (W231) I OP				
	Hancock	235	2	2	2.5 seg
	Rhinelander	84	2.5	2	2 seg
	4. (W639) I OP				
	Hancock	253	2	2	1.5 seg
	Rhinelander	129	1.5	2.5	1
	5. (W853) I OP				
	Hancock	269	2	2	1.5 seg
	Rhinelander	105	2.5	1.5	2.5 seg
	6. (Merr) I OP				
	Hancock	252	2	2	2 seg
	Rhinelander	179	2	2	3

Appendix A-1 (continued):

		Yield (cwt/acre)	Vigor	Haulm uniformity	Haulm maturity
7.	(T-874) I OP				
	Hancock	206	1.5	2	1.5 seg
	Rhinelander	170	2	2	3
VIII.	[4x x (4x x 2x)] II OP				
1.	[W639x(W643xJ)] II OP				
	Hancock	231	2	2	3
	Rhinelander	170	1.5	2	3
IX.	(4x clone) II OP				
1.	(Platte) II OP				
	Hancock	236	2	2	1.5 seg
	Rhinelander	169	1.5	2	1
2.	(W744) II OP				
	Hancock	222	2	2	3
	Rhinelander	131	2	1.5	3
3.	(W760) II OP				
	Hancock	265	1	2	2.5 seg
	Rhinelander	111	2.5	2	3
4.	(W639) II OP				
	Hancock	237	2	2	2 seg
	Rhinelander	126	2	2	3
X.	[4x x (4x x 2x)] selfed				
1.	[W639x(W643xJ)] selfed				
	Hancock	233	2.5	1.5	3
	Rhinelander	110	1.5	1.5	3
2.	[W582x(W5293.3xKenn)] selfed				
	Hancock	201	2	1	1
	Rhinelander	104	2	1	1
3.	[W639x(W643xJ)] selfed				
	Hancock	184	2.5	1.5	1.5 seg
	Rhinelander	92	1.5	2	3
4.	[W639x(W643xJ)] selfed				
	Hancock	223	1	2.5	2 seg
	Rhinelander	101	2.5	2	3

Appendix A-1 (continued):

		Yield (cwt/acre)	Vigor	Haulm uniformity	Haulm maturity
	5. [W639x(W643xJ)] selfed				
	Hancock	178	2	1.5	1
	Rhinelander	108	2	1.5	2.5 seg
	6. [W639x(W643xJ)] selfed				
	Hancock	228	1	1.5	2 seg
	Rhinelander	121	1.5	2	3
XI.	(4x clone) selfed				
	1. (Merr) selfed				
	Hancock	217	1	1.5	2 seg
	Rhinelander	86	2	1.5	2.5 seg
	2. (W639) selfed				
	Hancock	231	2	2.5	2 seg
	Rhinelander	77	1.5	2	3
	3. (W853) selfed				
	Hancock	241	2	2	1
	Rhinelander	89	1	2	1.5
	4. (W744) selfed				
	Hancock	215	2	1.5	1
	Rhinelander	94	2.5	2.5	2 seg
	5. (W231) selfed				
	Hancock	181	2	1.5	3
	Rhinelander	96	2.5	1	3

CHAPTER II.

FACTORS INVOLVED IN OPEN-POLLINATED TRUE POTATO SEED PRODUCTION

INTRODUCTION

McGregor (1973) pointed out that probably less than one percent of the world's food supply depends upon insect pollination. According to his estimates, one-third of the total diet in developed countries is derived either directly or indirectly from insect pollinated plants. Therefore, as the diet of the developing countries improves in quality, an increase in dependence on pollinating insects may be expected.

The extent of use of hybrid seed depends mainly on controlled pollinations to produce the seed. In crops such as carrot and onions, successful hybrid seed production is currently achieved through the utilization of honey bees as pollinators (Free 1970). However, failures have been reported using pollinating insects. Usually, they result from the lack of knowledge of the behavior of the pollinator in regard to the biological characteristics of the parental materials (Erickson 1982). Thus, understanding the complexities of pollinator foraging behavior and the pollinating requirements of the seed parents is of utmost importance in the development of entomophilous hybrid seed production programs.

MacArthur (1972) reported that insects when gathering food, encounter a wide spectrum of resources, from which they select to forage the species where the expectation of yield for the bee is greatest. He also emphasized that in certain situations insects are forced to expand their feeding habits and diets when resources are limited due to either seasonal variations in flowering or competition from other foragers. Alford (1975) indicates that bumblebees select plants where the yield expectation of pollen or nectar are highly desirable, but with no consistent specialization on either nectar or pollen over a long period of time. In one foraging flight, predominant pollen gatherers will also collect nectar. In potato, bumblebees act as pollen gatherers and are recognized as pollinators of this crop (Free 1970). Buchmann (1977, 1982) described an effective mode of pollination used by bees while foraging on flowers having anthers with terminal dehiscence as in Solanum species. This form of pollination has been termed "buzz pollination," since it characterizes the audible buzz component of bee behavior during the flower visitation. Bees which are able to buzz (i.e. bumblebees), first land on the corolla or directly on the anther cone, then grasp the stamens tightly, with their wings held stationary over the thorax and abdomen. By rapidly contracting and relaxing their flight muscles they transmit vibrations which cause the entire flower to vibrate, resulting in rapid expulsion of most pollen grains from the anthers pores onto the abdomen of the bee. The existence of an electrostatic field around the bee at the time of the visit has been proposed to explain the efficiency of this type of pollen collection (Buchmann and Hurley 1978). Buzz pollination is extensively utilized by bumblebees when visiting potato flowers.

Sanford and Hanneman (1981) tested the possibility of using domestic honey bees for intermating potato species. The behavior of the bees was observed before and after applying honey to some of the flowers to encourage visitation. The presence of this "attractant" induced the bees to visit flowers but only for a short period. Honey bees did not collect pollen and were not observed using buzz pollination. Since no fruits developed with this attempt, it was concluded that domestic honey bees are not suitable for intermating Solanum species. Supporting these results, Buchmann (1982) has reported that honey bees are physiologically incapable of using buzz pollination; therefore will not likely act as pollinators in potatoes.

The flower-visitor relationship is established by means of attractants which start a reaction chain in the bee that creates an urge, such as feeding. Primary attractants are considered pollen and nectar, secondary attractants are odor and visual attraction (Faegri and van der Pijl 1979).

Pollen, as a floral reward, is apparently more selective than nectar in attracting bees (Buchmann 1982). According to Lepage and Boch (1968), some lipids act as phagostimulants for pollen recognition in some bees. Honey bees are able to discriminate among feeding sources, and frequently show a high level of constancy in time for a given source (Grant 1950). Erickson and Peterson (1978), when studying the production of seeds by several male sterile and male fertile carrot lines, observed marked differences within genotypes of the carrots in seed setting ability. These differences were associated with non-random foraging activity of honey bees due to their preference and constancy to certain carrot lines. Parents selected for entomophilous hybrid seed production should therefore offer similar means of attraction to the pollinator in order to avoid reductions in seed set and to increase outcrossing. Secondary attractants such as odor and visual attraction may play different roles in increasing visitation, however, odor when present seems to be more important (Faegri and van der Pijl 1979).

Presently, in potato large scale intermatings must be done by hand or by the uncontrolled activity of bumblebees. The full applicability of the technology of production of potatoes from true seed (TPS) in developing countries requires, besides the development of appropriate breeding methods, practical and economical large scale controlled intermatings of tuber-bearing Solanums by bumblebees in order to obtain the desired tetraploid hybrids. Peloquin (1982) proposed breeding methods for TPS production suited to obtain highly heterozygous and uniform 4x progenies from 2x x 4x and 4x x 2x crosses by using 2x parents capable of producing 2n gametes via first division restitution (FDR) mechanism. The 2x x 4x breeding method is designed to generate hybrid TPS progenies using bumblebees as pollinators. The male fertility and self incompatibility system of the 2x parent would offer enough pollen to attract the bees and prevent self-seed production. Moreover, the ability of the 2x parent to produce high frequency of 2n eggs would result in higher seed set. Effective outcrossing will be assured by the high degree of male fertility of the 4x pollen parent. All seed produced on the 2x parent by this breeding method will be therefore tetraploid and of hybrid origin.

To complement the potential of this method, studies on the foraging behavior of bumblebees in a potato field, and the means of attraction establishing an effective flower-pollinator relationship are required in order to apply this knowledge in potato hybrid seed production.

Data on amount of flowering, percent stainable pollen, fruits per plant and seeds per fruit were obtained in an attempt to determine the relationship between these variables in the production of TPS under field conditions.

This research was undertaken to obtain initial information about the behavior of bumblebees when intermating potatoes, and to establish the relative efficiency of different potato clones for production of open-pollinated seeds.

MATERIALS AND METHODS

The experiments were initially conducted at both Hancock and Rhinelander Experiment Stations, during the summer of 1982. Due to the poor bumblebee activity during the flowering season at Hancock, only the data obtained at Rhinelander will be considered.

A. Experimental materials.

One-hundred and eighty potato clones, representing cultivars and advanced selections particularly from the Wisconsin Potato Breeding project involved in a yield trial in a randomized complete block design with two replications provided the plant materials for this experiment. These clones are listed in Appendix B-3.

