THE STERILITY-INCOMPATIBILITY COMPLEX IN SWEET POTATO

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SUMMARY

Compatibility relations in sweet potatoes were assessed from the results of hand pollinations and ultra violet flourescence microscopy. Environmental conditions influenced compatibility reactions. Abnormal growth of pollen tubes in styles was common. Pollen sterility was assessed by germination on solid and liquid media and by staining with acetocarmine, lactophenol blue and tetrazolium salts and is not important. Female sterility however is a major factor determining the low seed set and seed viability.

RESUME

Les rapports de compatibilité dans la patate douceont été évalués à partir de résultats de pollinisations à la main et de microscopie flurescente ultraviolette. La croissance anormale des tubes polliniques dans les styles était fréquemment observée. La stérilité des pollens a été évaluée par la germination en milieu solide et liquide et par coloration aux sels acétocarmins, lactophénols bleus et elle n'est pas importante. Toutefois is stérilité femelle est un facteur important déterminant la formation lente des boutures et leur viabilité.

RESUMEN

Las relaciones de compatibilidad se determinaron a partir de resultados obtenidos por polinizacion manual y microscopía ultravioleta, fluorescente. El crecimiento anormal de tubos polínicos en los estilos fue común. La esterilidad del polen, la cual no es importante, se determinó mediante germinación en medio liquido y sólido y por coloración con acetocarmin, lactofenol azul y sales de tetrazolio. La esterilidad femenina, sin embargo, es un factor importante que determina la baja producción y viobilidad de simillas.

INTRODUCTION

Martin[5] has reviewed previous studies on incompatibility in sweet potatoes. Most authors have attributed poor fruit set to incompatibility, and have classified cultivars into distinct compatibility groups based on results of pollination between them. However, there have been discrepancies between the classifications of different authors suggesting either errors or differences due to experimental conditions or systems of classifying data.

Martin and co-workers were the first to recognize that a more complex system is responsible for poor fruit and seed set. In various publications[6,7,8] they pointed out that in sweet potato, beside the incompatibility system, there is a sterility complex which acts at different stages in the sexual cycle.

A study was started in 1969 at the Centre for Agricultural Research in Surinam to determine the relative importance of incompatibility and sterility mechanisms in reducing fruit set and seed formation in the sweet potato. This study included:

1. *In vivo* determination of compatibility relations.
2. Assessment of compatibility relations using fluorescence microscopy.
3. Pollen viability studies.
4. Female sterility studies.

METHODS AND RESULTS

Selfings and intervarietal crosses

About 35 cultivars of different origin were originally entered in the field pollination programme. Some of them flowered very poorly under our conditions and were excluded, when it appeared that classic ways to stimulate flowering, such as grafting on to non-tuberiferous *Ipomoea* species, shortday treatment, and nitrogen application, had little or no effect. This left only 27 clones in the programme. All clones were planted on ridges and trellissed along chicken wire to promote flowering and to facilitate crossing. Pollinations were carried out between 7.00 and 9.00, since it had been established previously that pollinations made later, under sunny conditions, caused a further reduction in fruit set.

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As far as possible clones were selfed and crossed in all combinations. Altogether some 24,000 hand pollinations were made covering 404 out of a total of 702 possible combinations. Taking into account only those combinations that had been made at least twenty times, 378 combinations were available for analysis, comprising about 23,000 pollinations.

Fruit set was recorded about 10 days after pollination when unfertilized ovaries had already abscissed, whereas fertilized ones were already visibly swollen. Fruits ripened four to five weeks after pollination but many fruits dropped before ripening.

To decide whether a combination is compatible or not is difficult. Some investigators set a threshold of 5 of 10% seed set beyond which a combination is considered to be compatible. This leads to an inextricable mixing of the effects of incompatibility and sterility components. However, considering a combination compatible only if it results at least in fruit set, might lead to an underestimation of compatibility, as incompatibility may be overcome under certain environmental and physiological conditions.

It was therefore decided to classify the intervarietal combinations into three provisional categories:

1. Incompatible. Combinations completely failing to give capsule set.
2. Compatible. Combinations with a percentage capsule set of two with a minimum of one ripe capsule.
3. Indefinite. Combinations not belonging to 1. or 2.

The compatibility relations between a number of cultivars are presented in Table 1. In some instances striking differences were found between reciprocal crosses (Table 2), but unilateral compatibility was not the rule.

Results of field pollinations were considerably influenced by environmental factors (Table 3) and therefore no attempt has been made to group them.

Besides unravelling compatibility relationships as such, it is interesting to learn the extent to which compatible combinations lead to capsule and seed set. Figure 1 represents the distribution of 278 crosses over fertility classes.

Table 4 clearly shows that distinct differences exist between clones in respect of capsule set, seed set and number of seeds per pollination.

Of the capsule sets, 75 percent were harvested. Generally they contained only one or two seeds; occasionally three seeds were found. Average number of seeds per capsule depended on the mother clones, varying from 1.07 for cultivar Hopi to over 1.50 for cultivars USA 130, Louisiana 6 and A28/7. The overall average was 1.34. No correlation was found between the number of seeds per pollination and the number of seeds per capsule.

Microscopic observations

The second method of establishing compatibility relations was based on *in vitro* tests of (i) pollen germination on the stigma and (ii) pollen tube penetration into the style.

To follow the pollen tubes in the stylar tissue, use was made of fluorescence microscopy. Penetrated pollen tubes could be distinguished from the stylar tissue by a yellowish fluorescence of callose plugs in them

To date, 461 combinations, comprising 28 different clones have been studied. Each cross was done in triplicate and most were repeated once or more. In all instances the total number of pollen grains remaining on the stigmatic surface, the number of grains germinated, and the number of tubes in the upper, middle and lower part of the style were counted. On this basis the cultivars were classified into five groups (Table 5).

