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BOTANICAL AND AGRONOMIC STUDIES IN DIOSCOREA TRIFIDA L.f.

(Suggested short title)

STUDIES ON BOTANICAL AND AGRONOMIC CHARACTERISTICS IN CUSH-CUSH (*DIOSCOREA TRIFIDA* L.f.)

by

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A thesis submitted to the Faculty of Graduate Studies and Research in partial fulfilment of the requirements for the degree of Doctor of Philosophy.

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Montreal.

July, 1967.

ACKNOWLEDGEMENTS.

It is a pleasure to acknowledge my sincere appreciation to all who rendered assistance and provided facilities during the course of this research programme. My thanks are extended to Dr. H. A. Steppler, Head of the Agronomy Department, McGill University, whose encouragement and advice have been a source of strength since the inception of the programme. I would like to thank Dr. J. Bubar and the other members of the staff of the Agronomy Department, Macdonald College, for their help and encouragement, given freely at all times.

I owe special debts of gratitude to Dr. W. F. Grant of the Genetics Department and his staff for providing facilities and assistance during the course of the cytological investigations; - Mr. Ian Ogilvie was especially helpful with the photomicrographic and photographic work; and to Drs. E. O. Callen and R. H. Estey of the Plant Pathology Department for advice and facilities.

I wish to express my appreciation to McGill University and the University of the West Indies for concluding an arrangement whereby I was permitted to complete one year of study at the latter University and carry out field investigations under supervision of its personnel. My gratitude must be expressed also to the External Aid Office of the Government of Canada for assistance in financing the final year of study at Macdonald College.

Finally, I would like to thank the Government of Trinidad and Tobago for granting me leave to complete these studies and all my colleagues at Central Experiment Station, Trinidad, who maintained an encouraging interest during the course of the programme.

ABSTRACT.

Ph.D. Vann Courtenay Ryce Henry. Agronomy.

STUDIES ON BOTANICAL AND AGRONOMIC CHARACTERISTICS IN CUSH-CUSH (*DIOSCOREA TRIFIDA* L. f.)

The gross morphology of the Cush-cush plant (*Dioscorea trifida* L. f.) was studied. A plant description with emphasis on agronomically important characteristics is presented.

A technique for counting the chromosomes in root tip squashes was developed. Chromosome numbers observed were 2n = 72 in 4 male clones, 2n = 72 in 3 female clones, and 2n = 81 in 1 hermaphrodite clone. A chromosome count of 2n = 54 was observed in an open-pollinated seedling.

Several tests indicated slow and irregular germination in cush-cush but percentage germination of fresh seed is high. Phase change is characteristic of seedling development and change from juvenile to adult phase involves transitional phenotypes.

In low flowering populations male plants outnumbered female. A ratio of 1:1 was obtained with over 60% flowering. Some hermaphrodite plants were observed.

No relationship between sex and tuber yield was determined.

Differential yielding ability was observed between clones. Closer within-row spacings gave highest yield.

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INTRODUCTION

Cush-cush (Dioscorea trifida L.f.) is a monocotyledonous twining vine plant well adapted to growing conditions in the Caribbean area. It is a member of the Yam family and produces edible, starchy tubers which are very popular in West Indian diets. There is evidence that cush-cush was a very important yam species in Tropical America around 1900 (Jumelle, 1910) and it is still regarded as the best edible yam originating in the New World (Burkill, 1960). Since Sagot (1871) first described cush-cush as the principal yam species grown in French Guiana, many favourable comments have been made on its eating qualities. Fairchild (1899), Agricultural Explorer in the United States Department of Agriculture, regarded it as superior to other yams and recommended its serious consideration by the Florida truck farmers and Louisiana planters as a vegetable to be grown for the highest priced or fancy markets. Prain and Burkill (1936-1939) described the tubers as excellent when cooked, having a flavour not possessed by the larger yams.

It might be expected that a foodstuff with such a distinct consumer appeal would be produced in large quantities and make a significant contribution to local food production. In fact, at the present time the production of cush-cush throughout the islands of the West Indies is severely limited and, in Trinidad, the demand for it so far exceeds supply that it has become a high-priced, luxury item in local dishes.

The low production of this vegetable largely results from the primitive and uneconomical cultural methods still used by cush-cush

growers and the unimproved low-yielding cultivars they grow. Botanical information on the cush-cush plant is scanty; its growth habits and requirements for successful development and tuber production have not been recorded; and the range of variation of characters which may provide scope for improvement by selection is not known.

The overall objective of the programme of research reported herein is to provide botanical and agronomic information on which a crop improvement programme may be based. The botanical part of the project involved studies in 3 major divisions of botany, viz., morphology, cytology and plant physiology. The morphological studies were directed toward providing as complete a description as possible of the external characteristics of the plant noting the range of variation in characters of agronomic importance. Anatomical investigations were undertaken whenever these seemed essential for a clearer understanding of external features. The cytological studies involved the development of techniques for determining chromosome numbers in the species. The plant physiological studies were restricted to investigations on germination and seedling growth.

The second part of the programme consisted of agronomic investigation of the efficiency of Dioscorea trifida as a tuber producer. Seed size and spacing studies were conducted. Different clonal types of cush-cush were tested for yielding ability and the species was also compared with other common yams (D. alata).

Finally, sex expression in Dioscorea trifida was investigated and the relation between sex and tuber yield was examined.

For convenience these several areas of study shall be considered

separately in the review of pertinent literature, the description of materials and methods, and the presentation of experimental results.

REVIEW OF LITERATURE

Nomenclature

The name Dioscorea trifida first appeared in "Supplementum plantarum systematis vegetabilium" by Linnaeus, fil. (1781). Since that time many synonyms have been used. de Noter (1913) referred to Dioscorea triloba Linné which he stated was synonymous with D. affinis Kunth, D. truncata Miguel and D. trifida Meyer. He also claimed to have received specimens of D. triloba Linné from China bearing the name D. Dregeana. Knuth (in Engler, 1924) recorded 9 synonyms of D. trifida L.f. which have also been used to designate the species. These are as follows:

D. triloba Lam.

D. brasiliensis Willd.

D. palmata Juss.

D. brasiliana Poir.

D. quinquelobata Vell.

D. articulata Steud.

D. goyazensis Griseb.

D. affinis Kunth.

D. ruiziana Klotzsch.

The species described by de Noter (1913) was probably Dioscorea trifida L.f., although the authorities cited, Meyer and Linné, have not been seen associated with the names D. trifida and D. triloba elsewhere in the literature. D. dregeana, according to Burkill (1960), is an African species.

Relatively few common names of Dioscorea trifida have been recorded in the literature. It has been called Indian Yam, Cush-cush and Yampee (or Yampi) in Trinidad (Hart, 1898) and Jamaica (Harris, 1906). Jumelle (1910) mentioned the names Cousse-couche (used in the French Antilles) and Aje (used in Cuba). In French Guiana, Indian Yam is the name most commonly used (Sagot, 1871), and the species is known as Mapuey in Puerto Rico. It is probable that the yam which Kinman (1921) called Mapuey Morado is D. trifida. In a personal communication, Taylor (1964) cited Cara mimosa as the common name given to D. trifida by Pio Correia in Diccionario Plantas Uties do Brasil.