Four clones were present more than once in each replication. These were treated as separate materials in the yield trial and in this experiment, since the origin of the tubers for planting were from different sources. The total number of entries included in this experiment were therefore 190. Each replication consisted of 20 plants 0.30 m apart. The distance between each 20 hill unit was 1.20 m and the distance between rows was 0.90 m.

B. Field observations

1. Bumblebee behavior in a potato field

Procedures adopted to observe the behavior of bumblebees were to locate a bee during a foraging flight and follow it along the field until the flight was completed. All data was obtained using a portable cassette recorder in order to avoid distraction from watching the bee by having to write notes. Fifteen foraging flights were recorded. The foraging pattern between plants was observed in order to determine flower color preference if any, and average working time per flower based on 50 flowers. Time of day and general sky conditions were also recorded.

2. Manual transfer of pollen

Fresh pollen from clones producing a large amount of fruit was applied to anthers of male sterile plants, but having flowers with normal appearance, in order to observe if this procedure would encourage bee visitation to the male sterile clones. Pollen was either placed on the surface of the anthers or into a gelatin capsule attached to the anthers to avoid wind dispersal.

3. Odor

Flower odor was determined in the field by smelling five to ten flowers of each clone in both replications. The following scale was used: 0 = no odor detected; + = odor detected.

Flowers from five *Solanum* hybrid species growing under greenhouse conditions were also utilized to detect the origin of odor within the potato flower. Procedures and results obtained are presented in Appendix B-1.

4. Flowering

Visual observations to estimate the amount of flowering in each clone were made in a three week period when more than half of the clones were flowering. The following scale was used:

0 = no flowering
1 = poor flowering
2 = medium flowering
3 = good flowering.

C. Pollen stainability

During the flowering period, three open flowers were picked at random from each clone in each replication and put into a coin envelope. Following transportation to the laboratory, pollen was obtained from each of the three flowers using a vibrator, to put the pollen onto a clean glass slide. It was stained with an aceto-carmine-glycerol solution and scored for pollen stainability. Percent stainable pollen was calculated based on observation of at least 400 pollen grains. Only plump, evenly stained pollen grains were scored as stainable pollen. Data was not obtained from clones that did not flower, or had very little pollen.

D. Fruit set

Data on fruit set were obtained from the first and end hill of each 20 hill plot. To prevent fruit loss, all naturally pollinated inflorescences were wrapped with cheesecloth after the starting of fruit enlargement. Fruits of each replication were harvested at approximately four weeks following natural pollination. The number of fruits on two plants in each clone and each replication were counted, therefore the fruit number figure represents the number of fruit on two plants.

E. Seed set

Six fruits of each clone from each replication were selected at random to obtain data on seed set. Seeds were extracted and counted on an individual fruit basis. Seeds were not extracted from dried fruits. In clones where all fruits had dried up, no data was obtained. These probably represented fruits with a very low number of seed.

F. Statistical analysis

Simple correlations were determined between percent pollen stainability and seed set, between pollen stainability and fruit set, and between fruit set and seed set. A multiple correlation was also calculated for these three variables. Linear regressions for these variables were also obtained and a linear regression line was fitted for each case. Pollen samples were grouped by classes of percent pollen stainability, i.e. 0-1.9; 2-3.9 etc. and plotted against their respective mean values of fruit set and seed set. All data was analyzed using programs of the Minitab computer located at the Dairy Science Computer Center, University of Wisconsin.

RESULTS AND DISCUSSION

A. Bumblebee behavior in potato fields

1. Time of day

A peak of bumblebee activity in the field was usually observed from 10:30 AM till noon under sunny and clear skies. A consistent decline in activity was observed associated with high temperatures. Under conditions of cloudy skies and rain bumblebees either had little activity or were absent. The same low level of activity was observed early in the morning and after sunset.

2. Average visit time per flower

Observations on mean visit time per flower of bumblebees in potato clones from 15 foraging flights expressed in seconds/flower are presented in Table 1. Data from each flight was obtained by dividing the total time spent while visiting 50 potato flowers. The overall mean time was calculated as 4.7 seconds per flower.

3. Visual attraction

Visual attraction by means of flower color was not observed in any of the foraging flights. All suitable flowers regardless of their color were equally visited suggesting that this was not an important factor in the attraction process.

4. General flight pattern

Figure 1 summarizes the results of visual observations on 15 foraging flights of bumblebees when visiting a potato field. Upon arrival to a row (see IN), bumblebees will first make several circular observatory flights around one or two inflorescences. If

Table 1. Mean visit time per flower of bumblebees in potato clones.

Number of flights	Mean time per flower* (sec/flower)
1	4.4
2	4.9
3	5.1
4	4.3
5	5.3
6	4.7
7	4.6
8	4.5
9	4.8
10	4.7
11	4.5
12	4.8
13	4.7
14	4.5
15	4.7

Overall mean = 4.7 sec/flower

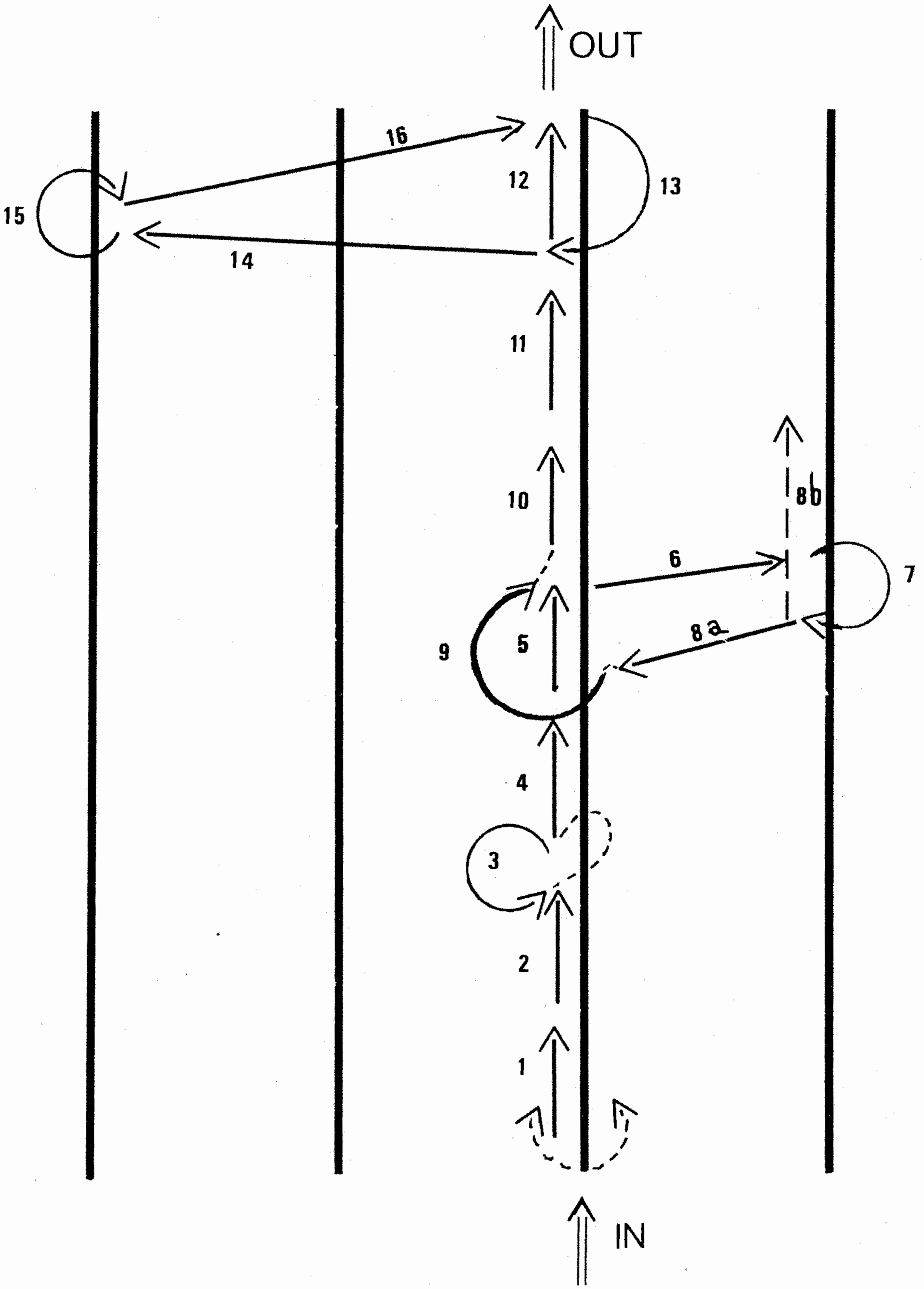
*Data based on 50 flowers.

FIGURE 1

GENERAL FORAGING PATTERN OF

BUMBLEBEES IN A POTATO FIELD

-Parallel lines represent rows of potato clones.
-Numbered arrows indicate the direction of the flight.
-Circular flights are indicated by curve arrows.


OUT
16
12
13
15
14
11
10
8b
6
7
9
5
8a
4
3
2
1
IN

found attractive, the bee will start the foraging flight plant by plant working every suitable flower in each inflorescence. In all cases, higher inflorescences were worked first. While working in one row, the bee may change to a different row (position N°6) but always moving in one direction.