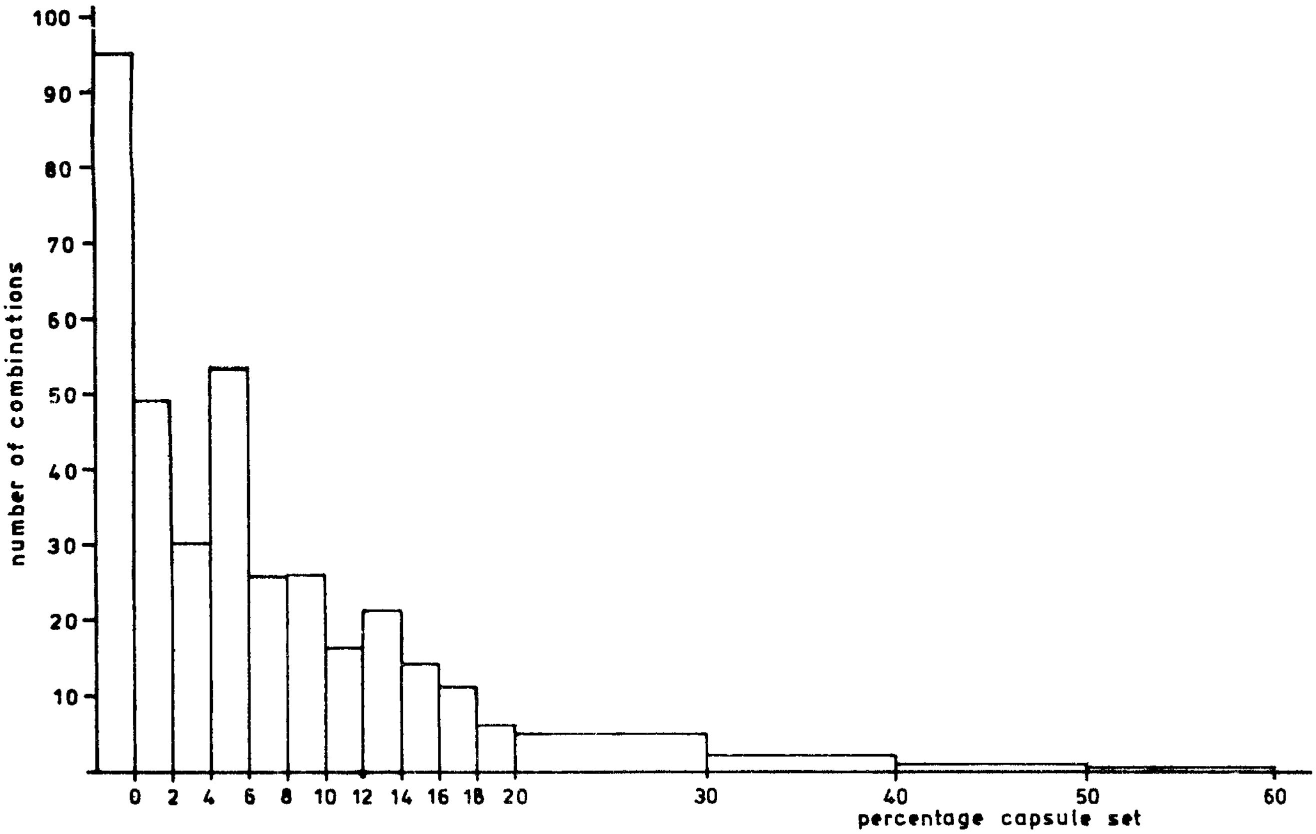
Group I consists of clones with a weak incompatibility system. In intra-group pollinations, often some pollen grains germinated and sometimes a few penetrated the stylar tissue. Germination depended very much on external conditions; in a particular combination it once failed entirely, whereas at a later date germination was abundant. In inter-group combinations germination and tube growth were profuse.

Group II includes only three related clones, two of which, cultivars Genjem 1 (1968) and Genjem 1 (1970), may be identical, though the latter resembles cultivar Genjem 2 in its abundant flowering. In this group a weak unilateral incompatibility against all clones of group I was observed. When used as maternal parent, the cultivars Genjem behaved similarly to the members of group I pollinators however. They were completely compatible with all other clones but were self-incompatible. This justifies, in our opinion, their separate classification.

Group III consists of four unrelated intra-incompatible, inter-compatible cultivars.

Group IV includes five cultivars with a very pronounced reaction pattern: almost complete failure of pollen germination in intra-group crosses but a high rate of germination and pollen tube growth in inter-group matings.

Group V comprises a number of cultivars that were, with a few exceptions, compatible in all matings, but in selfs pollen generally failed to germinate. Only cultivar Sunny Side appeared self-compatible. Some members of this group, i.e. cultivars Blauwkop and Sunny Side gave considerable capsule set in the field,