Distribution and Origin

In the original description, Linnaeus, f. named Surinam as the habitat of Dioscorea trifida. Several reports have since appeared in the literature indicating fairly wide distribution of the species throughout tropical America. It has been reported as far south as 16° South latitude in Mato Grosso in Brazil (Knuth, 1924) and as far north as 23° North latitude in Cuba (Jumelle, 1910). It is found between 52° West longitude in French Guiana (Grisebach, 1864; Sagot, 1871; and others) and 79.50° West longitude in Balao, Ecuador (Knuth, 1924). D. trifida is also known in most of the West Indian islands as well as in the South American countries of Guyana (formerly British Guiana - Hart, 1898), Peru, and the Rio Negro and Amazonas regions of Brazil (Knuth, 1924).

Prain and Burkill (1936-1939) reported that the only region outside tropical America in which Dioscorea trifida has found prominence is in Ceylon where it was established since around 1917. Attempts to

grow it in Calcutta and elsewhere in India have failed. Prain and Burkill suggested that perhaps the smallness of its tubers has in the past hindered its transportation to the Old World.

A few authors have offered suggestions as to the place of origin of Dioscorea trifida. de Candolle (1882) considered the name Indian Yam in Surinam to be indicative of origin in that country. Jumelle (1910) referred to the species as originating in Tropical America, and Britton and Wilson (1924) called it a native of South America. Burkill (1960) also indicated its New World origin.

Taxonomy

Dioscorea trifida is a member of the botanical family Dioscoreaceae. The plants in this family have been described in Gray's Manual of Botany (Eighth Edition, 1950) as usually having "twining stems from large tuberous roots or knotted to smooth rhizomes and ribbed and netted veined petioled leaves, small dioecious 3- or 4-androus and regular flowers, with 6-cleft calyx-like perianth adherent in the pistillate plant to the 3-locular ovary, styles 3, distinct."

Dioscoreaceae belongs with 8 other families (including Liliaceae, Amaryllidaceae and Iridaceae) to the botanical order Liliales (Burkill, 1960). It is a family of mainly tropical and warm temperate plants (Hutchison, 1934). Its evolution and phylogenetic relationships with other members of the order have been traced by Burkill (1960) who also noted the unsatisfactory state of taxonomy within the Dioscoreaceae itself. While a number of taxonomic arrangements have been proposed (notably by Grisebach, 1864; Uline in Engler and Prantl., 1897; Knuth in Engler,

1924), there has been no general agreement on a single classification of the family. Burkill (1960), after a comprehensive review of the relevant literature, proposed, as a first step in clarifying the position, the subdivision of the family into the para-Dioscoreeae and the Dioscoreeae. The following is an abridged version of Burkill's proposal:

Plants with hermaphrodite flowers . . . the para-Dioscoreeae

Plants dioecious . . . . . the Dioscoreeae

Fruit a capsule . . . . . Dioscorea

Fruit a samara . . . . . Rajania

Fruit a berry . . . . . Tamus

Knuth (1924) reported 654 species in the Dioscoreaceae. Of these, 614 belong to the genus Dioscorea. New species have been identified and added to this list since Knuth's publication.

Dioscorea trifida belongs to the subgenus Eudioscorea and section Macrogynodium (Knuth, 1924). The following abridged and modified extracts from Knuth's (1924) Key to the Dioscorea indicate the taxonomic relationships existing between the section Macrogynodium and other sections comprising many of the species of Dioscorea mentioned from time to time in this dissertation.

Dioscorea L.

The Subgenera

A. Seeds with long wing below . . . . . Subg. I. Helmia

B. Seeds encircled by a slightly wavy membranous wing . . . . . Subg. II. Eudioscorea

C. Seeds winged above. Tubers entirely below ground . . . . . Subg. III. Stenophora

D. Seeds winged upwards. Tubers partly above ground, large, ligno-suberized externally . . Subg. IV. Testudinaria

Subg. II. Eudioscorea Pax.

A. Capsule obovate, elliptical or almost orbicular.

Leaves entire, sometimes lobed.

a. Fertile stamens 6.

a'. Capsule large.

I. Male flowers in cymose clusters.

Rudimentary style large. - Mexico, Central and South America . . . . . Sect. 18. Macrogynodium
Incl. D. trifida
D. bernoulliana

II. Male flowers in dense clusters or heads, rarely solitary, sessile.

Rudimentary style usually absent.

1. Stamens of the same length.

+ Capsule longer than broad.

Mexico, South America . . . . Sect. 19. Apodostemon
Incl. D. mexicana
D. spiculiflora

++ Capsule . . . . . .

2. Stamens 3 long, 3 short. - Mexico
Sect. 21. Heterostemon
Incl. D. composita
D. floribunda

. . . . . .

V. Male flowers solitary, rarely in clusters. Stems ± prickles. Leaves entire. - Asia and Trop. Pacific Islands
Sect. 24. Combilium
Incl. D. esculenta

. . . . . .

b. Fertile stamens 3, with alternating staminodes.

a'. Glabrous. - America

I. Male flowers solitary . . . . .

II. Male flowers pedicellate, in clusters.

1. Stamens long . . . . .

2. Stamens short, staminoides thread-like. Stigmas short. - Central America, Brazil . . . . . Sect. 32. Brachystigma Incl. D. simuata.

III. Male flowers sessile, in heads, rarely scorpoid. Mexico to Argentina . . . Sect. 33. Lychnostemon Incl. D. polygonoides

b'. Pilose. - Africa . . . . . Sect. 34. Macrocarpaea Incl. D. preussii

. . . . . .

B. Capsule broader than long. Leaves entire, uppermost lobed.

a. Leaves alternate. Male inflorescence branched. Stamens epipetalous. - America.

a'. Male flowers sessile, membranous . . . . .

b'. Male flowers pedicellate, not very fleshy.

I. Stamens 6.

1. Style very short . . . . .

2. Style long . . . . . Sect. 47. Lasiogyne Incl. D. discolor

. . . . . .

d. Leaves opposite, rarely alternate. Spikes simple to compound, usually in compact whorls in leaf axils. Stamens central, short. - Asia, Africa, America.

a'. Stamens 6, rarely 3 aborted, pilose.

I. Stellate hairs. Perianth segments about equal. - Africa . . . . . Sect. 51. Asterotricha
Incl. D. hirtifolia

II. Plain hairs (with one exception). Perianth segments unequal. - Asia, Africa, America . . . . . Sect. 52. Enantiophyllum
Incl. D. alata
D. cagensensis
D. batatas
D. abyssinica
D. japonica
D. minutiflora
D. rotundata

It is interesting to note that while a prominent characteristic of Dioscorea trifida lies in its deeply lobed leaves, the majority of the species associated with it in the section Macrogynodium have entire leaves. The obvious dissimilarity between D. trifida and other members of the section was commented on by Prain and Burkill (1936-193) who, however, made no recommendations for its inclusion in any other section.

Morphology

The Seed

The information in the literature on the seeds of Dioscorea trifida is meagre and refers only to the fact that they are completely surrounded by a membranous wing (Knuth, 1924). Indeed, little has been written about the seeds of any of the species of Dioscorea. Burkill (1960) discussed the function of wings in evolution of the Dioscoreaceae

and advanced the view that seeds entirely encircled by wings, like the seeds of D. trifida, glide on very light air and are therefore well adapted for dispersal in regions of high forests. Such seeds would have preceded those with more limited wing development in the evolutionary process.

