QUEENSLAND DEPARTMENT OF PRIMARY INDUSTRIES
DIVISION OF PLANT INDUSTRY BULLETIN No. 401

EFFECTS OF CHROMOSOME DOUBLING ON RONPHA GRASS, A NATURAL PENTAPLOID PHALARIS HYBRID

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SUMMARY

Fertile amphidiploids (2n = 70 chromosomes) were produced by chromosome doubling induced by colchicine treatment. Pollen grain size in the C_0 and C_1 generations was 18-19% higher than in the initial hybrid, and percentage of stainable pollen grains was increased from 2-4% to 88%.

A return to fertility in the C_0 to C_2 generations was evidenced by seed production.

I. INTRODUCTION

Irrigation has extended the use of temperate pasture species into the subtropical sub-coastal area of Central Queensland, which is beyond their generally recognized region of adaptation. The requirements for a pasture grass suitable for these conditions include vigorous cool-season production, moderate summer dormancy and compatibility with Ladino white clover (*Trifolium repens* var. *latum*), the most productive and persistent clover variety under these conditions. Temperate grasses, such as ryegrasses, cocksfoot and *Phalaris tuberosa,* have a short season of active growth in this environment and their persistence has been poor in Ladino clover swards.

A number of species and varieties of the genus *Phalaris* were introduced and tested in order to find material suited to these conditions. They included both indigenous and bred strains from the Mediterranean environment, South Africa and the United States of America. *P. arundinacea* is winter-dormant, although it provides a seasonal balanced pasture with Ladino clover from October to the frosts of the following winter.

An introduction from South Africa, Ronpha grass, apparently a sterile natural interspecific hybrid between *P. tuberosa* L. var. *stenoptera* (Hack.) Hitchc. and *P. arundinacea* L., has exhibited attractive agronomic characteristics, namely superior leafiness, cool-season growth, and compatibility with Ladino clover in mixed sward. To facilitate establishment, the production of a fertile strain of Ronpha grass seemed desirable, and to this end the possibilities of utilizing an amphidiploid were considered. This report is an account of the work initiated in 1957-58 following the introduction of the spontaneous hybrid.

II. REVIEW OF LITERATURE

Reference to natural and artificial hybrids between species of the genus *Phalaris* has been made by a number of workers.

A natural 42-chromosome hybrid, *P. arundinacea* x *P. tuberosa* var. *stenoptera,* was described by Love and Mohrdieck (1955). Earlier, the occurrence of natural hybrids between *P. minor* and *P. tuberosa* and between plants of *P. arundinacea* and *P. tuberosa* in South Australia was reported by Trumble (1935). The production of fertile derivatives from the cross *P. arundinacea* x *P. tuberosa* was considered desirable by Trumble because "of the attractiveness of some plants," and "new possibilities are indicated in the breeding of improved strains for irrigated or extended rainfall districts".

Liebenberg (1956) described a pasture species propagated by vegetative means in the Transvaal region as a sterile hybrid of *P. tuberosa* and *P. arundinacea.* Codd (Anon. 1956) claimed that the grass was developed on Mr. T. Wassenaar's farm in the Middleburg district, Transvaal. The name Ronpha is derived from the first syllables of Rondevallei, the name of the farm, and *Phalaris.* Codd suggested that one of the parent species was a particularly leafy strain of *P. tuberosa* selected by himself over a period of years on the Prinshof Experiment Station, Pretoria.

In Nyasaland, Ronpha grass is claimed to be suited to low-rainfall areas and has a desirable winter growth habit (Anon. 1957). The South African Department of Agriculture (personal communication, 1959), indicated that Ronpha grass has been grown in South Africa with varying success under fairly diverse climatic conditions. The grass is frost-resistant; it has withstood temperatures of —5° C and is considered more frost-resistant than *P. tuberosa* var. *stenoptera.* In summer-rainfall areas, irrigation is necessary to maintain growth through a long winter. Its superior leafiness and high protein content make it a desirable supplementary winter stock feed in the summer-rainfall regions of South Africa and it is said to stand up well to heavy grazing.

Fertile reciprocal crosses between *P. arundinacea* and *P. tuberosa* were reported by Jenkin (1931) and Jenkin and Sethi (1932). It appeared that fertilization occurred much more readily when *P. arundinacea* was used as the female parent, and relatively few seeds were obtained when the cross was attempted using *P. tuberosa* as the female parent.

Trumble (1935), while investigating the possibility of a hybrid origin for *P. tuberosa,* carried out a series of interspecific crosses between *P. arundinacea, P. tuberosa, P. minor, P. coerulescens* and *P. paradoxa*. Hybridization was readily effected in most cases, the only exceptions being *P. coerulescens* x *P. paradoxa* and *P. coerulescens* x *P. arundinacea.*

A hexaploid ($2n = 42$) variety of *P. arundinacea* x *P. tuberosa* has been bred at the Welsh Plant Breeding Station. The F_1 was only partially fertile but subsequent breeding produced a highly fertile variety, S.230 (Jones 1959; Vose 1959).