If this new row is found more attractive, the bee will temporarily switch to this working position (position N°8b). Once this area is visited, the bee will return to the previous row, to the same position from which it departed (position N°5) and continue working here in the same direction. The same returning pattern was observed if the bee did not find the row rewarding enough to be worked (position 7 and 8a). Before leaving each row several circular flights are made (position N°13) around the last plant. The bee may also fly to the adjacent row or two to three rows away (position N°14) from where, after making several observatory circular flights it returns to finish working the last plant (position N°12), and finally the bee moves to a different row, or leaves the field.

4a. Inflorescence working pattern in potato

The bumblebee approaches the inflorescence by circular flights in order to determine if it is rewarding enough to start a foraging flight. In order to harvest the pollen, a bee will first land on the anther cone, its body weight making the flower hang downwards. By vibrating the anthers, the pollen is discharged from the terminal pores, and falls on the abdomen of the bee. Later while moving to another flower, the pollen obtained is brushed from the abdomen to the corbiculum. This process was also observed while the bee works a flower that offered enough pollen to extend the visitation.

B. Manual transfer of pollen

All attempts to encourage bee visitation by manually transferring pollen from a male fertile clone to a male sterile clone resulted in complete failure. Rather than being encouraged, bees indicated no interest in working the flowers with pollen from a male fertile clone.

C. Odor

Field data on flower odor for potato clones is presented in Table 2. Odor was detected in 29% of the clones. Results from greenhouse experiment presented in Appendix B-1 indicate that the odor of potato flowers when present, originates from the anthers. Relatively large amounts of fruit and seed set were obtained from clones with different values for percent pollen stainability, regardless of the presence of flower odor (Table 3). Odor was also detected in some clones with very low percent pollen stainability.

D. Flowering

Results of amount of flowering for all clones are presented in Table 4. Only two percent of the clones did not flower, and 12% had poor flowering. Overall flowering was therefore good at Rhinelander. This would most likely increase the probability of obtaining a large number of open pollinated fruits in the field. However, despite the good flowering observed in some clones, their corresponding values for fruit set were low, as indicated in Table 5.

Table 2. The presence of odor in flowers from potato clones at Rhinelander.

Odor class	Number* of clones	%
Odor detected	54	29
No odor detected	133	71
TOTAL	187	

*Three clones did not flower.

Table 3. Percent pollen stainability, seeds per fruit, fruit set and flower odor characterization of 20 potato clones.

Clone	Percent pollen stainability	Seeds per fruit	Number of fruits from two plants	Odor*
W744	34.1	296	309	+
W780	29.1	225	269	0
W793	10.7	105	100	0
W815	9.2	159	108	+
W824	6.5	153	108	+
W847	4.6	112	81	0
W861	13.0	266	122	0
W862	33.5	255	436	0
W870	2.5	117	95	0
W877	30.4	283	89	+
W879	29.6	348	189	0
W882	16.4	277	158	0
W883	45.1	275	99	0
W76-11	6.5	134	161	0
W76-13	17.4	278	139	0
W76-15	2.9	234	93	+
W76-16	1.9	117	129	0
W76-29	22.9	224	101	0
W76-32	22.6	300	99	+
W76-56	9.3	192	146	0

*Scale: + = odor detected; 0 = no odor detected.

Table 4. Amount of flowering in potato clones at Rhinelander.

Flowering	Number of clones	%
Good	128	67
Medium	37	19
Poor	22	12
No flowering	3	2
TOTAL	190	

Table 5. Percent pollen stainability, fruit set and flowering of 12 selected potato clones.

Clone	Percent pollen stainability	Number of fruits from two plants	Flowering*
W907	22.9	39	3
Butte	2.6	10	3
W76-44	23.8	41	3
Chipbelle	7.9	27	3
W76-33	8.0	26	3
R. Pontiac	17.2	4	3
W76-4	18.5	44	3
Lemhi	7.7	23	3
W831	18.1	29	3
W742	14.7	24	3
W623	2.5	14	3
W809	4.4	17	3

*Scale: 0 = no flowering; 1 = poor; 2 = medium; 3 = good.

E. Pollen stainability, fruit set and seed set

General data for percent pollen stainability, fruit set and seed set are presented in Appendix B-3. Distribution of percent pollen stainability for potato clones is presented in Table 6. Forty-eight percent of the clones had between 10-40% pollen stainability and 52% had less than 10% stainable pollen.

Fruit set varied from 0-477 fruits per clone (two plants in one replication) with an overall mean of 65 fruits. Seed set varied from 0-400 seeds per fruit with an overall mean of 140 seeds. Parthenocarpic fruits were obtained from 2% of the clones, but none of these clones had many fruit.

The mean seed set and fruit set by classes of percent stainable pollen are indicated in Table 7. Seeds per fruit averaged 111.2 when the percent of stainable pollen was 10% and below, indicating that practical levels of seed set for open pollinated seed production were obtained. Even below 5% stainable pollen, the average seeds per fruit was 88.1. Mean fruit set per clone was low at this level of percent stainable pollen. However, relatively male sterile clones with high values for mean seed set and fruit set were detected (Table 8). This suggests the possibility that the efficacy of insect pollinators increased the levels of cross-pollination and facilitated seed set in these clones.

Linear correlation coefficient values for seed set and percent stainable pollen; fruit set and seed set; fruit set and percent stainable pollen, and multiple correlation coefficient for these

Table 6. Distribution of percent pollen stainability for potato clones at Rhinelander.

Percent pollen stainability	Number of clones*	Percent of clones
<10%	95	52
10-20%	48	27
20-40%	36	20
>40%	2	1
TOTAL	181	

Range = 0.1-45.1%.

*Data was not obtained from clones that did not flower or had very little pollen.

Table 7. Mean seed set and fruit set by classes of percent pollen stainability.

Classes of percent pollen stainability	Number of clones*	Mean seeds per fruit	Mean number of fruits
0-1.9	27	100	16
2-3.9	20	101	37
4-5.9	9	91	9
6-7.9	9	143	55
8-9.9	14	121	50
10-11.9	6	148	33
12-13.9	9	110	42
14-15.9	6	110	77
16-17.9	13	125	68
18-19.9	12	171	56
20-21.9	4	174	60
22-26.9	14	196	77
27-31.9	12	130	116
32-41.9	5	190	186
42-45.9	2	170	88

*Data was not obtained from clones where fruits had dried up.

Table 8. Seed set, fruit set and odor of eight selected clones with low percent pollen stainability.

Clone	Percent pollen stainability	Mean seeds per fruit	Number of fruits from two plants	Odor
W76-15	2.9	234	93	+
W76-56	9.3	192	146	0
W815	9.2	159	108	+
W824	6.5	153	108	+
W76-11	6.5	134	161	0
W76-16	1.9	117	129	0
W870	2.5	117	95	0
W847	4.6	112	81	0

Table 9. Correlations between seed set, fruit set and percent pollen stainability.

	Percent pollen stainability	Seed set	Fruit set
Seed set (y)	0.311**		
Percent pollen stainability (x_1)			0.479**
Fruit set (x_2)		0.28**	

Multiple correlation $R_{yx_1x_2} = 0.343$

**Significant at the 0.01 level.

variables are presented in Table 9. A modest linear positive correlation ($r = 0.479$) was found only for fruit set and percent stainable pollen. Results from regression analysis are presented in Appendix B-2.

The following graphs illustrate the relationships between: seed set and percent stainable pollen (Figure 2); fruit set and percent stainable pollen (Figure 3); and seed set and fruit set (Figure 4). Significant relationships were found in all cases.

Considerable variation in mean seed set at all values of percent pollen stainability and fruit set were found. The differences in magnitude of the standard error bars illustrated in Figures 5 and 6, respectively, indicate the extent of this variation. The mean seed set from 18.0-45.9% pollen stainability was significantly higher than the mean seed set from 0-9.9% (t-Test significant at the 0.01 level). The increase in seed set observed from 18.0-45.9% pollen stainability may be due to an increase in self-seed production, whereas the seed set observed from 0-9.9% could be an indication of effective outcrossing..

The coefficients of determination (r^2) presented in Appendix B-2, indicate that percent pollen stainability accounted for 9.6% of the variation in seed set. Fruit set accounts for only 7.8%. Percent stainable pollen and fruit set jointly accounted for 11.8%. Other factors different from those involved in this study seem to account for most of the variability observed in seed set.