Regarding other components of the Dioscoreaceous seed, Smith (1916) depicted the embryo of Dioscorea villosa L. as roughly pear-shaped with a cone-like apical region and an expanded terminal region, the cotyledon. The embryo is located in a large fissure in the surrounding endosperm and thus is provided with room for the rapid growth of the cotyledon at the time of germination. Endosperm cells contain abundant reserves of hemicellulose, protein and oil. Burkill (1960) reviewed reports on the seeds of many Dioscoreaceae, including D. villosa, and found all the embryos to be similar.

The Root System

The roots of the Dioscoreaceae have received little attention in the literature, and those of Dioscorea trifida, none at all. Watt (1963) stated that the root system of yams is not extensive. Burkill (1960) recognized two different kinds of roots in the root system of Old World species of the Dioscoreaceae, viz., long, exploring, diageotropic roots which spread in the surface soil, and relatively short-lived rootlets which ramify among and below the long roots. Martin and Ortiz (1963) described the adult roots of D. floribunda and D. spiculiflora, two New World species, as adventitious roots which develop from the tuber and replace the primary fibrous root system. These adventitious

roots branch into fibrous roots and new adventitious roots continually arise from the cortex of the tuber. Old roots persist for long periods of time but their growth gradually decreases and they often die. Martin and Ortiz observed that primary and adventitious roots of Dioscorea species have well-defined vascular cylinders each limited by a double-layered endodermis. Each layer of the endodermis is marked with a Casparian strip, and conjunctive tissue encircles the individual vascular bundle. According to these authors large idioblasts with raphides are to be found in the thick starchy parenchymatous cortex. They also reported suberization of the outermost layers of cells of larger roots.

An interesting observation by Burkill (1960) was that in some Old World species the short roots may lignefy internally and, after the cortex has sloughed off, develop into thorns which protect the tuber. In some other species, the long roots may similarly develop into protective thorns.

The Stem

The stem of Dioscorea trifida is angular (Grisebach, 1864; Britton and Wilson, 1924; and others) and winged (Linnaeus, f. 1781; Grisebach, 1864; and others). Knuth (1924) maintained that the wings are confined to the lower parts of the stem and Britton and Wilson (1924) claimed that the stem is 4-angled and 4-winged. Williams and Williams (1951) and Hawley (1956) observed that stems and wings are green although the wings may be flecked with purple.

Like many members of the Dioscoreaceae, Dioscorea trifida climbs by twining. Burkill (1960) observed that stem-twiners commonly

have rough stems, purposely to prevent slipping. He expressed the view that the roughness in the Dioscoreaceae takes the form of ridges which make the stem angular in cross section.

The stem of Dioscorea trifida twines to the left (Uline, 1897; Knuth, 1924; Prain and Burkill, 1936-1937). That is to say, the twining is "sinistrorsum externe visus". (Burkill (1960) described the twining as sinistrorse or "to the left" if it appeared to an observer looking at the plant that the stem climbs toward the left hand side, or from right to left on its support. Allard (1946, 1948) and Williams and Williams (1951) used the term clockwise.) The direction of twining has been regarded by some taxonomists (Ulins, 1897; Knuth, 1924; Burkill, 1960) as an important diagnostic character in the Dioscoreaceae, and sections which have been separated on various morphological grounds have revealed these additional correlations of twining behaviour (Allard, 1948). Burkill (1960) considered the taxonomic value of twining direction to be unquestionable in respect of Old World species but contended that in the light of present knowledge, it appeared to be a less reliable character among New World species.

Regarding the internal structure of the stem of Dioscorea, Martin and Ortiz (1963) reported that the epidermis is two-layered, and a multilayered cortex of collenchyma is laid down by activity of the primary thickening meristem which also gives rise to the primary vascular tissue. The vascular bundles which are found in ground parenchyma, form a central core of several to many layers of bundles arranged in a loose ring. The vigour of the plant determines the number of such rings and upon these, in turn, depends the thickness of the stem. There is

no true secondary growth. This general view of the anatomical pattern in the stem of Dioscorea does not conflict greatly with that provided by Burkill (1960) for the family Dioscoreaceae as a whole. There is in Burkill's discussion, perhaps, a suggestion of greater orderliness in the arrangement of the vascular rings. Burkill provides additional anatomical features. He observed that the thickness of the cortex varies from species to species and a very pronounced endodermis defines the cortex inwards. The zone of vascular tissue generally starts with a girdle of sclerenchyma which frequently engulfs the common bundles but lie against and a little external to the cauline bundles. Common and cauline bundles differ structurally. And, no species has a constant number of bundles from the base of the stem to the apex. Burkill also noted that in the Dioscoreaceae, ridges and wings in the stem invariably overlie vascular bundles. A similar finding was reported by Brouwer (1953).

Burkill (1960) pointed out that although the stem of the Dioscoreaceae is provided with a great many axillary buds, it branches very sparingly. He advanced the view that the buds are under apical dominance and the more active the apex, the less the branching.

Burkill (1960) concluded that the typical stem of the Dioscorea species measures up to 1 cm. in diameter. Aerial parts of the stem may be thickest at ground level and taper upwards. On the other hand, the tendency of some stems to become thicker progressively upwards to the first assimilating leaf is not uncommon. According to this author the stem survives above ground for 6-12 months.

The Leaf

Burkill (1960) stated that the fact that so much of the foliage is heteroblastic is a family character in the Dioscoreaceae. He cited the distinction which Goebel (1900) made between heterophylly and heteroblasty; heterophylly being the production of two forms of leaves, each form serving divergently a purpose for which it is designed, while heteroblasty occurs when energy for growth fails leaving the leaf unfinished according to the measure of its failure. Burkill noted that lobing characterizes the juvenile leaves of Dioscorea sansibarensis Pax (syn: D. macroura Harms), a very large African species. He maintained that in view of this phase change in the leaves of the Dioscoreaceae, special care should be taken in selecting adult leaves whenever characterization of a species is contemplated.

Burkill (1960) stated that the typical Dioscoreaceous leaf has the following:

(a) a long petiole with a pulvinus at each end,

(b) a broad lamina with arcuate primary nerves of which only three reach the apex of the leaf,

(c) a water pore or water pores on a projecting leaf tip - a tip which develops before the rest of the leaf and which subsequently stops growing and dies also before the rest of the leaf,

and (d) reticulate nervation between the primary nerves in the leaf.

The cush-cush leaf as described in the literature is highly variable in size and shape. The petiole may or may not be winged (Williams and Williams, 1951) and may or may not be angular (Knuth, 1924). It varies in length from 5 to 18 cm. (Knuth, 1924). The leaf blade is

membranous (Knuth, 1924), 3-5 lobed, and deeply cordate at the base (Grisebach, 1864; Jumelle, 1910; Knuth, 1924). Jumelle (1910) considered the upper leaves to be mainly 3-lobed whilst the lower ones are mainly 5-lobed. The nerves on the dorsal side of the lamina may be slightly pilose and punctuated by pellucid lines (Grisebach, 1864; Knuth, 1924; Britton and Wilson, 1924). Up to 13 nerves have been observed in the leaf (Knuth, 1924) and the 3 central ones are located in the middle lobe (Grisebach, 1864; Knuth, 1924). The central or middle lobe has been described as oblanceolate (Knuth, 1924), or ovate-lanceolate to elliptic or oval (Britton and Wilson, 1924) and may be 9 to 25 cm. long (Knuth, 1924; Britton and Wilson, 1924). The lateral lobes are somewhat shorter and some of them may be suppressed or absent (Knuth, 1924). The overall width of the leaf varies from 8 to 25 cm. (Britton and Wilson, 1924; Knuth, 1924).