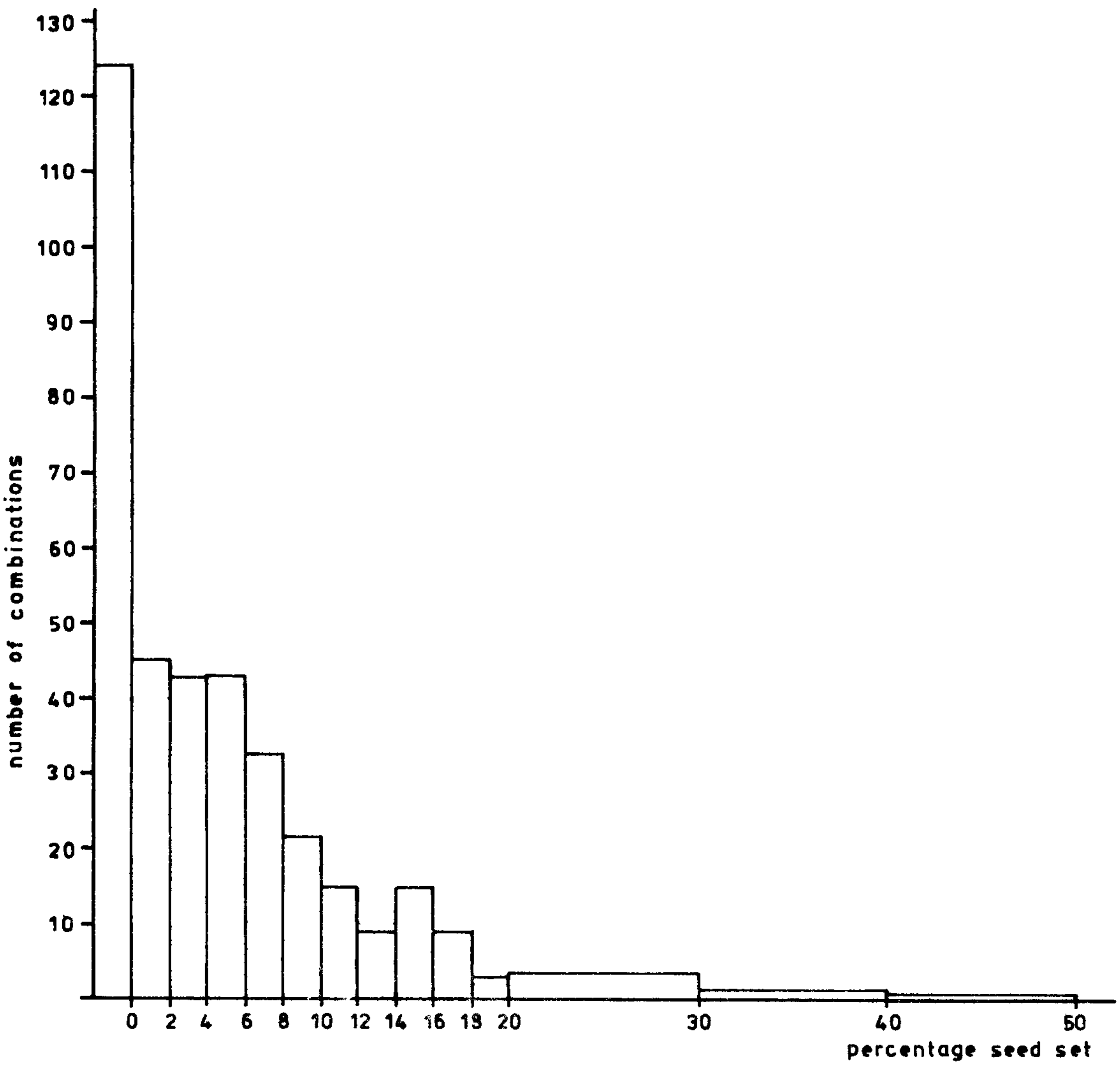


Fig. 1. Distribution of capsule-set and seed-set data in 378 intervarietal combinations and selfings of sweet potato.

whereas cultivars USA 130, Georgia Red and Lousiana 6 did not. Possibly this group should be subdivided into a self-compatible group and one or more small intra-incompatible group(s).

Between the various clones there was a large variation in average number of pollen grains per stigma, germination percentage, style penetration and number of pollen tubes in different regions of the style (Table 6).

On the whole only one out of five germinated pollen grains penetrated the style. Occasionally some pollen tubes with swollen tips were noticed on the stigma. More common were tubes with a thickened tip ending somewhere in the stylar tissue. This occurred in styles of nearly all clones. Only in two instances did pollen tubes continue to grow after swelling. This points to the existence of a second growth-inhibiting mechanism. The sharp decline in number of pollen tubes in the mid and lower style regions also indicates this. Generally, the relative decrease was larger between upper and mid-style than between mid and lower style, indicating that the inhibitor operates in the upper style.

In Table 6 seed-set data are included, both as obtained in the field and as computed, for compatible combinations (based on *in vitro* assessment) irrespective of whether they actually set seed or not. Assuming that all the tubes found in the lower style enter the ovary, our expectation based on microscopical observations is that average seed production per compatible pollination is about 1. However, only one tenth of this figure has been realized in our field crosses (Table 6). This implies that a further sterility component is operating in the ovarial region.

Of the 360 combinations assessed both in the field and *in vitro*, 270 (75%) behaved similarly. Of the remainder, 58 were compatible *in vitro* but did not give capsule set in the field, whereas 32 combinations were incompatible *in vitro* yet gave seed from capsules set in the field.

The failing of capsule set in combinations showing satisfactory pollen germination *in vitro* may have been caused by various factors such as female sterility because of heavy impediment of tube growth in stigma and style, failure of fusion between egg cell and male gamete, or seed abortion (Goldrush, Butikatoka), semi-sterile pollen (Goldrush), weak incompatibility genes, or chance. A majority of the failures related to mother clones with less than 0.05 seeds per pollination (27 cases) or a semi-sterile pollinator (6 cases).

The combinations which were incompatible *in vitro*, but still gave capsule and seed set are more remarkable but may be explained by more favourable external conditions or by physiological changes in the plant, or perhaps by occasional contamination with foreign pollen. In all instances the percentage capsule and seed set have been below 2.1. Of the remainder, some, but not all, are related to clones with a weak incompatibility allele.

Germination *in vitro*

Pollen germination *in vitro* was studied using a large range of liquid and solid media.

Several forms of pseudo-germination were observed, such as bursting, the formation of curling plasm strands, and, sporadically, bulging of the pollen grains within the exine wall. Once a distinct nucleus was found in such a bulge (Figs 2 and 4).

Pseudo-germination to some extent decreased with increasing saccharose concentration and higher temperatures. On agar, the percentage pseudo-germination rapidly decreased and very few cytoplasm protrusions were found when saccharose concentrations exceeded 25%. Boron did not influence this phenomenon, nor did salts of Ca, Mg and K or stigma-style press juice. Cultivars Djarak, Hopi and USA 130 all behaved similarly in this respect.

None of the media tested produced germination, though a small number of pollen grains was detected having tube-like structures covered by the intine wall (Fig. 5). These stopped growing after a few hours and they were observed only in concentrated saccharose solutions (35%) and on agar.

Pollen stainability

Pollen of the cultivars Djarak, Butikatoka and USA 130 was tested for its stainability with acetocarmine. All except Djarak were also stained in lactophenol cotton blue.

Pollen was collected at 8.00 and 10.00 h. and immediately stained. The results are compiled in Table 7. The mean percentage of stainable pollen was somewhat lower for USA 130 than for Djarak and Butikatoka and about 10 percent higher in cotton blue than in acetocarmine. Time of pollen sampling did not affect the stainability. However, as acetocarmine and cotton blue are non-vital stains, they differentiate mature from immature rather than viable form unviable pollen.

Tetrazolium salts are claimed to give a better estimation of viability. They are reduced to insoluble coloured products by the action of respiratory dehydrogenase enzymes, and therefore are commonly used to determine seed viability.