FIGURE 2

RELATIONSHIP BETWEEN SEED SET

AND POLLEN STAINABILITY

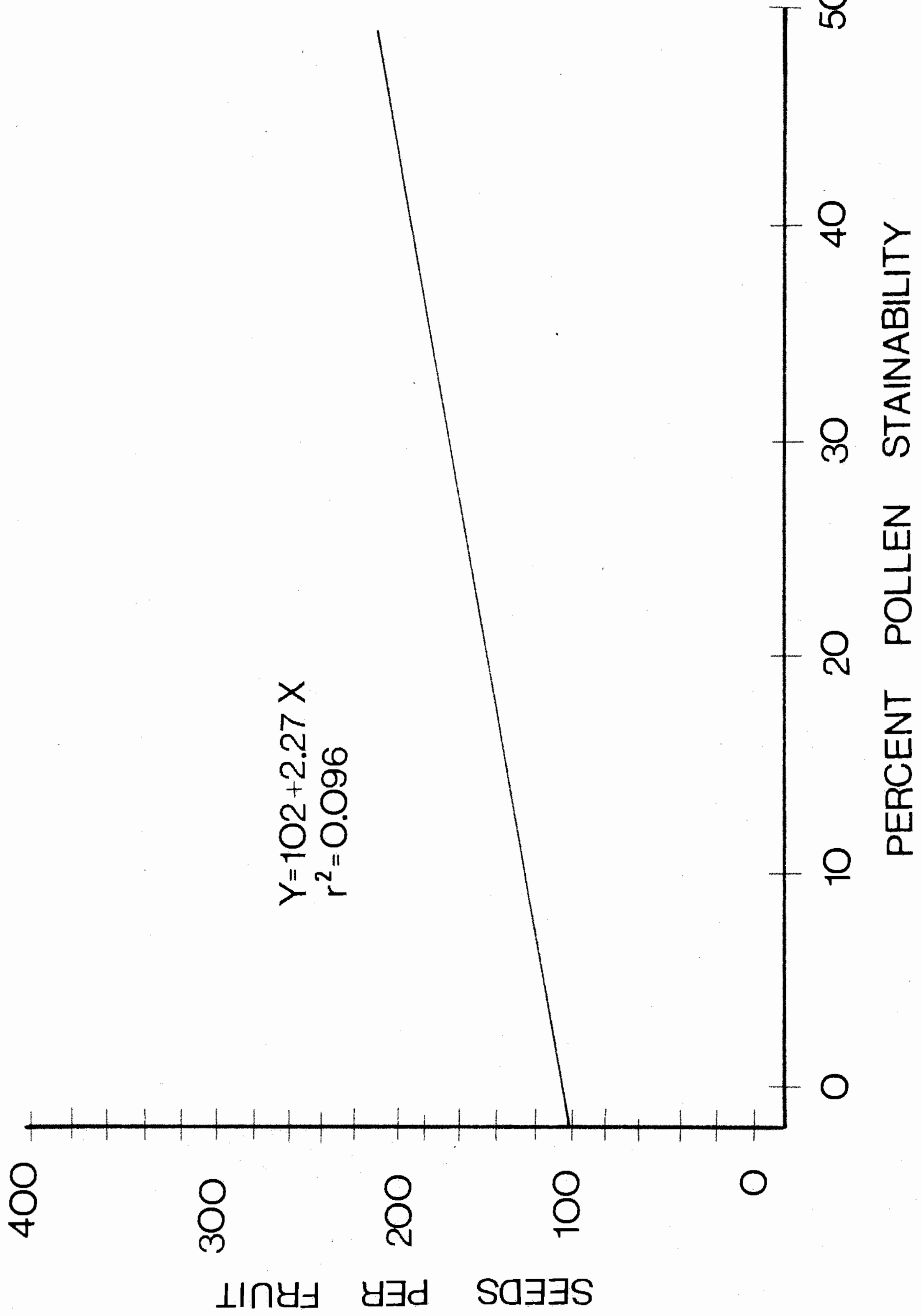

Y=102+2.27 X
r^2=0.096
SEEDS PER FRUIT
400
300
200
100
0
PERCENT POLLEN STAINABILITY
0
10
20
30
40
50

FIGURE 3

RELATIONSHIP BETWEEN FRUIT SET AND

PERCENT POLLEN STAINABILITY

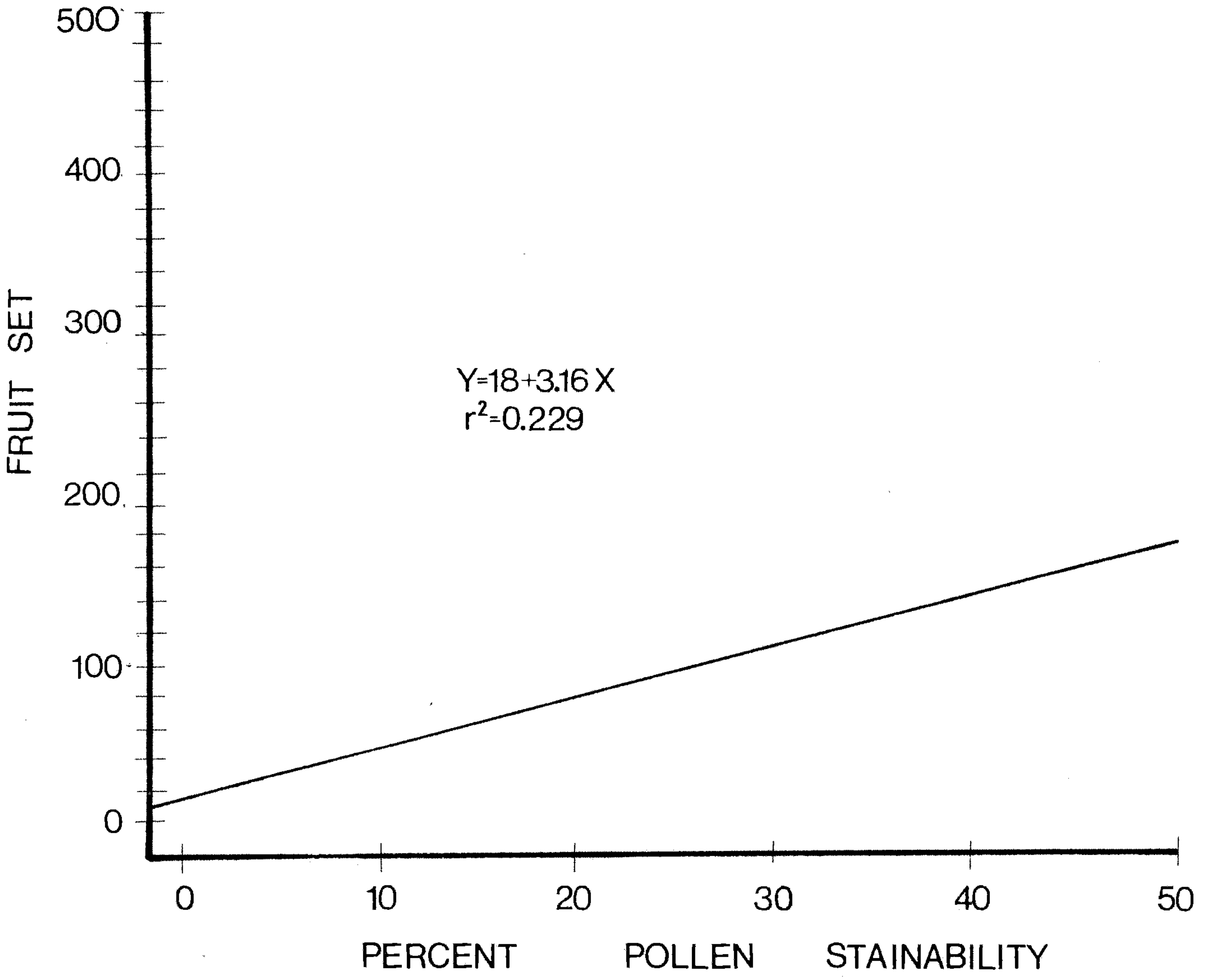

500
400
300
200
100
0
FRUIT SET
Y=18+3.16 X
r²=0.229
0
10
20
30
40
50
PERCENT POLLEN STAINABILITY

FIGURE 4

RELATIONSHIP BETWEEN SEED SET

AND FRUIT SET

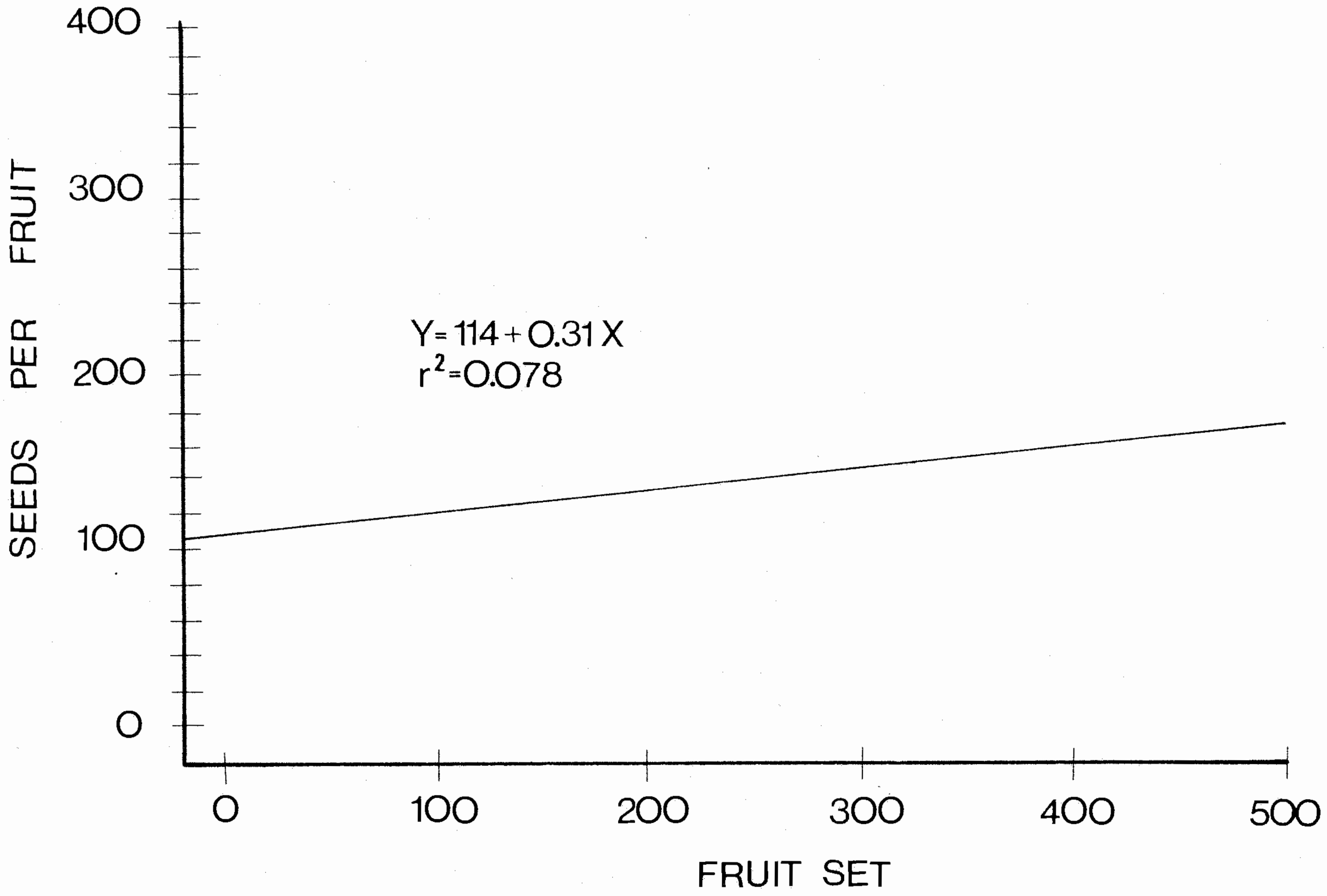

400
300
200
100
0
SEEDS PER FRUIT
Y= 114 + 0.31 X
r^2=0.078
0
100
200
300
400
500
FRUIT SET

FIGURE 5

VARIATION IN SEED SET IN RELATION

TO PERCENT POLLEN STAINABILITY

Means were determined after grouping seed set by class of percent pollen stainability (i.e. 0-1.9%, 10-11.9% . . . 42-45.9% pollen stainability).