The Inflorescence

Burkill (1960) reported that in most of the Dioscorea species the male flowers are borne in cymes.

The inflorescences of Dioscorea trifida have been variously described by Grisebach (1864), Knuth (1924) and Britton and Wilson (1924). Grisebach and Knuth described the female inflorescence as a spike whilst Britton and Wilson called it a long, slender raceme. The male inflorescence was defined by Grisebach as a slender, simple raceme, and by Knuth as a raceme occurring in clusters of 3 to 5. Britton and Wilson described it as a long, slender, sometimes whorled, panicled spike. Knuth reported that the male flowers may be solitary or somewhat clustered

on the axis of the inflorescence and that the leaves on the reproductive branches are short and nearly sessile. Prain and Burkill (1936-1939) contended that whenever two male flowers appeared to occur at the same site on the axis of the inflorescence, the second flower arose on the short pedicel of the first.

There is general agreement among taxonomists that the axes of male and female inflorescences of Dioscorea trifida are hairy. Britton and Wilson (1924) pointed out that male and female inflorescences are subtended by lanceolate, acuminate bracts about 2 mm long.

The Flower and Pollination

Burkill (1960) described the general floral characteristics in the Dioscoreaceae in the following floral formulae:

$$K_3 C_3 A_{3+3} \bar{G}_3 \quad \text{or} \quad K_3 C_3 A_{3+0} \bar{G}_3$$

Knuth (1924) used the term perianth in place of corolla and calyx in his description of the flowers of Dioscorea trifida. He stated that the perianth segments are oblong-lanceolate, acuminate or acute and about 3 mm. long. The male flowers have 6 fertile stamens with long filaments curved inwards inserted at the base of the perianth segments.

The anthers are oblong, curved, introrse and there is a thick, conical 3-lobed rudimentary style. In the female flower there are 6 rudimentary stamens, a densely hairy ovary, a prominent stylar column with a 2-lobed apex and terete deeply curved stigmas. The floral descriptions reported by Britton and Wilson (1924), although less comprehensive, are in general agreement with Knuth's (1924) statement (above).

Burkill (1960) noted that the hermaphrodite flowers of the para Dioscoreeae are larger than the unisexual flowers of the Dioscoreeae. He commented that there is nothing unusual in the reduction in the size of the flower when one sex is missing. He cited the female flowers in the gynodioecious Labiatae which are smaller than the hermaphrodite flowers and reasoned that an interlocking of greater size with bisexuality characterizes the flowering plants. In this connection, it is interesting to note Martin's (1966) report that a hermaphrodite hybrid from the cross Dioscorea floribunda x D. composita had smaller flowers than a female hybrid and that the stamens were somewhat shorter than those of the corresponding male hybrid.

Burkill (1960) maintained that the insects which pollinate the flowers of the Old World Dioscoreaceae must be flying insects since they must fly to get from male to female plants. He mentioned the flower of Dioscorea ovinala Baker which is set among hairs in such a manner as to make the approach by flying easier than by crawling.

Burkill (1960) recorded the usual diameter of the flowers of the Dioscoreaceae as 2 to 5 mm. but noted that reports of much larger dimensions had been made.

The Fruit

Jumelle (1910) described the fruit of Dioscorea trifida as a 3-lobed capsule with a persistent style on its upper end. Prain and Burkill (1936-1939) called it a reflexed, elongated capsule. Knuth (1924) reported minute pubescence on the capsule which he observed to be oblong in shape with a rounded base and sub-acute apex. The reported

dimensions of the capsule are 27 to 30 mm. long (Jumelle, 1910; Knuth, 1924) and 17 mm. wide (Knuth, 1924).

The Tuber

Burkill (1960) advanced the view that some species of Dioscorea produce tubers and others produce rhizomes. The rhizome or tuber grows out from some part of the hypocotyl of the germinating seedling and thereafter develops by plagiotropic lobing.

Dioscorea trifida produces tubers (Linnaeus, 1871; Jumelle, 1910; Prain and Burkill, 1936-1939; and others). Prain and Burkill (1936-1939) stated that the tubers, which are produced in clusters, are relatively small, the maximum length being about 12 inches. They found the average tuber to be about 9 inches long and 3-4 inches in diameter. Jumelle (1910) noted that some tubers are cylindrical in shape while others are round. Williams (1925) reported tubers which are hand-shaped, pear-shaped, and testiculate. Flesh colour in cush-cush tubers may be white or purple (Williams, 1925).

Williams and Williams (1951) observed that cush-cush forms a rosette of more or less fleshy structures above the main tubers and smaller tubers may be formed at the ends of these structures.

Cytology

No report on the chromosomes of Dioscorea trifida has been observed in the literature. However, it is evident that many other dioecious species of the Dioscoreaceae have been regarded by cytologists

as favourable material for studying chromosomes, especially sex chromosomes.

Prochromosomes

Swanson (1957) described prochromosomes as specialized portions of the chromatin which, unlike other portions, stain deeply during interphase. They are sometimes called chromocenters and the word heterochromatin was first coined to designate this precocious chromatin. Riley (1948) noted that the prochromosomes may be fewer, or more numerous, than the chromosomes but frequently exist in the same number.

Suessenguth (1921), in his work on nuclear divisions in certain Monocotyledons, gave special attention to the condition of the chromosomes in the vegetative cells of Dioscorea sinuata Vell., a subtropical South American species. He reported prochromosomes with distinctly marked contours in the resting nucleus. Generally, 20 to 25 prochromosomes were observed in the cell nuclei of root tips, but if the prochromosomes were large only half this number could be seen. Neurman (1925) also working with D. sinuata, found that the number of prochromosomes in the resting nucleus varied from 3 to more than 30. In 1937, Smith discussed the cytology of 13 species of Dioscorea and maintained that the nuclei of these species are of Manton's (1935) vesicular type with a single large nucleolus and prochromosomes arranged about the periphery of the resting nucleus. Smith did not attempt to count the prochromosomes but noted that they were more numerous in the species with the higher numbered metaphase complements. Martin and Ortiz (1963) observed that a preponderance of root tip cells with well-developed prochromosomes of the vesicular type made counting of chromosomes in root tip squashes in

13 species of Dioscorea confusing and tedious.

Chromosome Numbers

The evidence in the literature suggests that at least 3 basic chromosome numbers are to be found in the genus Dioscorea, and that these basic numbers may be associated with different geographical regions. For convenience, the chromosome numbers and probable origin of species reported in the literature are summarized in Table I. The author of each report and the year of publication are also stated in the Table.

The first reports on chromosome numbers in Dioscorea species were conflicting. Suessenguth (1921) reported that D. sinuata has 2n = 24 chromosomes. Meurman (1925), on the other hand, stated the number to be 2n = 35 chromosomes in the same species. The investigations of Nakajima (1933, 1936) and Smith (1937) produced counts of 2n = 20, 40, 60, 61, 64, 80, 81, 140 and 144 chromosomes in 17 species most of which originated in the Old World. It was evident that chromosome numbers which are multiples of 10 predominate, and Smith (1937) advanced the view that 10 is the basic chromosome number in the genus Dioscorea. He pointed out that only 4 out of the 17 species examined by himself and earlier investigators have diploid chromosome numbers which do not fall into a regular series of 10. Two of these aberrant species were reported as having heterogenous elements in their somatic complements which may be associated with sex determination, and the other two had large numbers of small chromosomes and the accuracy of the counts reported may be in doubt. Further support for the view that 10 is a basic chromosome number in Dioscorea species was derived from

TABLE 1.