Hutton (1953) produced fertile allopolyploids by hybridization and subsequent chromosome doubling from *P. tuberosa* x *P. minor* and *P. coerulescens* x *P. minor.* The allopolyploids were obtained by cutting tillers back to 2 cm from the base and painting with an excess of an aqueous solution containing 0·2% colchicine and 0·1% of the spreader "Gardinol K". These treatments were repeated for six successive days. About one panicle in 20 that developed from such plants produced one or two seeds possessing the doubled chromosome number.

Covas and Cialzeta (1953, 1954) and Cialzeta and Covas (1954) described a method of intercrossing *P. tuberosa* and *P. arundinacea* for the production of commercial interspecific hybrids. The F_1 of this cross, which was extremely vigorous but sterile, when treated with colchicine gave rise to a fertile amphidiploid which was successfully crossed with the parent species.

Interspecific hybrids between *P. tuberosa* and *P. arundinacea* at the tetraploid ($2n = 28$) and pentaploid ($2n = 35$) level were produced by Starling (1961) and McWilliam (1962) respectively, and in each case amphiploids were induced by colchicine treatment. Both authors reported on the cytological behaviour of the hybrid and the amphiploid.

The somatic chromosome number of *P. arundinacea* has been reported as 28 by seven investigators (Myers 1947). Others found chromosome numbers varying from 27 to 56. Apparently the chromosome number of *P. tuberosa* has invariably been reported as $2n = 28$.

Hutton (1953) reported a strain of *P. arundinacea* (C.P.I. 7594) as having 42 chromosomes. Hanson and Hill (1953) found a range from 27 to 35 in somatic chromosome number for *P. arundinacea.* Carnahan and Hill (1956) found 28 to 56 chromosomes in the progenies of natural pentaploid *P. arundinacea.*

McWilliam and Neal-Smith (1962) have recorded the existence of two chromosomes races of *P. arundinacea,* one tetraploid ($2n = 28$) and the other hexaploid ($2n = 42$). They have also established that the hexaploid hybridizes freely with *P. tuberosa*; under Australian conditions it has a longer growing season and is more productive in the autumn and winter than the tetraploid races.

III. MATERIALS AND METHODS

The hybrid material used was intermediate between the parental species in several morphological characters (Figure 1). Brief notes on the species and hybrids are given in Table 1.

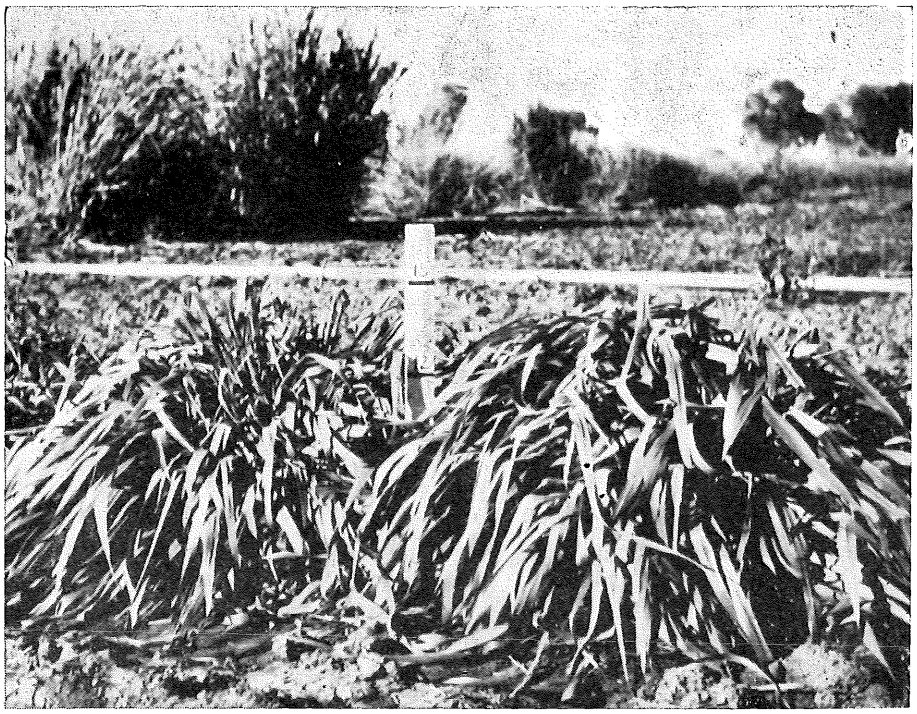

Fig. 1.—Ronpha grass, the sterile interspecific hybrid.