*The value of the mean is based on the number of clones indicated in the numerator and the number of clones that either did not set fruit or dried up before harvesting the seed are indicated in the denominator.

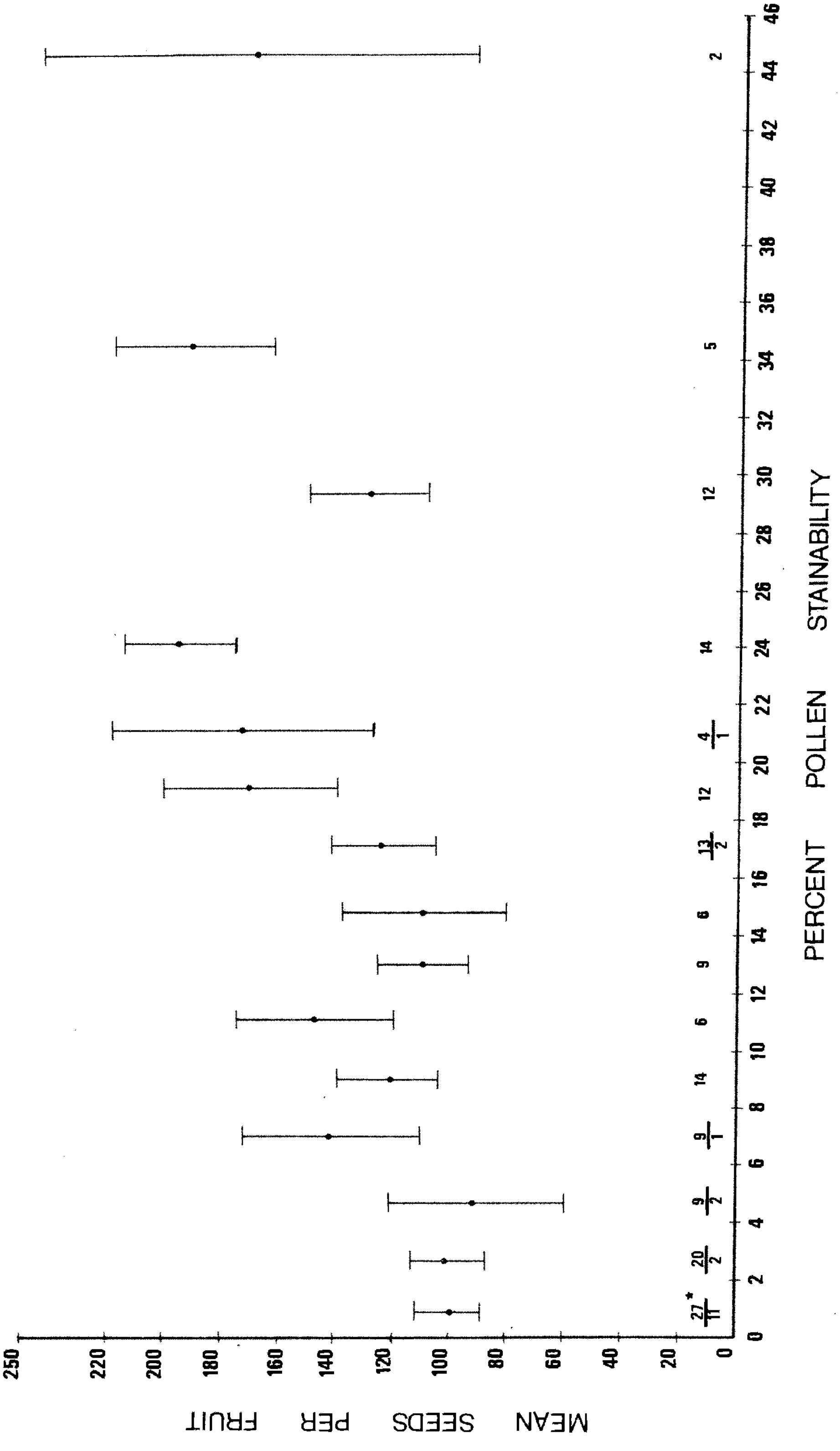
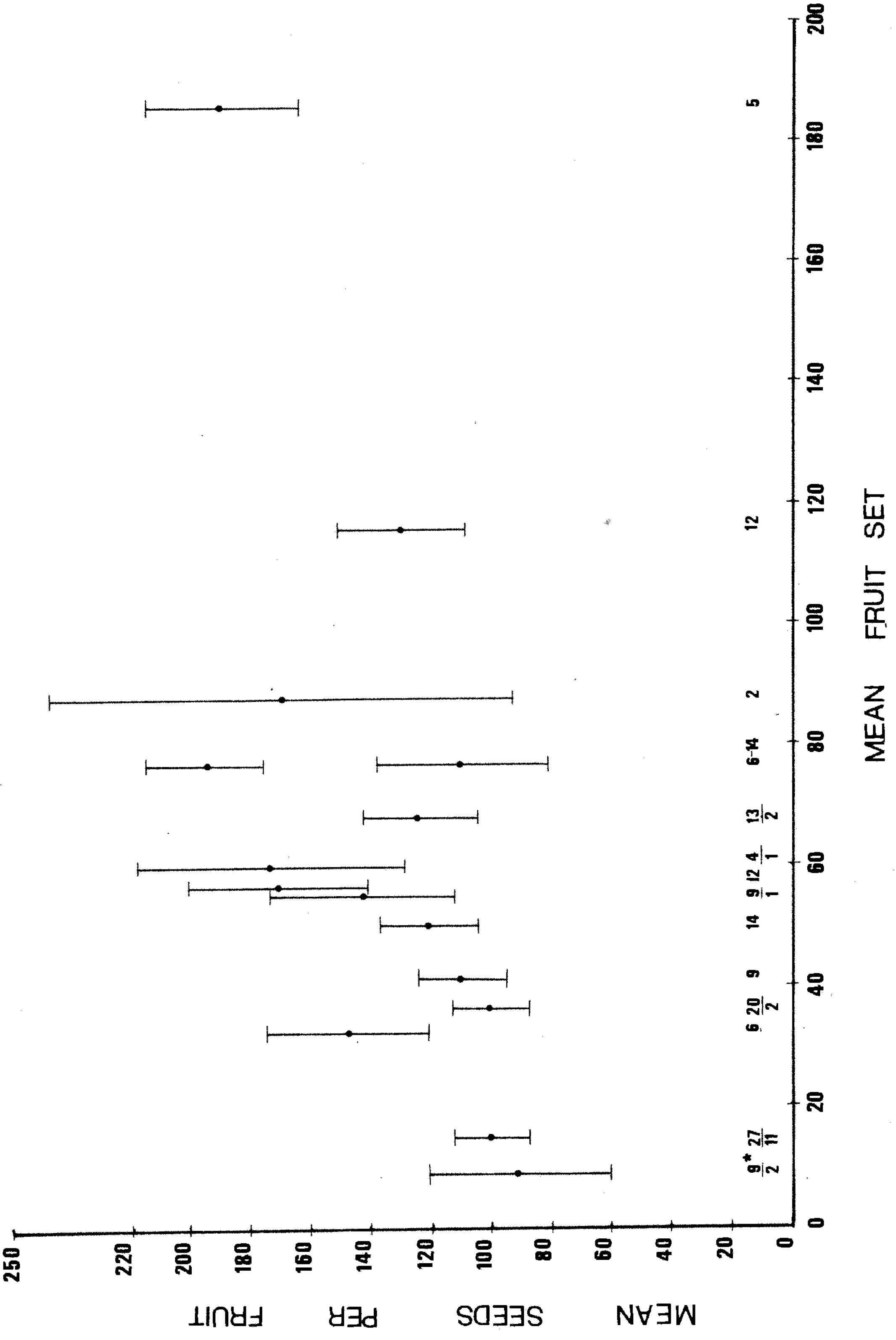

MEAN SEEDS PER FRUIT
0
20
40
60
80
100
120
140
160
180
200
220
250
PERCENT POLLEN STAINABILITY
0
2
4
6
8
10
12
14
16
18
20
22
24
26
28
30
32
34
36
38
40
42
44
46
27*/11
20/2
9/2
9/1
14
6
9
8
13/2
12
4/1
14
12
5
2

FIGURE 6

VARIATION IN SEED SET IN RELATION TO FRUIT SET

*The value of the mean is based on the number of clones indicated in the numerator and the number of clones that either did not set fruit or dried up before harvesting the seed are indicated in the denominator.