Chromosome numbers and probable geographic origin of Dioscorea species previously reported in the literature.

Dioscorea species	Probable Geographic Origin	Chromosome Number (2n)	Authority
1. D. abyssinica Hoch.	West Africa	40	Miege, 1952
		40	Martin and Ortiz, 1963
2. D. aculeata Webster.	Africa	40	Martin and Ortiz, 1963
3. D. alata L.	South-east Asia	30	Sharma and De, 1956
		40	Miege, 1951
		40	Simmonds, 1954
		40	Sharma and De, 1956
		40	Raghavan, 1958
		40	Ramachandran, 1962
		40	Martin and Ortiz, 1963
		50	Sharma and De, 1956
		60	Raghavan, 1958
		60	Ramachandran, 1962
		60	Martin and Ortiz, 1963
		70	Sharma and De, 1956
		80	Raghavan, 1958
		80	Ramachandran, 1962
		ca 81	Smith, 1937
4. D. balkanica Kosanin.	Albania	20	Miege, 1952
5. D. batatas Decne.	South-east Asia	140	Nakajima, 1933
		144	Smith, 1937
6. D. belophylla Voight.	India	80	Raghavan, 1959
7. D. bernoulliana Prain and Burk.	Guatemala	36	Martin and Ortiz, 1966

TABLE 1 (cont'd).

Dioscorea species	Probable Geographic Origin	Chromosome Number (2n)	Authority
8. *D. bulbifera* L.	Africa or Asia	36	Miege, 1952
		40	Miege, 1951
		40	Raghavan, 1959
		40	Martin and Ortiz, 1963
		54	Miege, 1952
		60	Miege, 1954
		80	Smith, 1937
		80	Raghavan, 1959
		80	Ramachandran, 1962
		80	Martin and Ortiz, 1963
		ca 98-100	Raghavan, 1959
		100	Ramachandran, 1962
9. *D. caucasica* Lipsky.	Asia Minor	20	Meurman (n=10), 1925
		20	Smith, 1937
		20	Miege, 1952
10. *D. cayenensis* Lamk.	Tropical Africa	ca 36	Miege, 1952
		ca 54	Miege, 1952
		ca 60-63	Miege, 1954
		ca 140	Smith, 1937
11. *D. ceratandra* Uline.	Brazil	36	Martin and Ortiz, 1963
12. *D. chouardii* Gaussen.	Pyrenees	24	Heslot, 1953
13. *D. composita* Hemsl.	Mexico	36	Martin and Ortiz, 1963
		54	Martin and Ortiz, 1966
14. *D. convolvulacea* Schlect. & Cham.	Mexico	36	Martin and Ortiz, 1963
15. *D. deltoidea* Wall.	India	40	Raghavan, 1939
16. *D. discolor* Hort.	South America	40	Smith, 1937
17. *D. dumetorum* Pax.	Tropical Africa	36	Miege, 1952
		40	Miege, 1951
		45	Miege, 1952
		54	Miege, 1952

TABLE 1 (cont'd).

Dioscorea species	Probable Geographic Origin	Chromosome Number (2n)	Authority
18. D. escuintlensis Matuda.	Guatemala	36	Martin and Ortiz, 1966
19. D. esculenta Burkill.	South-east Asia	40	Miege, 1951
		90	Raghavan, 1959
		90	Ramachandran, 1962
		100	Raghavan, 1959
20. D. fargesii France.	South-east Asia	64	Smith, 1937
21. D. floribunda Mart. and Gal.	Guatemala	36	Martin and Ortiz, 1963
		54	Martin and Ortiz, 1963
		54 *	Martin and Ortiz, 1966
		72 *	Martin and Ortiz, 1966
		144 *	Martin and Ortiz, 1966
22. D. friedrichsthalii R Knuth.	Costa Rica	36	Martin and Ortiz, 1963
23. D. friedrichsthalii R Knuth.	Guatemala	36	Martin and Ortiz, 1966
24. D. galeottiana Kunth.	Mexico	48	Cox, Corzo, Matuda and Duran, 1958
		52	Cox, Corzo, Matuda and Duran, 1958
		ca 104	Medellin Leal, 1959
25. D. gracillima Miq.	Japan	20	Nakajima, 1933, 1937
26. D. hastata Miege.	Tropical Africa	>120	Miege, 1952
27. D. hirtiflora Pax.	West Africa	40	Miege, 1952
28. D. hispida Dennst.	India	40	Raghavan, 1959
29. D. hondurensis R Knuth.	British Honduras	36	Martin and Ortiz, 1966

* Obtained by colchicine treatment and hybridization.

TABLE 1 (cont'd).

	Dioscorea species	Probable Geographic Origin	Chromosome Number (2n)	Authority
30.	D. japonica Thunb.	Japan	40	Nakajima, 1942
31.	D. macroura Harms. syn: D. sansibarensis Pax.	West Africa	40	Smith, 1937
32.	D. Mangenotiana Miege.	West Africa	ca 80	Miege, 1952
33.	D. mexicana Guillemin.	Mexico	36	Martin and Ortiz, 1966
34.	D. minutiflora Engl.	Tropical Africa	>120	Miege, 1951
35.	D. oppositifolia L.	East Indies, India	40 40 ca 140	Raghavan, 1959 Ramachandran, 1962 Smith, 1937
36.	D. paniculata Michx.	U.S.A.	36	Martin and Ortiz, 1966
37.	D. pentaphylla L.	Tropical Asia	40 40 80 80 ca 144	Raghavan, 1959 Ramachandran, 1962 Raghavan, 1959 Ramachandran, 1962 Smith, 1937
38.	D. polygonoides Humb & Bonpl.	Central America	36 54	Martin and Ortiz, 1963 Martin and Ortiz, 1963
39.	D. praehensilis Benth.	West Africa	40	Miege, 1952
40.	D. preussii Pax.	Tropical Africa	40	Miege, 1952
41.	D. pubera Bl.	India	40	Raghavan, 1958
42.	D. pyrenaica Bubani		24	Heslot, 1953
43.	D. quaternata (Walt) Gmel.	North America	36 54	Martin and Ortiz, 1966 Jensen (n=27), 1937
44.	D. quinqueloba Thunb.	Japan	20	Smith, 1937
45.	D. reticulata C. Gay.		ca 61	Smith, 1937

TABLE 1 (cont'd).

	Dioscorea species	Probable Geographic Origin	Chromosome Number (2n)	Authority
46.	*D. rotundata* Poir.	Africa	40	Martin and Ortiz, 1963
47.	*D. sativa* L.	South-east Asia	40	Sharma and De, 1956
48.	*D. sativa* L.f. *spontanea* Makino.	South-east Asia	60	Nakajima, 1936
49.	*D. sinuata* Vell.	South America	ca 24 ca 35	Suessenguth, 1921 Mourman, 1925
50.	*D. smilacifolia* de Wild.	Tropical Africa	>120	Miege, 1952
51.	*D. spiculiflora* Hemsl.	Mexico	20-28 36	Cox, Corzo, Matuda and Duran, 1958 Martin and Ortiz, 1963
52.	*D. spinosa* Roxb.	India	90	Ramachandran, 1962
53.	*D. Tokoro* Makino.	Japan	20	Nakajima, 1933, 1937
54.	*D. tomentosa* Koenig.	S. India	40 60	Ramachandran, 1962 Raghavan, 1959
55.	*D. villosa* L.	North America	ca 60	Smith, 1937
56.	*D. wallichii* Hook.	India	40	Ramachandran, 1962

the reports of Sharma and De (1956), Raghavan (1959), and Ramachandran (1962). These cytologists working with several Asiatic species recorded diploid chromosome numbers which are all multiples of 10.