Pollen of ten cultivars was treated with solutions of four tetrazolium salts, *viz.* TTC, TR, INT and

MTT. Pollen was collected at 7.00, 10.00 and 13.00 h. Their percentage stainability was compared with those in solutions of acetocarmine and cotton blue.

In most clones stainability did not decrease during the course of the day. Cultivar Brokopondo was an obvious exception. Stainability, as determined with tetrazolium salts, dropped strongly between 10.00 and 13.00 h. In the non-vital stains the percentage stained remained at the same level (Table 9). This is a further indication these stains do not measure viability properly.

The differences between the various stains make it difficult to decide on the actual viability. In TTC percentage stainabilities are considerably lower than the proportion of pollen grains which germinate in compatible matings for three of the examined cultivars, especially for cultivar Willemrank (Table 6).

Seed emergence

At the end of three consecutive years seeds were tested for viability. Scales, aborted seeds and abnormally developed specimens were excluded prior to sowing. Seeds were treated in concentrated sulphuric acid for 10 minutes, followed by prolonged rinsing in running tap water. They were sown in small pots filled with a mixture of sand, peat and clay, and covered with a small layer of coarse sand. Counting of emerged plants continued for three months. Emergence started two days from planting and culminated at about the fourth day. Over 90 percent of the germinating seeds emerged within 10 days. Small numbers of emerging plants was, however, observed 1 – 2½ months after showing. The results of the different tests were very similar and are, therefore, combined (Table 10).

Of a total of 1169 seeds 524 (46%) failed to emerge. Most non-emerging seeds were found in the lower seed weight classes, but also over 10% of the heaviest seeds (23 mg or more) did not germinate, indicating that instability or weakness of seeds occurs in all weight classes. Some seedlings, especially from lighter seeds, died shortly after emergence.

Clones differed considerably both for seed weight distribution and percentage non-germinating seeds. Emergence was by far the highest in cultivar Sunny Side, though this clone did not have the highest average seed weight.

DISCUSSION

The data confirm that poor seed set in sweet potato results from a complex of incompatibility and sterility mechanisms, in which sterility plays a dominant part. Pollen sterility appears to be of no importance except in some particular clones. Thus it was found that anthers of cultivars Jersey Orange did not dehisce and on mechanical opening shed very little pollen. Cultivars Goldrush and Puteri Selatan showed low percentages of pollen germination and tube growth even in compatible matings.

To explain low capsule and seed set, Martin and Cabanillas[7] proposed the action of two growth barriers, one of which inhibits the pollen tubes from passing the border between stigma and style, and the second operating in the ovary. No inhibitory mechanism in their view was active in the style. However, in our investigations it seems that at least in some cultivars an additional growth barrier is operating in the upper region of the style. Whether this prevents or merely retards tube growth is not clear, but the formation of swollen tips on the pollen tubes suggest that growth may be terminated.

Since there is no evidence for low pollen viability, germination of pollen on the stigma is a reliable basis on which to define one kind of compatibility reaction. Capsule and seedset data are too crude a basis for describing compatibility relationships since they depend upon external influences and to chance as well as to the cumulative effects of different sorts of incompatibility reaction.

Capsule and seed-set data in instances where pollen germination is normal give information on the efficacy of the concerted action of additional components of female dependant sterility or incompatibility mechanisms in the stigma, style and ovary. Further cytological and chemical investigations will be needed to determine the nature of the sterility mechanisms. Ting and Kehr[12] suggested that meiotic abnormalities may account for low fertility in sweet potato, but Jones[4], studying meiotic behaviour in 40 clones, found this to be normal.

Complete failure of pollen germination on liquid and solid media has previously been found by Fujise[2] and Martin and Ortiz[8]. According to Brewbaker[1] this behaviour is characteristic of trinucleate pollen.

Jones[4] claimed to investigate the pollen fertility of 28 sweet potato clones by staining in acetocarmine. The percentage of stained pollen ranged from 64–95% and the main range was between 80–95%. These values are of the same magnitude as those obtained in our experiments, but the interpretation is somewhat dubious.

Several authors have previously studied pollen viability by the use of tetrazolium salts[3,9,10] with indication that TTC and TR did not fully discriminate between viable and non-viable pollen, and that these salts may sometimes give an overestimation of viability. On the other hand, MTT was said to give very reliable viability percentages. In our trials, however, MTT gave much better indications of pollen viability than either TTC or TR. This anomaly needs further study.

Figure 2. *Pseudo-germination in sweet potato; pollen grain producing cytoplasmic strands (x 350).*

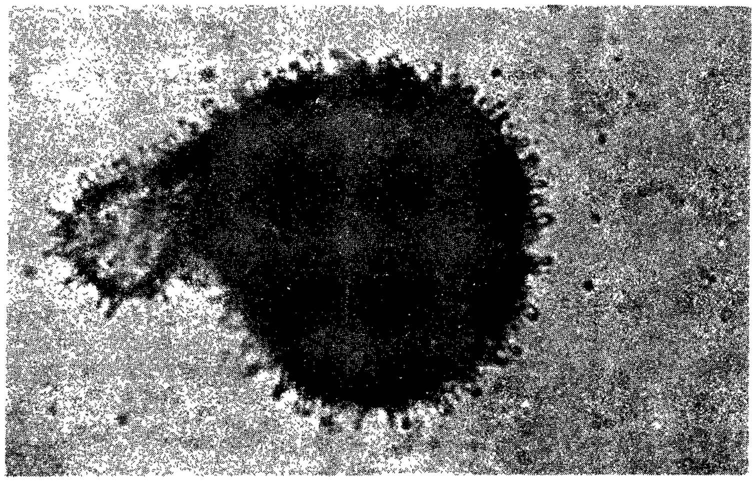


Figure 3. *Pseudo-germination in sweet potato; pollen grain showing a bulge covered by the exine wall (x 1000).*