TABLE 1

CHARACTERISTICS OF *P. tuberosa*, *P. arundinacea* AND RONPHA GRASS

Character	*P. tuberosa*	*P. arundinacea*	Ronpha Grass
Somatic chromosome number	28	28, 42	35
Occurrence	Mediterranean region, N. and S. Africa, S. America, Australia	Europe, temperate Asia, N. America, S. Africa	Transvaal (S. Africa)
Habit in Central Queensland	Winter growth	Summer growth	Winter and summer growth
Base of shoots	Bulbous	Not swollen	Bulbous
Colour of tip of radicle ..	White-green	Red (hexaploid)	Red
Wings on the glumes ..	Prominent	Absent	Prominent
Pubescence on lower glume	Absent	Present	Present
Sterile florets	Glabrous, one minute	Pubescent	Pubescent

In order to induce chromosome doubling in the initial hybrid, clonal material of Ronpha grass was subjected to three treatments with a 0·2% aqueous solution of colchicine (Grof 1960).

In one case, after cutting the top growth back to about 2 cm from the base, the tips of the tillers were immersed in a beaker containing 0·2% colchicine for 12 hr. After treatment, the tillers were rinsed with tap water, kept in water for 1 or 2 days and transplanted into pots. Optimum growing conditions were maintained before and after treatment.

In another case, tillers were treated similarly, but to increase the penetration and effect of colchicine, partial vacuum was applied for 3-4 min. The decapitated tillers were tied in small bundles of 3-6 tillers and were suspended, by threads tied round the roots, in a conical flask containing the aqueous solution of colchicine. The flask was corked and air was pumped out through the side-arm of the flask.

The third method employed involved the injection of colchicine into decapitated tillers with a hypodermic syringe. Strong, vigorously growing tillers were cut close to the base and the colchicine solution was injected into the base of the tiller. An excessive amount of colchicine solution was injected and it was held within the rolled leaves for several hours. The treatment was repeated on 4-6 successive days; each day the fresh growth made in 24 hr was cut back.

Pollen viability was estimated on the basis of its stainability in an iodine-potassium iodide solution. Pollen grains were rated as A, B or C depending upon their individual staining reactions. Grains representative of each of these classes may be described as follows:

Class A: Non-shrivelled grains with 90% or more of their contents intensely and uniformly stained.

Class B: Grains exhibiting some stain but considered abnormal due to shrivelling, mottling, partial staining (less than 90%) and/or low intensity of stain.

Class C: Grains exhibiting no stain.

Pollen was collected from 10 plants and in each case pollen grains in 10 microscopic fields of view were measured with the aid of an eyepiece micrometer scale. At the same time their staining reactions were recorded.

The length of panicles and seed numbers per 20 randomly selected panicles of each of six C_2 plants were also determined. These data were compared with similar data from commercial *P. tuberosa* grown at two localities.

Four replicate 100-seed-weight determinations of five C_2 progenies and commercial lines of *P. tuberosa* and *P. arundinacea* were made.

The germination capacity was recorded following prechilling of the seed. The technique used was the one developed by McWilliam (1960) to break the dormancy of seed of *Phalaris* species. From each of four C_1 plants, 50 seeds were taken and placed on moistened filter paper in petri dishes and vernalized in a household refrigerator in which alternating day and night temperatures of 14°C and 4°C respectively were maintained. After this treatment, seed was transferred to room temperature and germination percentages were recorded after 7 days at room temperatures.

Chromosome numbers of Ronpha grass and progenies of colchicine-treated hybrids were determined from root-tip smears. Root-tips were pretreated in alpha-bromo-naphthalene, fixed in 1:3 acetic-alcohol, and stained in aceto-orcein. Photomicrographs were made of chromosome configurations observed.

IV. RESULTS

(a) Response to Colchicine Treatment

The plants which responded to colchicine treatment were easily recognized. The growth of these plants became greatly retarded and they produced short, thickset shoots, dark green in colour. The base of the leaves enlarged and this part of the leaf took a characteristic cup shape. There was no indication that any of the colchicine treatments used were superior in effect to any of the others.

(b) Pollen Stainability and Fertility in C_0 and C_1 Generations

The first anthesis in colchicine-treated plants planted out into small plots in October and maintained under good growing conditions was observed on January 26. At flowering, some 6% of the treated plants exhibited normal anthesis (Figure 2).