MEAN FRUIT SET
MEAN SEEDS PER FRUIT
0
20
40
60
80
100
120
140
160
180
200
0
20
40
60
80
100
120
140
160
180
200
220
250
9*/2
27/11
6
20/2
9
14
9/1
12
4/1
13/2
6-14
2
12
5

GENERAL DISCUSSION

Increases in percent stainable pollen or fruit set were not found to account fully for the variability observed in seed set, as indicated by the low correlation coefficient values obtained (Table 9).

Schroeder and Peloquin (1983) explained that on the female side, several factors could contribute to the variation in seed set. These include differences in nutritive support within the inflorescences and differences in viability of the ovules in the ovary. Environmental factors such as temperature and relative humidity acting at the time of pollination were also emphasized. In the study herein reported, another factor contributing to the differences in seed set could be the existence of effective means of insect attraction originating from the potato flower, optimizing the pollinator-flower relationship and allowing for higher seed set to occur in certain clones.

Although general observations made by other authors indicate that bumblebees do not regularly visit male sterile flowers, eight male sterile or almost male sterile clones were found that produced an average of 115 fruits for two plants and 152 seeds per fruit (Table 8). This indicates that male sterility was not always an adverse factor in the natural pollination process. Bumblebees did visit a few male sterile clones. It is important to point out also that no parthenocarpic fruits were found in these clones. Moreover, the probability of selfing is very low considering their values for percent stainable pollen.

This is an indication that effective natural cross-pollination has taken place, therefore a high percent of the open pollinated seed if not all will be expected to be of hybrid origin.

The selection of these clones based on their values for seed set and low percent of pollen stainability for further utilization in TPS production appears highly feasible.

One of the breeding methods for TPS production using natural pollinators proposed by Peloquin (1982) could thus be used. This would involve the utilization of selected 4x male sterile cultivars in large scale synthesis of 4x progeny by 4x x 2x crosses. Bumblebees will effectively pollinate the seed parent avoiding the need of using hand pollinations. Low cost hybrid seed for utilization in production of potatoes from true seed will be therefore available. Selection of the 2x hybrid parent should consider those normally giving high seeds per fruit in 4x x 2x crosses.

An important factor for the economical production of hybrid seed is the knowledge of the optimum planting design to encourage effective large scale intermatings. Erickson, cited by Sanford and Hanneman (1981) reported that the tendency of bees to work up and down rows would prevent or reduce mating between rows of different plants. The observations made on bumblebee behavior in the present study indicate that although the tendency of the foraging flights were always in the same direction within the row, an effective between row foraging pattern was also observed if the adjacent rows were attractive enough to be worked. Future planting designs for hybrid seed production, if to be successful, should consider not only the most efficient planting ratios of pollen and seed parents, but also the foraging behavior of the bumblebees.

The use of open pollinated (OP) seed produced without control of the pollen parent, appears as a practical alternative in the production of potatoes from true seed if large amounts of hybrid seed cannot be economically produced. The expected yield, however, depends on the degree of heterozygosity of the seed parent (Peloquin 1979), the rate of outcrossing by which the seeds were produced, and the degree of bumblebee activity present during the flowering season. Tuber yields from open pollinated families are lower than those of hybrid 4x progenies as results presented in Chapter I of this thesis indicate. Glendinning (1976) reported that open-pollinated seed production may result in up to 80% of selfing in Andigena clones. This level of selfing would result in important tuber yield reductions.

The use of selected male sterile clones in OP seed production would increase tuber yields from open pollinated progenies. This type of production of true potato seed would have the additional advantage that the subsistence farmer could produce his own true seed in a very practical manner, without the complications that under his particular circumstances would imply the use of planting designs for hybrid seed production.

The fact that relatively large amounts of fruit and seed set were obtained regardless of the presence or absence of flower odor (Table 3) would indicate that flower scent was not a factor in attracting bumblebees. However it is known that bees can detect odors that man cannot with regard to certain organic compounds especially those that convey a message about nutritive value (Faegri and van der Pijl 1979). One way to evaluate the relative value of odor as an attractant would be to determine the organic compounds present in the structures of the flower at three stages: before anthesis; during anthesis, and after anthesis. This treatment would be applied to both: flowers with and without odor detected. Initial materials to utilize in this experiment could be the male sterile clones presented in Table 8 along with other selected male fertile clones. This experiment also may be complemented with flower biology studies for both male sterile and fertile clones in order to seek structural characteristics that could account for the attraction of bumblebees by particular male sterile clones.

Bees when visually attracted, will fly in a more or less straight line to the blossoms (Faegri and van der Pijl 1979). In the potato field, bumblebees showed lack of preference for flower color.. Also, irregular circular flights were consistently made by bumblebees when approaching the inflorescences. Moreoever, these flowers were not always worked, suggesting that visual attraction was not an important factor in the foraging activity.

Consideration should be given to the possibility of domesticating bumblebees to utilize them for TPS production. Some initial results have been reported in attempts to do this (Holm 1960; Medler 1960). However, the degree of success achieved is often disappointing (Alford 1975), and may not justify the time and effort involved.

Important conclusions can be derived from this research. First, the potential benefit of bumblebees as pollinators in potato, can be substantially increased through further research aimed to understand the complexities of the foraging behavior of this pollinator and the means of attraction involved in establishing an optimal flower-pollinator relationship.

Second, the fact that with values of percent stainable pollen below 5% a considerable amount of seed set was obtained, indicates that bumblebees do sometimes visit male sterile flowers. Effective outcrossing most likely occurs.

Third, it is possible that relatively male sterile clones producing significant amounts of seeds per fruit can be selected and effectively utilized in commercial production of potato hybrid seed using bumblebees as pollinators. This will greatly reduce the cost of hybrid seed production and increase its practicality.

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Appendix B-1. Detection of origin of flower odor in five Solanum hybrid species.

Entries from five Solanum hybrid species, growing under greenhouse conditions and displaying scent were utilized to detect the origin of odor within the flower structures.

Five flowers from each entry were picked at random and the following sets (treatments) were made: (1) Complete flowers; (2) Flowers with anthers emasculated; (3) Anthers only.

Each treatment was placed in separated glass vials, tightly closed to allow for scent expression and detection. The odor test was carried out with 25 individuals. Each individual was given one vial at a time to evaluate the presence of odor, allowing for intervals between treatments in order to avoid confounding effects in odor detection. The following scale was used: 0 = no odor detected; + = odor detected. Results are presented in Table 10. Odor was detected in all cases in vials containing complete flowers. Emasculated flowers displayed no odor. The presence of odor was consistently found in vials containing only anthers.

Table 10. Odor test on five Solanum hybrid species.

	Complete flower	Anthers	Flower emasculated
buk 1-10	+*	+*	0*
buk 1-3	+	+	0
mlt 3-1	+	+	0
mlt 2-10	+	+	0
vrn 2-1	+	+	0
vrn 1	+	+	0
chc 3-7	+	+	0

Rating: 0 = no odor detected; + = odor detected.

*Data based on results obtained with 25 individuals.

Appendix B-2. Results from analysis of regression.

I. Regression of seed set on percent pollen stainability.

Source	DF	SS	MS	F
Regression	1	162,697	162,697	17.1**
Residual	160	1,523,005	9,519	
Total	161	1,685,703		

$r^2 = 0.096$

II. Regression of seed set on fruit set.

Source	DF	SS	MS	F
Regression	1	132,565	132,565	13.6**
Residual	160	1,553,137	9,707	
Total	161	1,685,703		

$r^2 = 0.078$

III. Regression of fruit set on percent pollen stainability.

Source	DF	SS	MS	F
Regression	1	314,769	314,769	47.6**
Residual	160	1,057,047	6,607	
Total	161	1,371,816		

$r^2 = 0.227$

**Significant at the 0.01 level.

Appendix B-3. Percent pollen stainability, fruit set, seed set, flowering and odor characterization of potato clones in Rhinelander.