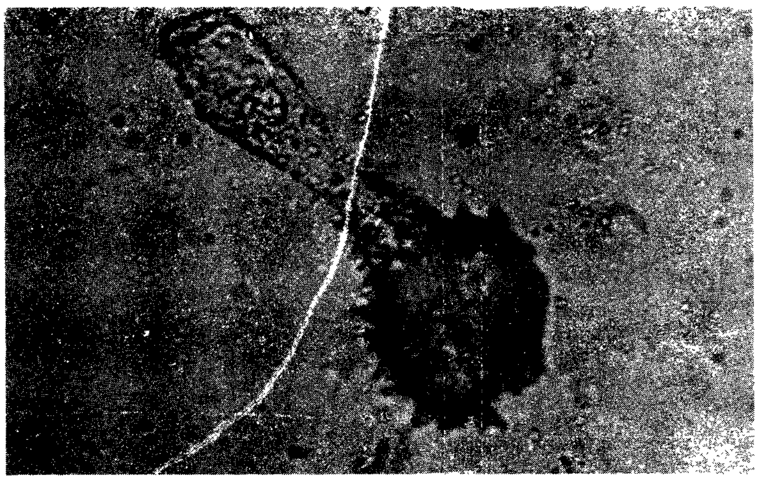


Figure. 4. *Pseudo-germination in sweet potato; protuberant pollen tube containing nucleus-like organ (x 1000).*

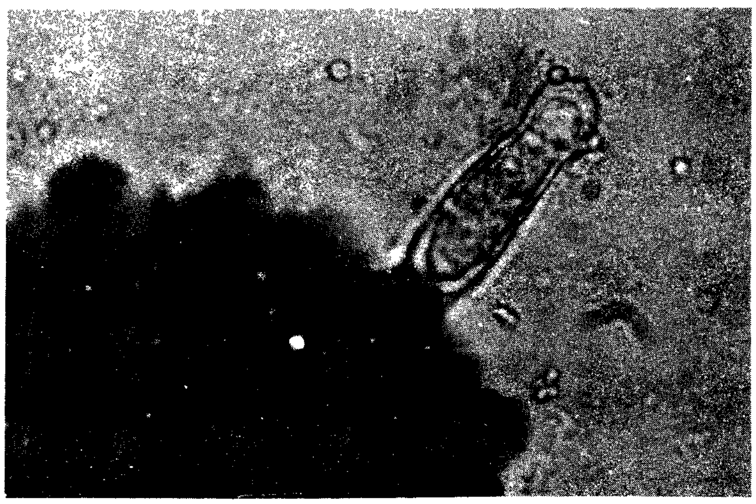


Figure 5. *Pollen grain of sweet potato cv. Dharak in 35% saccharose solution with small tube (x 1600).*

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Table 1. Compatibility relations between 23 sweet potato cultivars based on pollinations in the field.
+ = compatible ; — = incompatible ; ± = indefinite.
Incompatible combinations placed in brackets indicate 6–20 pollinations only.

♀ \ ♂		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23
Djarak	1	—	—	+	—	±	+	+	+	±	+	±	+	±	—	±	+	+	—	+	—	—	±	+
Hopi	2	±	—	+	—	—	+	+	—	+	±	+	+	—	±	+	+	+	+	±	—	±	±	—
U.S.A. 130	3	+	+	—	+	+	+	+	—	+	+	+	+	+	+	±	+	+	+	+	±	—	+	±
White Star	4	—	+	+	±	—	+	+	+	+	+	+	+	—	+	+	+	+	±	+	+	+	+	+
Butikatoka	5	—	—	—	—	+	+	—	—	—	±	+	+	—	—	—	—	±	±	—	±	+	+	—
Genjem 1	6	—	—	±	+	+	+	+	o	+	(—)	o	(—)	(—)	o	o	o	o	o	o	o	o	o	o
Genjem 2	7	—	+	—	+	±	—	+	o	±	—	(—)	o	(—)	o	—	—	—	o	o	o	o	o	o
Goldrush	8	—	—	—	—	—	—	(—)	±	—	—	(—)	(—)	—	o	—	—	(—)	o	(—)	o	+	o	o
Centennial	9	±	+	+	—	+	+	+	—	+	+	+	±	+	+	±	+	+	(—)	+	—	+	+	+
Georgia Red	10	+	+	+	+	+	+	+	—	+	±	+	+	+	±	+	+	+	(—)	—	+	o	(—)	o
Blauwkop	11	+	—	±	+	+	+	+	—	±	+	+	+	±	—	+	—	+	—	±	+	+	—	±
Egeida	12	o	o	o	+	+	+	o	o	o	o	o	+	o	o	o	o	o	o	o	o	o	o	o
Julian	13	+	+	+	±	+	+	o	o	±	(—)	o	—	—	o	o	±	o	o	(—)	o	o	o	o
Blanquita	14	—	±	(—)	o	o	o	+	o	(—)	+	—	o	o	—	o	o	—	o	o	o	o	o	o
Sunny Side	15	±	+	+	+	+	+	+	+	+	+	o	o	+	+	+	±	+	o	—	+	o	+	o
Willemsrank	16	+	+	+	+	+	+	—	—	—	+	+	+	+	+	+	+	±	+	+	+	+	±	—
Brokopondo	17	+	—	+	+	±	+	+	—	+	+	+	(—)	+	±	+	—	±	±	+	+	+	—	—
Louisiana 2	18	+	+	+	+	+	+	+	(—)	o	o	o	o	o	o	o	+	±	+	+	o	o	o	+
Louisiana 6	19	+	+	+	+	+	(—)	+	o	+	—	o	o	(—)	o	o	o	o	o	±	o	o	o	o
A 28/7	20	±	—	+	+	—	+	+	±	±	o	o	o	+	o	o	o	+	o	o	—	+	o	o
A 138	21	+	+	+	+	+	+	+	±	±	+	+	(—)	—	+	+	+	+	+	+	+	+	—	+
C 9/9	22	+	+	+	+	+	—	+	±	+	(—)	+	o	o	o	o	o	o	o	+	o	o	+	—
O 49	23	±	+	±	+	o	o	o	(—)	o	o	o	o	o	o	o	o	o	o	o	(—)	o	o	+

TABLE 2

Capsule and seed-set data for some intervarietal combinations showing striking reciprocal differences