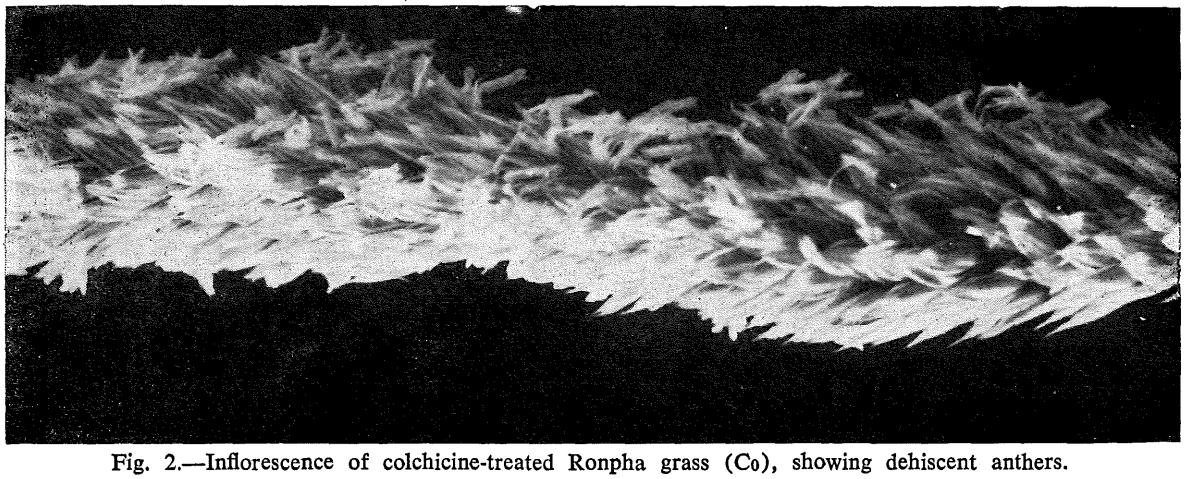

Fig. 2.—Inflorescence of colchicine-treated Ronpha grass (C_0), showing dehiscent anthers.

Very little pollen was found in the non-dehiscent anthers of the initial hybrid plants, and only 2–4% of the pollen was stainable. The mean diameter of stained pollen grains was 52μ. The dehiscent anthers of colchicine-treated plants contained 47–88% stainable pollen and the mean diameter of the pollen grains was 62μ.

Inflorescences on which anthesis occurred set seed.

Seeds of *P. tuberosa* and *P. arundinacea* develop within hard and stiff paleae of grey-brown colour and *P. arundinacea* seeds are usually the darker. The paleae of florets where the ovule has not been fertilized remain thin and white in both species, colored paleae indicating that ovule stimulation has occurred. This criterion, which was used by Jenkin (1931) to determine the rate of fertilization which occurred in *P. arundinacea* x *P. tuberosa* back-crossed to *P. tuberosa,* was also used in this study.

The collection of mature seeds was carried out daily, the first appearing a fortnight after the completion of anthesis. Altogether, numerous seeds were found with colored paleae which had caryopses in various stages of development. In the present study, only those seeds which contained a fully developed caryopsis were collected and counted.

The percentage seed set varied considerably among the individual inflorescences in the colchicine-treated material. The range was from 22 to 278 seeds per 100-cm length of inflorescence.

The coloured seeds of colchicine-treated plants showed high viability. The mean germination percentage of four progenies following prechilling of the seed ranged from 69·1 to 85·7% in 7 days.

The C_1 progenies were established as spaced plants in small plots. A wide range of variability was noted in height and vigour, date of seedhead emergence and anthesis. Inflorescences emerged from October onwards and emergence was continuous until February. In some cases seedheads were not produced at all in the first season. The late-flowering and non-flowering types exhibited very high vegetative vigour (Figure 3). The C_1 progenies extruded anthers which dehisced normally and a high percentage of apparently good pollen was found (Figure 4).

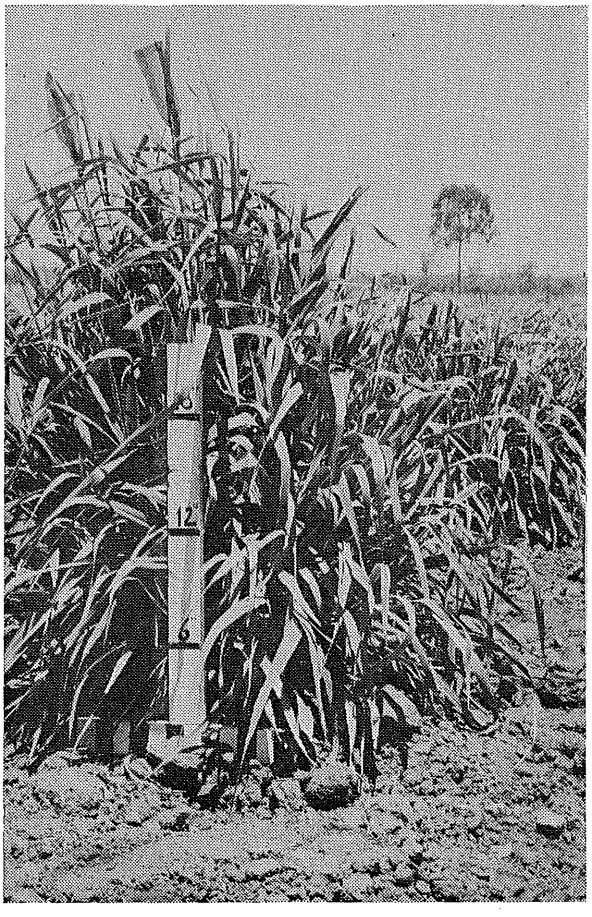

Fig. 3.—A vigorous amphidiploid plant.