Clone	Rep	Percent pollen stainability	Mean seeds per six fruits	Number of fruits from two plants	Flowering	Odor
Allagash	I	11.5	--*	0	1	0
	II	9.5	--	0	1	0
Atlantic	I	5.4	41	4	3	+
	II	9.6	51	28	3	+
Belchip	I	3.1	207	12	3	+
	II	2.8	45	3	3	+
Belrus	I	--**	--	--*	0	0
	II	--	--	--	0	0
Butte	I	3.3	--	9	3	+
	II	2.6	135	10	3	+
Chipbelle	I	7.9	11	27	3	+
	II	6.4	37	2	3	+
Crystal	I	18.8	26	14	3	+
	II	16.8	43	47	3	+
La Chipper	I	1.6	--	0	2	+
	II	0.5	--	0	2	+
La Soda	I	4.5	0	9	2	0
	II	3.9	--	2	3	0
Lemhi	I	7.7	274	23	3	0
	II	7.1	171	11	3	0
Monona A***	I	9.9	51	34	2	+
	II	13.1	--	6	2	+
Monona B	I	12.1	59	60	3	+
	II	14.5	62	42	3	+

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*No data available.

**No data was obtained from clones that did not flower or had very little pollen.

***Letter following the cultivars indicate that the tuber came from different source.

Appendix B-3 (continued:

Clone	Rep	Percent pollen stain-ability	Mean seeds per six fruits	Number of fruits from two plants	Flowering	Odor
Norchip	I	11.7	18	1	1	0
	II	9.6	--	0	3	0
Nooksak	I	32.5	98	186	3	0
	II	26.9	153	181	3	0
Norgold	I	.9	--	0	1	+
	II	1.5	50	2	1	+
Norland A	I	--	--	--	0	0
	II	--	--	--	0	0
Norland B	I	--	--	--	0	0
	II	--	--	--	0	0
Norland [Red Norland] A	I	23.4	63	19	2	0
	II	16.2	--	0	2	0
Norland [Red Norland] B	I	14.3	98	2	1	0
	II	11.3	35	3	1	0
Oceania	I	17.7	42	11	1	0
	II	14.3	117	7	1	0
Oneida	I	5.8	--	0	3	+
	II	4.2	107	5	3	+
Ontario	I	5.1	128	4	2	0
	II	4.2	--	0	3	0
Red Pontiac	I	24.6	--	1	3	0
	II	17.2	42	4	3	0
Rhinered	I	8.2	218	23	3	+
	II	8.2	162	66	3	+
Rideau	I	17.4	--	0	1	0
	II	16.2	--	0	1	0
Russette	I	7.4	112	32	2	+
	II	8.5	228	49	3	+
Russet Burbank A	I	4.2	--	0	3	0
	II	5.0	0	8	3	0

Appendix B-3.(continued):

Clone	Rep	Percent pollen stain-	Mean seeds per six fruits	Number of fruits from two plants	Flowering	Odor
Russet Burbank B	I	18.1	0	15	3	0
	II	17.0	--	0	3	0
Russet Burbank C	I	--**	--	--	3	0
	II	--	--	--	3	0
Russet Burbank D	I	0.1	--	6	3	0
	II	0.1	49	6	3	0
Russet Burbank E	I	0.1	--	7	3	0
	II	0.1	0	9	3	0
Superior A	I	7.8	--	0	2	+
	II	6.0	--	0	1	+
Superior B	I	15.3	--	1	2	0
	II	12.8	83	4	2	0
Superior Late	I	6.1	103	34	3	+
	II	5.2	77	16	3	+
Simcoe	I	--	--	--	0	0
	II	--	--	--	1	0
F 1154	I	21.2	206	202	3	0
	II	25.5	80	156	3	0
ND-146-4R	I	44.8	59	85	2	0
	II	44.1	177	33	3	0
ND-388-1	I	4.5	--	0	2	+
	II	4.5	--	0	3	+
ND-534-4	I	3.9	--	0	1	0
	II	4.2	--	0	1	0
W576-Sp	I	0.1	57	21	2	0
	II	--	--	--	-	-
W623	I	2.2	41	14	3	+
	II	2.5	36	14	3	+

Appendix B-3 (continued):

Clone	Rep	Percent pollen stain-ability	Mean seeds per six fruits	Number of fruits from two plants	Flowering	Odor
W629	I	14.8	104	78	3	+
	II	14.6	112	43	3	+
W703	I	10.4	153	55	2	0
	II	11.8	150	85	2	0
W710	I	14.8	147	36	2	0
	II	17.5	91	29	2	0
W716	I	38.7	206	108	3	0
	II	28.7	178	51	3	0
W718	I	17.6	203	36	1	0
	II	14.7	--	52	1	0
W723	I	19.6	124	65	2	+
	II	21.7	96	35	2	+
W726	I	11.4	73	63	3	+
	II	7.7	100	41	3	+
W729R	I	2.9	217	57	3	+
	II	10.4	342	49	3	+
W738	I	3.3	301	64	3	0
	II	3.2	120	69	3	0
W742	I	14.7	74	24	3	0
	II	15.3	56	12	3	0
W744	I	32.4	214	186	3	+
	II	34.1	296	309	3	+
W752	I	0.1	40	3	3	+
	II	0.4	--	20	3	+
W756	I	.9	--	0	1	0
	II	1.0	162	6	1	0
W760	I	17.1	128	341	3	+
	II	16.9	177	170	3	+

Appendix B-3 (continued):

Clone	Rep	Percent pollen stain-ability	Mean seeds per six fruits	Number of fruits from two plants	Flowering	Odor
W774-R	I	36.7	176	121	3	0
	II	31.5	172	71	3	0
W779	I	25.2	190	116	3	0
	II	23.9	204	153	3	0
W780	I	30.1	214	447	3	0
	II	29.1	225	269	3	0
W785	I	22.4	275	57	3	0
	II	18.1	333	12	3	0
W793	I	10.7	105	100	3	0
	II	9.6	125	30	3	0
W795	I	2.5	105	32	3	0
	II	3.2	122	71	3	0
W797	I	22.5	324	12	2	0
	II	21.1	--	0	2	0
W806-R	I	9.7	121	105	3	+
	II	17.1	201	171	3	+
W807-R	I	23.8	164	20	2	0
	II	15.4	122	16	2	0
W809	I	4.4	84	17	3	+
	II	2.4	--	4	3	+
W811	I	9.5	93	52	2	0
	II	7.4	29	8	2	0
W813	I	.5	--	3	3	+
	II	.3	73	8	3	±
W815	I	7.7	156	54	3	+
	II	9.2	159	108	3	+
W822	I	.8	--	3	2	0
	II	.7	--	0	2	0

Appendix B-3 (continued):

Clone	Rep	Percent pollen stain-ability	Mean seeds per six fruits	Number of fruits from two plants	Flowering	Odor
W823	I	32.0	2	4	2	0
	II	30.7	20	33	2	0
W824	I	11.6	163	80	3	+
	II	6.5	153	108	3	+
W826	I	1.2	--	0	2	0
	II	.9	--	1	2	0
W829	I	8.1	57	24	3	+
	II	11.7	49	100	3	+
W831	I	18.1	93	29	3	+
	II	13.3	52	29	3	+
W832	I	31.0	87	56	2	0
	II	32.6	156	44	2	0
W833	I	17.5	261	4	1	0
	II	19.5	400	18	1	0
W837	I	27.0	62	3	2	0
	II	29.0	--	6	2	0
W838	I	6.9	--	0	2	0
	II	8.3	148	21	2	0
W839	I	37.7	117	232	3	+
	II	40.0	113	149	3	+
W842	I	21.7	162	69	2	+
	II	26.0	222	31	2	+
W843	I	--	--	--	3	+
	II	--	--	--	3	+
W844	I	2.0	27	16	2	+
	II	3.0	48	27	2	+
W845	I	5.0	89	141	3	0
	II	7.0	119	30	3	0

Appendix B-3 (continued):

Clone	Rep	Percent pollen stain-ability	Mean seeds per six fruits	Number of fruits from two plants	Flowering	Odor
W846	I	.7	--	105	3	+
	II	.8	29	5	3	+
W847	I	4.6	112	81	3	0
	II	2.4	124	20	3	0
W848	I	.6	--	0	3	0
	II	.9	--	0	3	0
W849	I	5.5	166	28	2	0
	II	7.0	53	58	3	0
W853	I	28.3	220	88	3	+
	II	30.9	137	198	3	+
W854	I	3.0	--	1	3	0
	II	4.2	41	2	3	0
W855	I	0.1	64	1	1	0
	II	0.1	--	1	1	0
W856	I	19.4	76	89	3	+
	II	14.4	89	50	3	+
W858	I	16.1	142	48	3	0
	II	11.3	--	7	2	0
W860	I	20.0	227	75	3	0
	II	24.6	141	90	3	0
W861	I	13.0	266	122	3	0
	II	5.6	120	62	3	0
W862	I	33.5	255	436	3	0
	II	29.6	171	193	3	0
W863	I	2.3	147	55	3	+
	II	4.1	83	44	3	+
W866	I	1.2	30	55	3	0
	II	1.7	--	15	3	0

Appendix B-3 (continued):