Combination A x B	% capsule/% seed set A x B	B x A
Djarak x A 138	0/0	17.4/17.4
Djarak x C 9/9	1.9/0	18.1/ 9.5
Hopi x Brokopondo	23.5/22.1	0/0
Hopi x Louisiana 6	0.9/0.9	16.7/12.1
Hopi x 0 49	0/0	12.1/ 5.2
USA 130 x Butikatoka	10.4/4.5	0/0
USA 130 x A 28/7	5.7/0	35.0/31.7
White Star x Louisiana 2	1.9/0	51.9/42.9
Butikatoka x Georgia Red	2.0/0	22.0/18.0
Butikatoka x Sunny Side	0/0	37.7/28.5
Butikatoka x Willemsrank	0/0	17.1/20.7
Butikatoka x Louisiana 2	1.9/0	43.5/32.6
Butikatoka x Louisiana 6	0/0	30.2/26.4
Genjem 2 x Centennial	1.7/0	32.2/27.1
Genjem 2 x Sunny Side	0/0	16.0/12.0
Centennial x Blauwkop	1.6/0	17.8/11.1
Centennial x Brokopondo	20.7/15.5	2.7/0

TABLE 3

Capsule-set percentages for a number of combinations performed in different periods

Combination	1969	1970	1971	1972	1973
Djarak x Georgia Red	0	45.4	-	-	-
USA 130 x Djarak	1.1	45.6	-	0	-
USA 130 x Hopi	0	30.3	-	0	-
USA 130 x White Star	0	47.4	-	0	-
USA 130 x Georgia Red	0	41.7	-	-	-
Butikatoka x Blauwkop	0	-	-	20.0	-
Genjem 2	-	-	20.8	-	0
Willemstank x USA 130	-	-	0	33.3	-
Willemsrank x A 28/7	-	-	-	0	9.7
Louisiana 6 x Genjem 2	-	-	-	0	23.3
A 27/8 x USA 130	-	-	-	5.0	50.0
A 28/7 x Julian	-	-	0	0	33.3
C 9/9 x USA 130	-	-	0	0	42.9

Mother clones	Combinations	Pollinations	Capsule set	Seed set	Seeds obtained	% capsule set	% seed set	Seeds per pollination	Seeds per capsule
Djarak	13	945	86	67	82	9.1	7.1	0.09	1.22
Hopi	12	874	76	56	60	8.7	6.5	0.07	1.07
U.S.A. 130	19	1492	139	80	126	9.3	5.4	0.08	1.58
White Star	19	1445	190	154	213	13.1	10.7	0.15	1.38
Butikatoka	6	402	21	19	21	5.2	4.7	0.05	1.11
Genjem 1	2	114	8	8	12	7.0	7.0	0.11	1.50
Genjem 2	3	240	24	24	33	10.0	10.0	0.14	1.38
Goldrush	1	41	2	2	3	—	—	—	—
Centennial	16	895	102	75	97	11.4	8.4	0.11	1.29
Georgia Red	13	658	99	80	101	15.0	12.2	0.15	1.27
Blauwkop	13	820	97	69	86	11.8	8.4	0.10	1.24
Julian	3	123	14	11	14	11.4	8.9	0.11	1.27
Sunny Side	12	719	122	97	130	17.0	13.5	0.18	1.34
Willemsrank	20	1272	152	101	130	11.9	7.9	0.10	1.20
Brokopondo	14	840	71	55	75	8.5	6.5	0.09	1.36
Louisiana 2	9	537	129	105	145	24.0	19.6	0.27	1.38
Louisiana 6	7	398	66	55	83	16.6	13.8	0.21	1.51
A 28/7	5	265	37	32	51	14.0	12.1	0.19	1.59
A 138	19	1318	224	167	228	17.0	12.7	0.17	1.37
C 9/9	9	548	48	34	40	8.8	6.2	0.07	1.18
D 49	3	127	19	12	15	15.0	9.4	0.12	1.25
Okinawa 2	1	46	6	5	6	—	—	—	—
U.S.A. 21 X	3	151	33	33	45	21.9	21.9	0.30	1.36
total *		13428	1659	1247	1668	—	—	—	—
average *		—	—	—	—	12.4	9.3	0.12	1.34
range *		—	—	—	—	5.2-24.0	4.7-19.6	0.05-0.27	1.07-1.59

* exclusive clones with less than 5 combinations

Table 4. Capsule- and seed-set data of fertile matings with over 20 pollinations per combination.

Table 5. Classification of 30 clones of sweet potato into compatibility groups.
+ = compatible; high rate of germination and/or pollen tube growth; (+) = semi-compatible; low rate of germination and/or pollen tube growht;
(—) = semi-incompatible; occasional germination and/or pollen tube formation; — = incompatible; no germination;
* = small numbers of pollen grains per stigma (≥20)