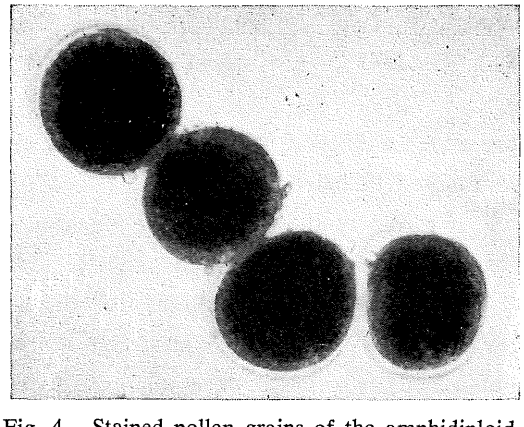

Fig. 4.—Stained pollen grains of the amphidiploid.

The mean diameter of pollen grains was 61·5μ. Pollen grain measurement of C_0 and C_1 plants showed 19 and 18% increases respectively over the pollen diameter of the initial hybrid. The results of pollen analyses are presented in Table 2.

TABLE 2

POLLEN STAINABILITY IN THE C_1 GENERATION

Plant No.	No. of Pollen Grains Examined	Percentage Pollen Grains		
		A	B	C
1	266	86·5	5·6	7·9
2	125	88·0	0·0	12·0
3	284	77·8	5·3	16·9
4	393	88·0	2·5	9·5
5	104	90·4	1·0	8·6
6	110	85·5	10·0	4·5
7	100	83·0	9·0	8·0
8	111	78·4	0·0	21·6
9	432	74·1	8·6	17·3
10	244	79·5	5·3	15·2
Means:	..	83·1	4·7	12·2

In spite of the generally high percentage of stainable pollen found among plants of the C_1 generation, seed-setting of these plants was very variable. Open-pollinated C_1 plants showed a range of types varying from low to high seed-setting ability.

The highest number of seed set in the C_1 generation was 63 per inflorescence. The self-pollinated C_1 plants showed a reduction in seed-set relative to open-pollinated plants, the maximum number of seeds obtained by self-pollination being 6 per bagged inflorescence.

The main characters of the fertile floret of the colchicine-induced amphidiploid are as follows:—

Colour: Grey-brown, not as dark as *P. arundinacea.*

Shape: Broadly lanceolate.

Length: 4–4·75 mm.

Breadth: 2 mm.

Pubescence: Covered by fine hairs except distinct bald patch in lower third.

Venation: Finely striate with 5 more or less lighter colored veins.

Sterile florets:

1st—Small, dark brown.

2nd—Somewhat larger.

Appendage present on both sterile florets, 1–1·5 mm long, covered by hairs.

The dimensions of the seed were found greater than those of either *P. tuberosa* or *P. arundinacea.*

(c) Morphological Characteristics and Fertility of the C_2 Progenies

Some 500 progenies of the C_2 generation were examined. They showed considerable variation in vigour, type of growth and percentage seed-set. However, all progenies were found to possess the winter/summer-growing habit and the winter hardiness characters of Ronpha grass. Selection was carried out in this generation for the combined characters of high vegetative vigour and seed yield.

Four C_2 progenies selected for high seed production significantly ($P<0·01$) outyielded the locally grown commercial *P. tuberosa,* but all progenies examined produced less seed than the *P. tuberosa* control grown at Hermitage in southern Queensland (Table 3). The seed set of the best-yielding amphidiploid was 74% of the maximum seed set observed in the Hermitage *P. tuberosa* control.

TABLE 3

SEED PRODUCTION OF C_2 RONPHA GRASS

Sample	No. of Seeds per Panicle	No. of Seeds per 100 cm Length of Panicle	
Control I. *P. tuberosa* ex Hermitage	190·1 ± 20·61	2,345 ± 172·6	A
C_2 Ronpha grass (1)	140·6 ± 9·47	1,364 ± 84·0	B
C_2 Ronpha grass (2)	82·4 ± 8·12	866 ± 80·0	
C_2 Ronpha grass (3)	91·6 ± 7·58	799 ± 60·8	C
C_2 Ronpha grass (4)	93·0 ± 7·99	746 ± 57·1	
Control II. *P. tuberosa* ex Biloela ..	19·9 ± 5·44	374 ± 92·1	
C_2 Ronpha grass (5)	52·2 ± 10·10	355 ± 65·5	D
C_2 Ronpha grass (6)	45·1 ± 9·12	277 ± 52·4	

A> >B> >C> >D

The C_2 progenies exceeded the commercial lines of *P. tuberosa* and *P. arundinacea* in vigour and other readily measurable attributes, e.g. plant height, length of leaves and breadth of leaves. Hundred-seed-weights of the C_2 progenies showed 21–41% increase over the seed weights of the commercial *P. tuberosa* control and 145–185% increase over the 100-seed-weights of commercial *P. arundinacea* (Table 4). Similarly, the C_2 progenies exceeded the same controls in length of panicle.