Clone	Rep	Percent pollen stain-ability	Mean seeds per six fruits	Number of fruits from two plants	Flowering	Odor
W867	I	0.1	55	4	3	0
	II	0.1	--	1	3	0
W869	I	.9	104	11	3	+
	II	.7	--	1	3	+
W870	I	1.4	91	57	3	0
	II	2.5	117	95	3	0
W871	I	7.1	93	85	3	+
	II	9.2	50	53	3	+
W876	I	1.4	38	33	3	0
	II	3.9	27	8	3	0
W877	I	30.4	283	89	3	±
	II	29.2	42	82	3	+
W878	I	19.3	152	45	2	0
	II	18.9	134	23	2	0
W879	I	29.6	348	189	3	0
	II	22.8	308	188	3	0
W880	I	--	--	--	2	0
	II	--	--	--	2	0
W882	I	16.4	277	158	3	0
	II	14.1	41	95	3	0
W883	I	45.1	275	99	2	0
	II	41.4	--	134	3	0
W885	I	20.3	282	76	3	0
	II	15.4	138	17	3	0
W887	I	18.1	186	171	3	0
	II	19.3	--	166	3	0
W892	I	33.0	222	277	3	+
	II	31.3	188	273	3	+

Appendix B-3 (continued):

Clone	Rep	Percent pollen stain-ability	Mean seeds per six fruits	Number of fruits from two plants	Flowering	Odor
W894	I	12.3	171	3	1	0
	II	11.1	--	1	1	0
W896	I	.7	53	14	3	0
	II	1.2	45	9	3	0
W899	I	1.9	--	0	2	0
	II	1.6	--	0	2	0
W900	I	26.5	118	20	1	0
	II	25.7	92	54	1	0
W901	I	20.5	232	12	2	+
	II	25.0	182	32	2	+
W902	I	15.8	146	40	2	0
	II	18.9	93	19	2	0
W903	I	.3	--	0	2	0
	II	.2	--	0	2	0
W904	I	2.7	57	10	2	0
	II	3.8	48	13	2	0
W905	I	4.7	90	14	3	+
	II	6.1	41	14	3	+
W906	I	3.1	68	39	3	0
	II	2.9	42	36	3	0
W907	I	22.9	121	39	3	0
	II	22.7	114	38	3	0
W908	I	21.8	134	148	3	0
	II	33.4	90	78	3	0
W909	I	1.7	81	203	3	0
	II	3.5	94	158	3	0
W910	I	1.9	--	0	3	0
	II	1.5	--	0	3	0

Appendix B-3 (continued):

Clone	Rep	Percent pollen stain-ability	Mean seeds per six fruits	Number of fruits from two plants	Flowering	Odor
W911	I	2.0	54	2	3	0
	II	1.5	93	5	3	0
W912	I	1.9	--	0	3	0
	II	1.7	--	0	3	0
W913	I	13.3	107	7	1	0
	II	13.6	90	6	1	0
W914	I	19.2	--	0	1	0
	II	24.1	--	1	1	0
W915	I	1.5	--	0	2	0
	II	1.9	--	0	1	0
WHS-17	I	.8	187	16	3	0
	II	.3	--	0	3	0
W74-85R	I	11.7	131	37	2	0
	II	--	--	--	-	-
W76-1	I	18.9	114	89	3	0
	II	15.0	191	20	3	0
W76-2	I	14.4	135	81	3	0
	II	11.8	139	62	3	0
W76-3	I	18.6	83	64	1	+
	II	21.0	77	60	1	+
W76-4	I	18.5	42	44	3	0
	II	18.6	66	21	3	0
W76-5	I	28.6	107	236	3	0
	II	33.6	98	204	3	0
W76-6	I	13.6	106	51	3	0
	II	12.6	87	7	1	0
W76-7	I	10.7	--	8	1	0
	II	11.8	213	11	1	0

Appendix B-3 (continued):

Clone	Rep	Percent pollen stain-ability	Mean seeds per six fruits	Number of fruits from two plants	Flowering	Odor
W76-8	I	23.5	163	169	3	0
	II	22.4	163	105	3	0
W76-9	I	26.8	83	124	3	+
	II	28.1	181	80	3	+
W76-10	I	0.1	194	9	1	0
	II	0.1	--	3	1	0
W76-11	I	6.5	134	161	3	0
	II	7.0	92	151	3	0
W76-12	I	3.0	222	11	2	0
	II	1.6	162	28	2	0
W76-13	I	19.3	229	62	3	0
	II	17.4	278	139	3	0
W76-14	I	5.7	245	51	3	0
	II	6.8	191	82	3	0
W76-15	I	2.9	234	93	2	+
	II	2.4	80	6	3	+
W76-16	I	1.9	117	129	3	0
	II	2.0	--	44	3	0
W76-17	I	24.6	137	75	3	0
	II	22.0	--	22	3	0
W76-18	I	.7	60	4	3	0
	II	.7	139	7	3	0
W76-19	I	.4	32	12	3	0
	II	1.0	--	1	2	0
W76-20	I	1.7	--	1	2	0
	II	1.7	--	2	2	0
W76-21	I	.4	--	1	3	0
	II	.6	48	13	3	0

Appendix B-3 (continued):

Clone	Rep	Percent pollen stain-ability	Mean seeds per six fruits	Number of fruits from two plants	Flowering	Odor
W76-22	I	--	--	--	3	0
	II	--	--	--	3	0
W76-23	I	1.7	93	21	3	+
	II	2.7	58	18	3	+
W76-24	I	.6	--	0	2	0
	II	5.2	--	3	2	0
W76-25	I	2.3	63	13	3	+
	II	3.6	33	2	3	+
W76-26	I	2.4	--	0	1	0
	II	2.5	--	0	1	0
W76-27	I	21.9	118	67	3	0
	II	21.6	120	30	3	0
W76-28	I	28.2	186	51	2	0
	II	31.8	147	56	1	0
W76-29	I	22.9	224	101	3	0
	II	19.5	98	114	3	0
W76-30	I	20.8	72	116	3	0
	II	15.2	47	98	3	0
W76-31	I	19.6	171	98	3	0
	II	18.9	222	8	3	0
W76-32	I	22.6	300	99	3	+
	II	25.0	219	80	3	+
W76-33	I	8.0	122	26	3	0
	II	10.0	101	18	3	0
W76-34	I	.6	113	62	3	0
	II	.7	245	1	3	0
W76-35	I	1.6	135	16	3	+
	II	2.7	84	46	3	+

Appendix B-3 (continued):

Clone	Rep	Percent pollen stain-ability	Mean seeds per six fruits	Number of fruits from two plants	Flowering	Odor
W76-36	I	1.4	169	4	3	0
	II	1.2	146	8	3	0
W76-37	I	15.3	107	1	2	0
	II	14.9	--	0	2	0
W76-38	I	8.1	59	11	3	+
	II	9.9	60	11	3	+
W76-39	I	13.1	147	88	3	0
	II	13.9	115	62	3	0
W76-40	I	29.2	209	67	3	0
	II	26.0	46	61	3	0
W76-41	I	3.4	123	33	2	0
	II	2.4	105	12	2	0
W76-42	I	1.4	256	9	3	0
	II	0.9	--	1	3	0
W76-43	I	--	--	--	1	0
	II	--	--	--	1	0
W76-44	I	24.4	198	32	3	0
	II	23.8	182	41	3	0
W76-45	I	18.8	196	70	3	+
	II	19.6	284	56	3	+
W76-46	I	10.7	226	33	2	0
	II	12.3	214	6	2	0
W76-47	I	7.1	168	27	1	0
	II	9.8	178	14	1	0
W76-48	I	7.0	291	32	2	0
	II	1.9	268	7	2	0
W76-49	I	17.1	332	5	1	0
	II	19.9	235	5	1	0

Appendix B-3 (continued):

Clone	Rep	Percent pollen stain-ability	Mean seeds per six fruits	Number of fruits from two plants	Flowering	Odor
W76-50	I	24.4	261	6	2	0
	II	25.5	213	46	2	0
W76-51	I	1.4	--	0	3	0
	II	2.4	123	2	3	0
W76-52	I	1.2	197	9	2	0
	II	.9	132	27	2	0
W76-53	I	0.1	79	68	2	0
	II	0.1	108	24	2	0
W76-54	I	16.9	191	194	3	+
	II	14.4	99	256	3	+
W76-55	I	.9	110	9	1	0
	II	.6	118	20	1	0
W76-56	I	9.3	192	145	3	0
	II	9.5	113	35	3	0
W76-57	I	0.1	--	0	1	0
	II	0.1	--	0	1	0
W76-58	I	0.8	--	0	3	0
	II	1.2	99	17	3	0

University of Wisconsin–Madison

To Professors:

PELOQUIN, Chairman

HANNEMAN

GURIES

written

You are hereby requested to act as a committee for the oral examination of the candidate whose name is endorsed hereon.

By authority of the President of the University.

Robert M Bock
Dean

The Graduate School

Madison, February 18 1983
(Date of Examination)

To the Graduate Faculty:
We, the undersigned, report that as a committee we have examined

JOSE LUIS RUEDA

whose major field is PLANT BREEDING & PLANT GENETICS

We recommend that the candidate be admitted to the degree of

Master of SCIENCE

In partial fulfillment of the requirements of the Master's degree the candidate offers a thesis entitled: (If no thesis has been required, kindly indicate the fact.)

BREEDING METHODS FOR PRODUCTION OF POTATOES FROM TRUE SEED

We report that the candidate has failed to pass a satisfactory examination and is not recommended for admission to the Master's degree.