Heslot (1953) first suggested the occurrence of species of Dioscorea with a basic chromosome number other than 10. He reported 2n = 24 chromosomes in D. pyrenaica and D. chouardii, two species which are found in the Pyrenees, and maintained that 12 bivalents are formed regularly at heterotypic metaphase. Heslot considered that these results indicate that the Dioscoreaceae indigenous to the Pyrenees have a basic chromosome number of 12, whereas the evidence was increasingly in favour of a basic number of 10 for Dioscorea species. He drew attention to the fact that Miègeville, at the time of the original description of D. pyrenaica, indicated that this plant was different in several ways from other members of the genus Dioscorea and proposed its inclusion in a new genus which should be called Borderea. Heslot contended that the existence of a different basic chromosome number constituted an important argument in support of Miègeville's proposal for the establishment of the new genus Borderea which now should include the 2 species D. pyrenaica and D. chouardii redesignated Borderea pyrenaica and B. chouardii respectively. Heslot's view was supported by Miège (1954) who also reported 2n = 24 chromosomes in D. pyrenaica and D. chouardii.

Miège (1954) produced evidence indicating that 10 is not the only basic chromosome number in Asiatic and African species of Dioscorea. The chromosome complements of 11 African species studied by this worker vary from 2n = 36 in D. dumetorum to 2n >120 in D. hastata, D. minutiflora and D. smilacifolia. In D. dumetorum, Miège observed 2n = 36, ca 45,

and 54 chromosomes. Forms with 2n = 45 chromosomes are sterile. He concluded that a polyploid series exists in D. dumetorum ranging from 2n = 36 to 2n = 54 and suggested that the form with 2n = 45 is a hybrid in which chromosome sets of a tetraploid (9 x 4) and a hexaploid (9 x 6) are brought together. All of the other African species examined by Miège, with the exception of D. cayenensis, were found to have chromosome numbers which are multiples of 10. Regarding D. cayenensis, Smith (1937) had previously reported a chromosome complement of 2n = 140 in this species. Miège (1954), on the other hand, in a study involving 12 clones, observed some plants with 2n = 36 chromosomes and others with 2n = 54 chromosomes. Miège concluded that the species is hybrid in origin and is clearly in need of subdivision since, in addition to the cytological differences, it comprises many morphologically dissimilar forms.

Dioscorea bulbifera is believed by some authors to be actually two species, one African in origin and the other Asiatic. Other workers consider it to be a single species of Asiatic origin. Miège (1954) reported chromosome values of 2n = 36, 40, 54 and 60 in this species and contended that these counts imply the existence of two major groups or series in D. bulbifera; one series having 2n = 36 and 54 chromosomes and a basic chromosome number of 9, and another series with 2n = 40 and 60 chromosomes and a basic chromosome number of 10. Miège maintained that these cytological differences explain morphological variations and similarities in the species.

Martin and Ortiz (1963) recorded 2n = 36 and 54 in 7 New World species and 2n = 40, 60 and 80 in 6 Old World species of Dioscorea.

They noted that the chromosome numbers of the Old World species are multiples of 10 while those of the New World species are multiples of 9 and maintained that these results together with previous observations suggest that the progenitors of the New World species had a basic chromosome number of 9. Possible exceptions are the North American species complex, D. villosa, with 2n = 60 (Smith, 1937) and the South American species, D. discolor, which has 2n = 40 (Smith, 1937). In this connection however, Martin and Ortiz pointed out that D. quaternata, a part of the D. villosa complex, had been found to have 2n = 54 chromosomes (Jensen, 1937).

Martin and Ortiz (1963) noted that while the Asiatic species have chromosome numbers which are multiples of 10, those of the African species are multiples of 9 and 10. Moreover, two probably African species, Dioscorea bulbifera and D. cayenensis, both have tetraploid and hexaploid forms as well as chromosome numbers which are multiples of either 9 or 10. They maintained that these findings suggest that Africa was the centre of origin of the genus Dioscorea, and that there is a tendency for forms with the basic chromosome number of 9 to spread west, and forms with the basic chromosome number of 10 to spread east and north.

Martin and Ortiz (1966) presented further evidence in support of the view that 9 is the basic chromosome number of the genus Dioscorea throughout the Western Hemisphere. They determined the chromosome numbers in 10 named New World species, 5 of these for the first time, and found them all to be multiples of 9. They also reported for the first time the occurrence of octoploids among New World species represented by unidentified species from Costa Rica and Peru.

Speciation

Sharma and De (1956) discussed the role of polyploidy in speciation among representatives of the genus Dioscorea in Bengal, India. They stated that counts of 2n = 30, 40, 50 and 70 chromosomes which they had obtained for different individuals of D. alata demonstrated that individuals of a single species may behave as members of a polyploid series. They noted, however, that there were no marked phenotypic differences among these individuals and concluded that in Dioscorea, polyploidy alone does not result in the manifestation of detectable morphological characters. Polyploidy must have combined with other factors responsible for phenotypic changes in order to effect speciation in the genus. Sharma and De reasoned that these changes may have involved gene mutation only or, perhaps, gross structural changes in the chromosomes.

Meiotic irregularities have been observed in Dioscorea quaternata, a species with a chromosome complement of 2n = 54 (Jensen, 1937). Martin and Ortiz (1963) also reported meiotic abnormalities in two lines (with 2n = 54 chromosomes) of D. floribunda. At meiosis up to 9 quadrivalents were seen in this material as well as univalents, bridges, fragments and delayed separation of bivalents. They suggested that these anomalous lines with 2n = 54 chromosomes probably originate from backcrosses of an allotetraploid to one of its diploid progenitors followed by chromosome doubling as manifested by the quadrivalent pairing observed. However, noting subsequently the occurrence of single plants with 54 chromosomes among normal siblings, Martin and Ortiz (1966) questioned this hypothesis pointing out that production of the aberrant plants could be through the occasional fertilization of an unreduced

gamete although such an occurrence would not lead to quadrivalent pairing.

Chromosomes and Sex

The first report of sex chromosomes in Dioscorea was made by Meurman (1925). Working with D. simuata, Meurman observed an unpaired chromosome in metaphase and anaphase of the heterotypic division in pollen mother cells. He concluded that this unpaired chromosome was a sex chromosome and suggested that this could be a case of the Protenor or XO type of sex chromosomes. Meurman found no evidence of sex chromosomes in his studies of meiosis in D. caucasica. Nakajima (1937), in a study of meiosis in pollen mother cells in D. tokoro, D. gracillima and D. japonica, observed an unequal pair of chromosomes in side views of heterotypic metaphases in each of the species and assumed them to be sex chromosomes of the XY type. Jensen (1937) found no evidence of sex chromosomes in D. quaternata and contrasted meiotic abnormalities observed in the species with various accepted sex-determining apparatus to show that the latter are not justified as such. Smith (1937) reported heterochromosomes in the mitotic division figures of D. macroura, D. discolor, D. fargesii, D. reticulata and D. alata. He identified them as sex chromosomes pending investigation of the meiotic divisions of these species. He also found that D. reticulata (2n = 61) and D. alata (2n = 81) have chromosome numbers of 2n - 1 and classed them with D. simuata which Meurman (1925) suggested belongs to the Protenor (XO) type of sex chromosomes. Allen (1940) and Westergaard (1958) both commented on the suggestion that an XO type of sex mechanism exists in some species of Dioscorea. Allen stated that this type of allosome

complement is at most rare in angiosperms while Westergaard contended that Smith's (1937) demonstration of its occurrence could not be regarded as conclusive although the evidence is suggestive.