TABLE 4

SEED WEIGHT AND PANICLE LENGTH OF C_2 RONPHA GRASS

Sample	100-Seed-Weight (mg)	Length of Panicle (cm)
C_2 progeny A	246·4 ± 4·53	16·1 ± 0·41
C_2 progeny B	228·6 ± 3·65	14·4 ± 0·40
C_2 progeny C	221·2 ± 2·36	12·3 ± 0·25
C_2 progeny D	215·8 ± 2·53	11·5 ± 0·29
C_2 progeny E	212·1 ± 12·01	9·4 ± 0·27
Control I	175·2 ± 1·38	7·8 ± 0·43
Control II	86·4 ± 2·79	5·1 ± 0·27

Control I. For 100-seed-weight, *P. tuberosa* commercial Australian; for length of panicle, *P. tuberosa* ex Hermitage.

Control II. For 100-seed-weight, *P. arundinacea* commercial; for length of panicle, *P. tuberosa* ex Biloela.

Figures 5a and 5b illustrate relationships among seeds of *P. tuberosa*, *P. arundinacea* and the amphidiploid.

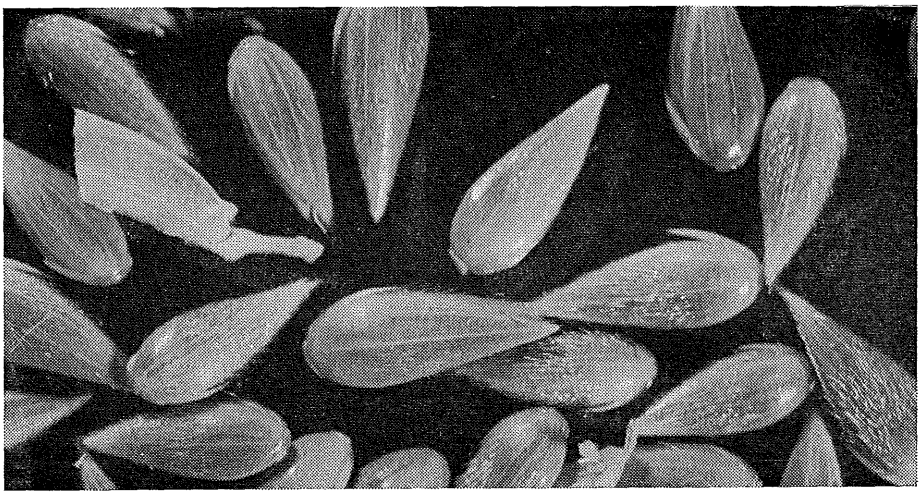

Fig. 5a.—Seeds of *P. tuberosa*.