	♀ \ ♂		I													II			III				IV					V				
			1	2	4	5	8	9	13	14	20	28	29	31	32	6	7	33	18	26	27	30	16	17	21	22	23	3	10	11	15	19
I	Djarak	1	(—)	(+)	(+)	(+)	—	(+)	(+)	—	(—)	(—)	—	—	—	+	+	+	+	(+)*	+	+	+	+	+	+	+	+	+	+	+	+
	Hopi	2	—	(+)	(—)	(—)	(—)	(+)	—	—	(+)	—	(—)	—	(—)	+	+	o	+	o	o	o	+	+	+	+	+	+	+	+	+	+
	White Star	4	(—)	(+)	(—)	—	o	+	—*	(—)	(+)	—	—	—	+	+	+	o	+	+	+	+	+	+	+	+	+	+	+	+	+	+
	Butikatoka	5	—	—	—	—	—*	(—)	(—)	—*	—*	—	—	—*	—	+	—*	o	+	+	(+)*	o	+	+	+	+	+	+	+	+	+	+
	Goldrush	8	—	(+)	—	(—)	—	+	o	(—)	(+)	—	—	o	—	+	+	o	+	o	o	o	+	+	+	+	+	+	+	+	+	+
	Centennial	9	(—)	+	(+)	o	(+)	(+)*	(—)*	—*	(+)	(+)	—	o	—*	+	+	o	+	+	+	(+)	+	+	+	+	+	+	+	+	+	+
	Julian	13	o	o	o	o	—	o	o	o	o	o	+	o	o	o	o	o	o	+	o	o	o	o	o	o	o	o	o	o	o	o
	Blanquita	14	—*	(—)*	o	—	—*	—*	(—)	—	—	o	o	o	o	+	+	o	+	+	o	o	+	+	+	(+)*	+	(+)	+	+	o	o
	A 28/7	20	(—)*	o	—	(—)*	—	—	o	(+)	—*	(+)	(+)	o	—	+	+	o	+	o	o	o	+	+	+	+	+	+	+	+	+	+
	Louisiana 3	28	—	(+)	—	—	(+)	(+)	o	—	(—)	—	—	—	o	o	+	+	+	o	o	o	+	+	+	+	+	+	+	o	+	+
	Louisiana 5	29	—	+	(—)	—	—	(+)	—	—	—	(—)	—	—	o	o	+	+	+	o	o	+	+	+	+	+	+	+	+	o	+	+
	Palumeu	31	—	—	(—)	—	—	—	o	o	—	—	—*	—	o	o	o	o	(+)	o	o	o	+	+	(+)	+	+	+	o	o	+	+
	Tox Paars	32	(—)	(—)	—	—	—	(—)	(+)	(+)	(—)	—	—	o	o	o	+	o	+	o	o	o	+	+	+	+	+	+	+	+	+	+
II	Genjem 1 (1968)	6	—	o	o	o	o	o	o	o	o	o	(+)*	o	o	—	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o
	Genjem 2	7	(—)	(+)	(+)	(—)	—	(+)	(—)	(+)	(+)	—	(—)	o	(+)	—	(+)	(+)	+	+	+	(+)	(+)	+	+	+	+	+	+	+	+	+
	Genjem 1 (1970)	33	(—)	+	(—)	—	—	(+)	—	(+)	(—)	—	(+)	o	(—)	o	o	+	+	+	(—)	+	+	+	+	+	+	+	+	+	+	+
III	Louisiana 2	18	+	+	+	+	+	+	o	+	+	+	+	o	+	o	+	o	—	o	o	o	+	+	+	+	+	+	+	+	+	+
	Okinawa 2	26	+	+	o	o	o	+	o	o	o	o	o	o	o	o	o	o	o	o	o	o	(+)	o	o	o	o	+	o	+	o	o
	U.S.A. 21 X	27	+	+	+	+	(+)	+	(—)	o	+	+	+	o	o	o	o	o	(—)	o	—*	o	o	+	o	+	o	+	+	o	+	o
	Puteri Selatan	30	+	o	+	+	—	+	o	+	+	+	+	o	+	o	+	o	—	—	—	—*	+	+	+	+	+	+	+	+	+	+
IV	Willemsrank	16	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	o	+	+	+	o	(—)	—	—	—	—	+	+	+	+	+
	Brokopondo	17	+	+	+	+	(+)	+	+	+	+	+	(+)	+	+	o	+	+	+	+	+	o	—	—	—*	—*	—	+	+	+	+	+
	A 138	21	+	+	+	+	+	+	—*	+	+	o	o	o	o	+	+	o	+	+	+	o	—	—	—*	—*	—	+	+	+	o	o
	C 9/9	22	+	+	+	+	+	+	o	+	+	+	+	+	+	o	+	o	+	+	(+)	+	—	(—)	—	—	—	+	+	+	+	+
	O 49	23	+	+	+	+	—	+	+	+	+	+	+	+	o	o	o	o	+	o	o	o	—	(—)	(—)*	—	(—)	+	+	o	o	+
V	U.S.A. 130	3	+	+	+	+	+	+	+	+	+	+	+	+	o	+	+	o	+	+	+	—*	+	+	+	+	+	—	+	+	+	+
	Georgia Red	10	+	+	+	+	+	+	o	+	+	+	+	+	+	+	+	o	+	o	o	o	+	+	+	+	+	+	—	o	+	—
	Blauwkop	11	+	+	+	+	o	+	+	+	+	o	o	o	o	+	+	o	+	+	+	o	+	+	+	+	+	+	+	—*	o	o
	Sunny Side	15	+	+	+	+	(+)	+	o	+	+	+	+	o	+	o	o	o	+	o	o	o	+	+	+	+	+	+	+	o	+	+
	Louisiana 6	19	+	+	+	+	(+)	+	o	+	+	+	+	+	+	o	+	+	+	+	+	+	+	+	+	+	+	+	(—)	o	+	—

Mother clones	Combi-nations	Grains per stigma	% germinated	% of germinated grains in upper style	Tubes per style			Seeds per pollination based on:	
					upper style	mid style	lower style	field data	in vitro assessment
Djarak	17	90	23.6	16.2	3.5	1.4	1.0	0.09	0.06
Hopi	13	79	21.2	15.6	2.6	1.0	0.3	0.07	0.04
U.S.A. 130	27	68	33.5	23.1	5.3	2.1	1.6	0.08	0.06
White Star	16	66	29.3	26.2	5.0	2.4	1.3	0.15	0.18
Butikatoka	14	52	34.9	13.4	2.4	0.1	0.0	0.05	0.02
Genjem 1 (1970)	14	115	13.3	9.0	1.4	0.8	0.7	(0.11)	—
Genjem 2	14	121	14.9	9.5	1.7	0.6	0.4	(0.14)	0.00
Goldrush	13	85	16.4	18.9	2.6	1.1	0.8	—	0.01
Centennial	16	94	27.6	20.0	5.2	2.6	1.3	0.11	0.14
Georgia Red	22	73	23.6	16.9	4.0	1.2	0.9	0.15	0.12
Blanquita	11	57	34.5	17.7	3.5	1.0	0.0	—	—
Blauwkop	20	35	50.1	23.6	4.2	1.5	0.7	0.10	0.06
Sunny Side	21	70	34.3	16.3	3.9	1.8	1.7	0.18	0.17
Willemsrank	23	75	42.0	23.3	7.4	4.0	2.4	0.10	0.09
Brokopondo	23	69	20.1	24.8	3.4	1.8	1.1	0.09	0.06
Louisiana 2	22	80	27.6	29.1	6.5	2.5	1.3	0.27	0.31
Louisiana 6	25	119	18.0	13.1	2.8	1.6	1.5	0.21	0.20
A 28/7	13	75	25.8	19.1	3.7	1.7	1.1	0.19	(0.42)
A 138	16	71	56.3	16.3	6.5	1.0	0.2	0.17	0.16
C 9/9	21	65	24.5	25.5	4.0	2.2	1.5	0.07	0.07
O 49	15	61	31.9	20.3	3.9	2.4	2.0	(0.12)	(0.10)
Okinawa 2	6	70	26.0	16.1	2.9	0.2	0.0	(0.13)	(0.09)
U.S.A. 21 X	14	123	17.1	18.8	4.0	2.4	2.3	(0.30)	(0.19)
Louisiana 3	11	144	16.6	15.0	3.6	1.9	1.8	—	—
Louisiana 5	13	118	14.5	23.2	2.2	1.3	0.8	—	—
Puteri Selatan	20	124	18.0	22.8	5.0	2.2	1.9	—	—
Palumeu	9	59	12.5	33.9	2.5	0.7	0.4	—	—
Tox Paars	12	115	16.5	19.4	3.7	2.2	1.8	—	—
average		85	25.9	19.5	3.8	1.7	1.1	0.12	0.10
range		35 – 144	12.5 – 56.3	9.0 – 33.9	1.4 – 7.4	0.1 – 4.0	0.0 – 2.4	0.05 – 0.30	0.00 – 0.42