Evidence of the presence of a sex mechanism based on XY balance in Dioscorea with strong male determining genes in the Y-chromosome and female determinants in the X-chromosome was presented by Ramachandran (1962). This worker drew attention to the similarities between the sex mechanism in Dioscorea and that in Melandrium album as discussed by Westergaard (1938 - 1948) and Warmke (1939 - 1946). In the somatic complements of the male plants of tetraploid D. tomentosa and D. pentaphylla, octoploid D. bulbifera and in the nine-ploid D. spinosa, Ramachandran observed one chromosome which is much larger than the others of the respective complements. These large chromosomes are absent in female plants and Ramachandran concluded that they are similar to the Y chromosomes in Melandrium. He noted that at the different levels of polyploidy there is only one Y-chromosome and suggested that this reduction is brought about by the preferential pairing of X's and Y's. Ramachandran identified the sex chromosomes morphologically in the somatic complements by virtue of their larger size. The X-chromosomes are larger than the autosomes but smaller than the Y-chromosomes. He observed that some of the X-chromosomes are indistinguishable from the autosomes and thought it possible that some of them are undergoing transformation into autosomes as suggested by Westergaard (1940). Ramachandran noted that in the microspore mother cells of D. tomentosa the Y pairs with a smaller X and the bivalent is characterized by its relatively large size, assymetrical shape and tendency to lie towards the periphery of the metaphase plate.

Martin (1966), in a study of sex ratios and sex determination in Dioscorea, found that a strong Y chromosome, actively engaged in sex determination, is suggested.

Chromosome Size and Shape

The chromosomes of Dioscorea species are very small (Meurman, 1925; Sharma and De, 1956; Miege, 1954; and others). Sharma and De (1956) recorded dimensions of 0.45μ to 1.55μ and Ramachandran (1962), 0.5μ to 2.0μ. Some authors reported constrictions in some of the chromosomes. In some cases these are quite distinct, in others they are not (Smith, 1937; Sharma and De, 1956; Ramchandran, 1962). Sharma and De (1956) observed satellites in D. alata. Owing to the minute size of the chromosomes, the satellites are not always visible and accurate counts are difficult.

In general, the chromosomes of all the species and varieties of Dioscorea show more or less similar morphological characters (Sharma and De, 1956; Ramachandran, 1962).

Sex Expression

No report on sex expression in Dioscorea trifida was found in the literature and the information relating to the Dioscoreaceae as a whole is meagre. An anonymous writer in the Gold Coast Farmer (1935) reported on sex ratios in 6 varieties of an unnamed yam species. In 3 of the varieties, 98-100% of the plants were female; two varieties had a preponderance of males (78-98%); and one variety segregated in a male

to female ratio of 1:1. Burkill (1937) contended that there is a numerical disproportion between male and female plants in Tamus communis. He cited Brenner (1914) as stating that males are two to three times as numerous as females. In a study carried out on wild stands of T. communis in the south of England, Burkill counted 134 female plants, 295 male plants, and 125 plants which had failed to flower after 3-4 years' growth. Burkill concluded that the ratio of male to female plants in this population would be about 2:1. Martin (1966) investigated sex ratios in 5 New World species of Dioscorea. He found that in four of the species, males outnumber females significantly in open-pollinated progenies. Martin examined the progenies of controlled crosses of one of these species, D. floribunda, and noted that they segregate in either a 1:1 or 3:1 ratio. The sex ratios of progenies from common females vary according to the male parent while those of progenies of a given male are constant. Martin suggested that these results indicate the heterogeneity of males.

Germination and Seedling Growth

Studies on germination in a few species of the Dioscoreaceae have been reported in the literature. (Dioscorea trifida is not among these species). Smith (1916) experienced great difficulty in inducing the seeds of D. villosa to germinate at Madison, Wisconsin. She overcame this difficulty by keeping the seeds in soil out of doors during the winter and bringing them into the greenhouse the following spring when apparently they germinated satisfactorily. Allard (1946) reported that he sowed some seeds of D. villosa (or, D. glauca) in Virginia on

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10th November, 1937 and they germinated on 10th February, 1938. Allard did not describe the conditions under which germination was carried out. Burkill (1937), in a discussion on germination in Tamus communis, maintained that the seed is not ready to germinate when freed from the fruit but requires a period of after-ripening. He sowed 200 newly-collected seeds in the autumn of 1931 in a garden-frame at Leatherhead, England. The resulting seedlings appeared above ground in the following order:

In June, 1932	1	seedling
In early July, 1932	3	seedlings
In April and May, 1933	97	"
In April and May, 1934	76	"
In April and May, 1935	5	"
In May, 1936	5	"
Total germinated	187	seedlings

Burkill described another experiment in which seeds of Tamus communis were germinated indoors under partially controlled conditions during the winter. Once more the majority of the seeds required over 6 months for germination while, in an appreciable number, germination was delayed for an additional 12 months. These experiments led Burkill to conclude that an after-ripening period of 6 months in moist conditions is essential for the germination of the seeds of Tamus communis. He maintained that his experiments demonstrated that seeds which fail to germinate at the end of the first after-ripening period will not do so until another 12 months have passed, even though kept uniformly moist. In other words, Tamus seeds show a tendency to sink into a second dormancy if conditions are not favourable for germination when the after-ripening is complete.

The process of germination as reported for species of the Dioscoreaceae is interesting. According to Smith (1916), the embryo in the mature seed of Dioscorea villosa is very small in proportion to

the size of the seed and in relation to the fissure in the endosperm where it is located. On germination, the cotyledon increases rapidly in size, filling the entire fissure. The cotyledon remains in the seed but the primary root emerges and soon begins to give off secondary roots. The first functional leaf elongates until its tip becomes free from the seed coats. Smith maintained that the leaf is not bent over while in the seed but assumes this position on freeing itself from the seed and retains it until well above ground. Burkill (1937) described a similar sequence of events in the germination of Tamus communis. He reported, however, that the primary root of Tamus, unlike that of D. villosa, remains unbranched. Burkill expressed the view that the primary root, and later, the primary bud are pushed clear of the seed coats by the growth of the cotyledon within the seed. The torn halves of the cotyledonary sheath are also pushed out in the early stages of germination.

Burkill (1937) observed that the epicotyl appeared shortly after the emergence of the cotyledonary sheath and gives rise to the tuber as a lateral swelling. He pointed out that the epicotyl is such a small part of the plant that growth on one side must involve some growth throughout and, possibly, a little in the hypocotyl. In a subsequent publication, Burkill (1960) indicated that, in fact, it is part of the hypocotyl which takes on growth and becomes the tuber. As the tuber grows, the cotyledon dies and the emptied seed coats decay.