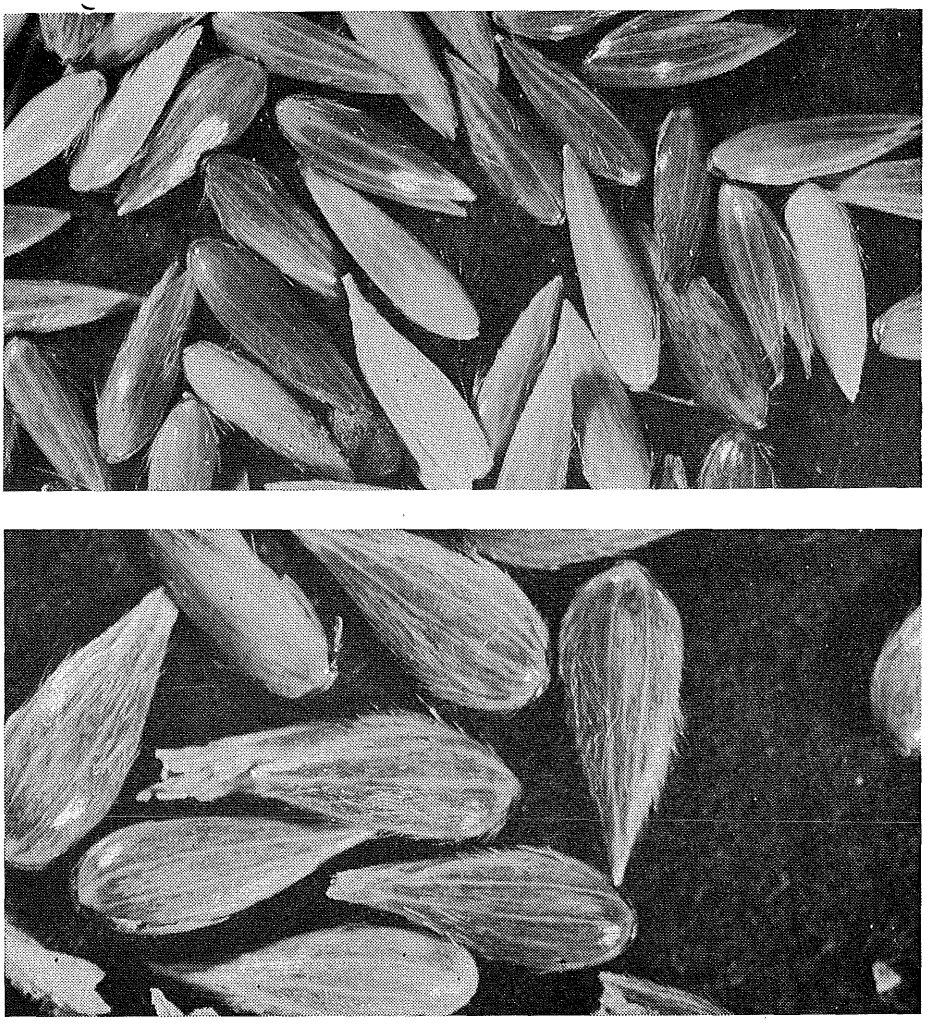

Fig. 5b—Seeds of *P. arundinacea* (top) and the amphidiploid (bottom).

(d) Somatic Chromosome Number of Ronpha Grass and the Amphidiploid

While the gross changes recorded in the experimental material indicate probable polyploidy, actual chromosome examination and counts were necessary to determine the degree of polyploidy.

The somatic chromosome numbers were determined in root-tip squashes of the hybrid and C_1 plants.

The hybrid has a chromosome complement $2n = 35$ (Figure 6). The chromosome number in the root tips of C_1 plants was determined as $2n = 70$ (Figure 7). These plants were amphidiploids, as evidenced by their double chromosome numbers relative to those of Ronpha grass ($2n = 35$).

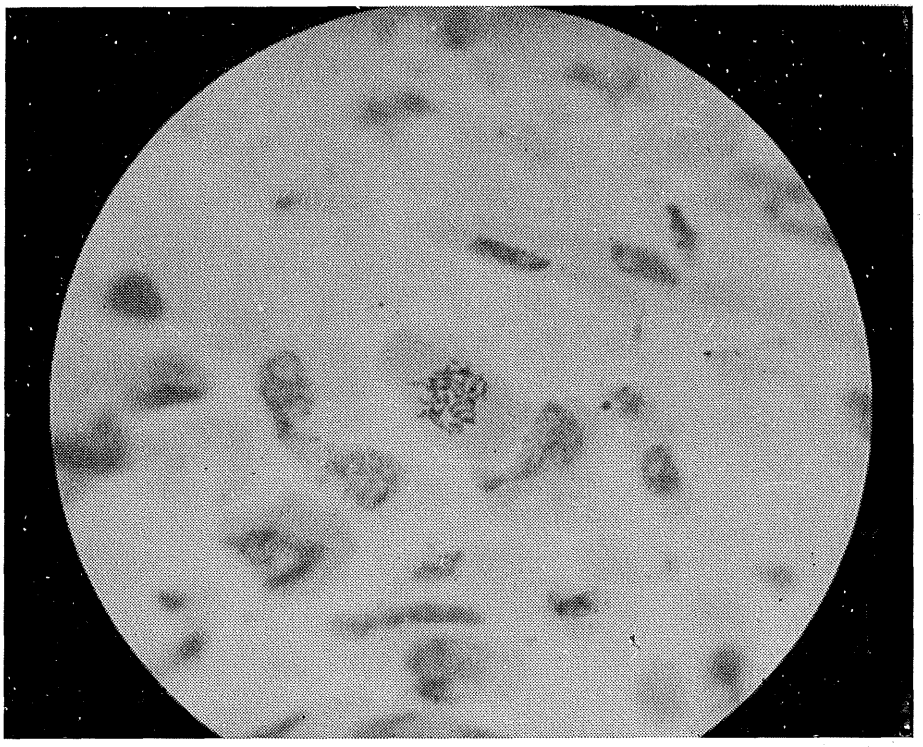

Fig. 6.—The chromosome complement of Ronpha grass ($2n = 35$) .x 450.

The cytological evidence supports the claims made by Codd (Anon. 1956) and Liebenberg (1956) that Ronpha grass is a hybrid presumably the result of a cross between a tetraploid *P. tuberosa* and a hexaploid *P. arundinacea* plant.

It is of interest that decaploidy has not previously been reported in *Phalaris,* and the C_1 plants with a somatic chromosome complement of $2n = 70$ apparently represent the highest recorded number of chromosomes in the genus *Phalaris.*

V. DISCUSSION

The primary objective, the production of fertile amphidiploids through colchicine-induced chromosome doubling in Ronpha grass, was accomplished. Of the colchicine techniques employed, the immersion of tillers in colchicine was found the most convenient for the mass treatment of clonal material. This technique has distinct advantages over the intermittent application of colchicine to individual tillers, especially when large numbers of plants are required for progeny evaluation, and results appear comparable.