Table 6. Average values of pollen germination, style penetration and pollen tube numbers in different regions of the style four hours after pollination in compatible matings of sweet potato. Seed set data are added for comparison.

Values in brackets are based on less than 5 cross-combinations.

TABLE 7

Stainability of pollen collected at 8.00 and 10.00 h in acetocarmine (AC) and lactophenol cotton blue (LC) for three sweet potato cultivars

	AC						LC	
	Djarak		Butikatoka		USA 130		Buti'ka	USA 130
	8.00	10.00	8.00	10.00	8.00	10.00	8.00	8.00
Number of flowers	24	25	29	17	19	15	10	11
Pollen grains counted	7161	8098	11633	7372	6952	5053	4884	3950
Well-stained	4967	5558	8170	5212	4238	2919	3966	2720
% well-stained	69	69	70	71	61	58	81	69

TABLE 8

Average percentages stainability in four tetrazolium salts (TTC, TR, INT and MTT), acetocarmine (AC) and lactophenol cotton blue (LC) of pollen from seven sweet potato cultivars. Averages computed from 10 replications

Clone	TTC 2%	TR 2%	INT 1%	MTT 1%	AC	LC	Average
Brokopondo	28	39	63	57	73	72	55
Willemsrank	15	24	37	42	33	58	35
Hopi	12	44	63	63	69	75	54
USA 130	19	40	63	64	79	81	58
White Star	29	48	63	66	69	81	59
Djarak	35	55	76	72	81	84	67
Butikatoka	56	69	74	71	75	77	70
Average	28	46	63	62	68	75	-

TABLE 9

Average percentages stainable pollen from cultivar Brokopondo collected at three different times

Solution	7.00 h	10.00	13.00
TTC 2%	28	23	9
TR 2%	39	38	17
INT 1%	63	65	46
MTT 1%	59	54	44
AC	73	77	70
LC	72	71	68

Mother clones	Seed weight (mg)								% not emerged
	≥10	11–13	14–16	17–19	20–22	23–25	26–28	total	
Djarak	5 (5)	6 (5)	7 (4)	29 (2)	23 (3)	–	–	70 (19)	27
Hopi	9 (9)	3 (3)	5 (3)	6	16 (1)	9 (1)	–	48 (17)	35
U.S.A. 130	19 (18)	6 (6)	11 (7)	43 (13)	29 (11)	11 (2)	–	119 (57)	48
White Star	4 (4)	5 (5)	6 (6)	18 (7)	47 (12)	7 (1)	1	88 (35)	40
Butikatoka	3 (3)	5 (4)	4 (3)	–	7 (2)	–	–	19 (12)	63
Genjem 1	5 (5)	1 (1)	2 (2)	2	2 (1)	1	–	13 (9)	69
Genjem 2	6 (6)	2 (2)	5 (5)	7 (1)	8 (1)	1	–	29 (15)	52
Goldrush	–	–	–	–	2 (1)	–	–	3 (1)	–
Egeida	–	–	2	8 (2)	1 (1)	–	–	11 (3)	27
Centennial	3 (3)	6 (4)	7 (4)	8 (5)	8 (1)	18 (5)	6 (1)	56 (23)	41
Georgia Red	6 (6)	6 (5)	19 (7)	22 (4)	11 (1)	–	–	64 (23)	36
Blauwkop	28 (28)	18 (11)	11 (1)	1 (1)	–	–	–	58 (41)	71
Julian	1 (1)	–	1 (1)	–	2	5	–	9 (2)	22
Sunny Side	–	7 (3)	16	16	1	–	–	40 (3)	8
Willemsrank	14 (14)	5 (5)	12 (4)	28 (8)	23 (1)	5	–	87 (32)	37
Brokopondo	6 (6)	4 (4)	7 (5)	5 (2)	16	10 (1)	3	51 (18)	35
Louisiana 2	16 (16)	11 (11)	8 (6)	13 (5)	38 (9)	23 (4)	–	109 (51)	47
Louisiana 6	2 (2)	–	2 (2)	4 (2)	4 (1)	3 (1)	–	15 (8)	53
A 28/7	4 (4)	6 (6)	6 (4)	6 (2)	–	–	–	22 (16)	73
A 138	44 (43)	40 (33)	51 (26)	69 (16)	17 (2)	1	–	222 (120)	54
O 49	2 (2)	–	–	–	–	–	–	2 (2)	–
C 9/9	5 (5)	4 (2)	10 (3)	2 (2)	–	–	–	21 (12)	57
Okinawa 2	–	–	1	–	–	–	–	1	–
U.S.A. 21 X	–	2 (2)	1	7 (1)	2	–	–	12 (5)	42
total	182 (180)	137 (112)	194 (93)	295 (75)	257 (48)	94 (15)	10 (1)	1169 (542)	46
% of grand total	15.6	11.7	16.6	25.2	22.0	8.0	0.9	100.0	
% not emerged	99	82	48	25	19	16	10		

Table 10. Percentages of emerged seeds and distribution over seed-weight classes for a number of sweet potato cultivars. Numbers in brackets indicate non-emerged plants.