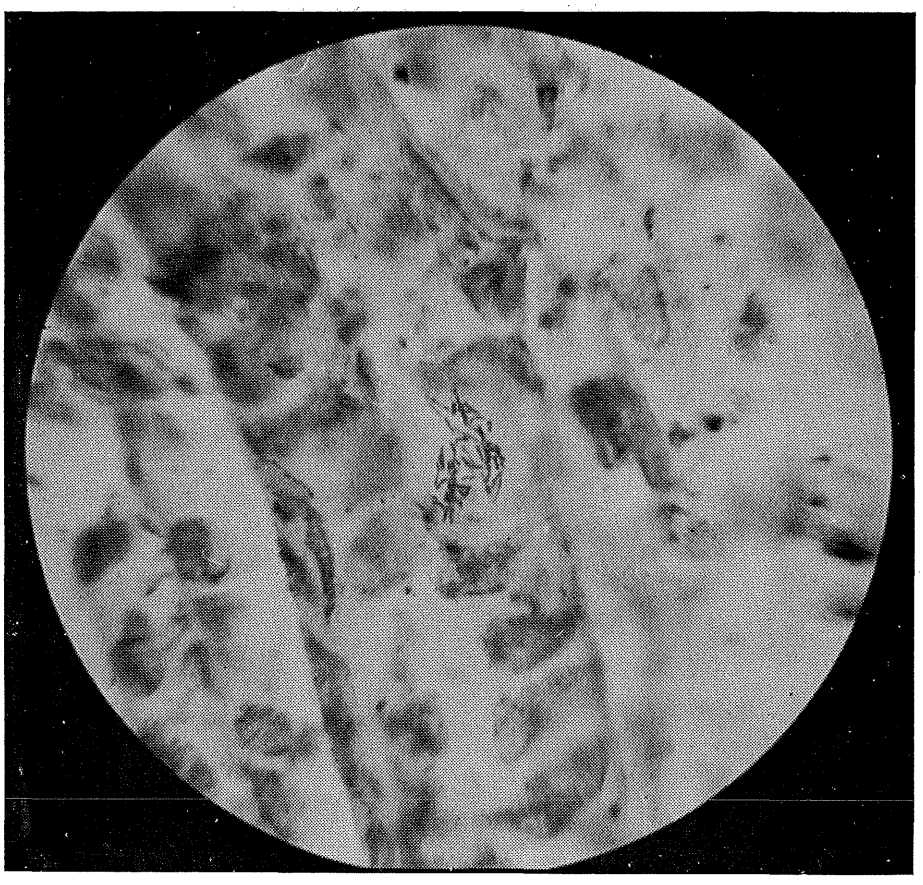

Fig. 7.—The chromosome complement of the amphidiploid ($2n = 70$) .x 450.

In view of the high frequency of bivalent associations observed in meiosis in F_1 hybrids produced by Starling (1961) and McWilliam (1962), and also in the pentaploid Ronpha grass material, considerable homology between *P. tuberosa* and *P. arundinacea* is indicated. The present work is also supporting evidence of the observation of these two authors that bivalency is the predominant chromosome association in the amphidiploid as well. Starling (1961), supported by McWilliam, suggests that "in these species of *Phalaris* a genotypically controlled tendency towards bivalent formation may be active".

Selections possessing the desirable characters and similar maturity times were assembled in polycross nursery plots where free intercrossing was assisted by replicated alternate-row plantings. Plants from C_1 to C_4 generations which perform well in the polycross progeny tests are being used for the development of synthetic varieties.

Because of the apparent homology between the chromosomes of the two parent species, selective pairing would not necessarily be expected. Indeed, the occurrence of univalents and bridges does suggest that pairing between homoelogous rather than homoelogous chromosomes does occur. Evidence of such relationships is reflected in the high degree of segregation observed in the amphidiploid progenies.

Of particular interest from a selection point of view is the occurrence of plants in the C_1 to C_4 generations which are more vigorous than the Ronpha grass. It is realized, however, that in view of the high chromosome number of the amphidiploid and the apparent nature of chromosome associations, development of an amphidiploid strain exhibiting any degree of uniformity is likely to be a very slow process.

Because of the variability of the amphidiploid material and the extreme difficulty of obtaining anything approaching a homozygous plant, the polycross is being used to compare selections in terms of winter yield and seed set. Plants from C_1 to C_4 generations which perform well in the polycross tests are being used for the development of synthetic varieties.

VI. ACKNOWLEDGEMENTS

Thanks are due to Departmental officers at the Biloela Research Station for their assistance in the field work, preparation of root-tip smears and micro-photography; to the late Mr. P. B. McGovern for the statistical analysis of the data; and to Dr. R. W. Downes, formerly Plant Breeder, Department of Primary Industries, for the many suggestions incorporated in the text. The helpful advice of Dr. A. J. Pritchard of the C.S.I.R.O. Cunningham Laboratory, Brisbane, on the cytological technique adopted, and his courtesy in making the initial chromosome counts in the hybrid and amphidiploid material, are also gratefully acknowledged.

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(Received for publication October 24, 1966)

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