Martin and Ortiz (1963) described the germination of the seeds of Dioscorea floribunda and D. spiculiflora. In both species the radicle and epicotyl emerge like those of D. villosa and Tamus communis leaving the cotyledon embedded in the endosperm of the seed. The radicle branches

to form a short-lived fibrous root system. Martin and Ortiz observed that the first bud which at first is enclosed in two scalelike sheaths develops into a short single-noded, single-leafed stem which remains the only shoot development for 2-4 weeks. In the meantime, the side of the hypocotyl opposite the primary shoot bulges to produce the tuber. Adventitious roots grow quickly from the young tuber and become the main root system displacing the primary one. Tuber growth continues by means of diageotropic or plagiotropic lobing and new shoots arise from positions axillary to the first shoot. D. spiculiflora may produce 5 or more such shoots before one, either old or new, elongates rapidly as a climbing stem. D. floribunda, on the other hand, produces only one secondary shoot which develops into a typical climbing stem.

Agronomy

Fairchild (1899) provided the following description of the field technique used in the cultivation of cush-cush in Jamaica, West Indies around the turn of the century:

> "The plants are propagated by means of the so-called "heads" consisting of groups or clusters of short roots just below the crown. These heads are planted in hills, six to eight feet apart in each hill. As soon as the vines are out of the ground, a stout stake or pole seven or eight feet long, is driven into the hill, near one of the heads and the various vines are trained up to it. If planted in rich soil they grow without attention other than the cultivation necessary to keep down weeds. Several vines spring from each single head, from which they at first draw their

nourishment, sucking it as dry as a sponge. By the time the vines are established on their own roots, they commence to form, underneath the heads, the fleshy roots which become the next crop. In the course of five or six months after planting, these roots are large enough to harvest and are gathered without destroying the vines, sometimes three or more crops being taken from one planting. After harvesting the deeply buried fleshy tubers, the upper roots are allowed to grow and make heads, and these are again used to start a new plantation, being cut into large pieces, each containing several buds. If not wanted for immediate planting, they are buried in a pit and covered with straw and leaves until the buds start, when they are set out in the hills, as just described. Several of the edible roots are produced from each head but the proportionate increase is small compared with sweet potatoes. The yield is not more than three or four roots per head planted. It is the custom in Jamaica to plant large heads since it is considered that these, or at least large cuttings of the roots, give better yields than small ones."

In its essential characteristics the system described by Fairchild (above) is still employed by cush-cush growers in the Caribbean area. Cush-cush is a yam and its cultivation is similar to that of other yams. Waitt (1963) in a review article on the Dioscorea species, discussed agronomic practices in yam production. While it is not proposed to consider here the general agronomy of yam production as a whole, some agronomic aspects must be mentioned as background for field studies reported later in this dissertation. Waitt drew attention to the fact

that yams are propagated vegetatively by tuber or tuber piece. He pointed out that a considerable range of "seed" weights is used varying from a few ounces to 6 lb. per piece. Waitt noted reports in the literature that a relationship exists between weight of seed piece and the rate and percentage of germination. Miège (1957) had stated that heavy seed pieces sprouted more quickly and vigorously than light ones, and the vines appeared to grow faster. Moreover, the gross yield is increased by planting heavier pieces although the relationship between seed weight and yield is not directly proportional.

Waitt (1963) noted that yams may be grown in "hills" or mounds, or in continuous rows in ridges or banks. Spacing distances vary according to soil type and climatic conditions and with the species of yam grown. Distances of 4 x 4 ft., 6 x 2 ft., 5 x 2 ft. and 4 x 2 ft., have been reported, the wider dimension generally indicating the distance between rows. Waitt mentioned the use of guinea corn and maize as supports for the growing yam vines and also noted that chicken wire had been used successfully for the same purpose in the cultivation of Dioscorea floribunda. Since the publication of Waitt's paper, Green and Soderholm (1966) reported the use of steel pipes, hog wire and bamboo poles for supporting the vines of D. composita in Florida. They found, however, that much hand labour was required to remove these materials from the field before the yam tubers could be located and harvested.

The total yield of tubers varies considerably from yam species to yam species. It also depends on the environment and the level of management practiced. Up to 16.5 tons per acre have been recorded in Trinidad from varieties of Dioscorea alata (Wood, 1933), and individual

tubers of this species have weighed 100 lb. or more (Young, 1923).

Waitt (1963) maintained that yams are costly to produce. He cited the high "seed" rate and excessive labour requirements as being the main reasons for this. He pointed out that in Nigeria where the average yield is approximately 3 tons of tubers per acre, at least 1 ton is required to plant an acre, and the normal labour input for this production is 150-240 man-days. This, he claimed, is a clear illustration of uneconomic yam production. No data of this kind is available in respect of cush-cush production. However, Hart (1898) reported that its yield is much lower than those of other species of yams and that it would not be profitable to grow it where a cheap supply of food is required. Fairchild (1899) also indicated that cush-cush is a fairly low yielder and that its demand for hand labour is considerable. Another undesirable characteristic was reported by Williams (1925) who considered its storage qualities inferior to those of other yams.

According to Cobley (1956), there are several varieties of cush-cush and they produce differently coloured tubers. Williams and Williams (1951) also referred to many varieties in Trinidad differing in shape and colour. Hart (1898) maintained that there are three or more varieties in Trinidad and mentioned the names Red, White, and Demerara cush-cush, the last named having the largest tubers. There is a suggestion in Fairchild's (1899) discussion that a single variety represented Dioscorea trifida in Jamaica at that time.

MATERIALS AND METHODS

The materials and methods used in this research may be considered most conveniently in the sequence in which they were required as the programme developed. The programme was carried out in 6 phases, as follows:

1. Collection of Material

   Collection of seeds and vegetative planting material (tubers) of Dioscorea trifida.

2. Plant Description - Observation and Measurements

   Establishment and maintenance of field plots of D. trifida for observation and measurement of plant characters.

3. Germination and the Seedling - Observation and Germination Tests

4. Studies on Sex Expression

5. Agronomic Studies

6. Cytological Investigations

Phases 1-5 were conducted at Central Experiment Station, Ministry of Agriculture, Trinidad, West Indies. Phase 6 was carried out in the Agronomy Department, Macdonald College.

Some indication of the prevailing climatic conditions at the experimental site in Trinidad may be obtained from the meteorological data in Appendix I. Descriptions of the three soil types found in the areas where field studies on cush-cush were conducted are given in Appendices II, III and IV.

1. Collection of Material

The first lot of cush-cush seed used in germination studies at Central Experiment Station were obtained in April, 1963 from Mr. John Gooding of the Regional Research Centre, University of the West Indies. These seeds were relatively fresh, having been harvested the previous February, and came from a small plot of Dioscorea trifida maintained in the Centre's yam collection at St. Augustine, Trinidad. Seeds became available from observation and experiment plots at Central Experiment Station commencing in January, 1964 and from this time onwards these were the only seeds used in the programme.

The collection of tubers and tuber pieces for planting commenced in April, 1963. There were two objectives. One was to get as variable a population of cush-cush as possible in order to make an assessment of the range of variation in the species; and, the other was to obtain enough of 3 or 4 cush-cush varieties to use as source material in agronomic trials.

A collection of variable material was made in Trinidad with the assistance of the Extension Service of the local Ministry of Agriculture. Extension Service field personnel collected tubers from individual plants in food gardens, semi-abandoned cacao plantations and secondary forests throughout the country. Since by the month of April most of the annual cush-cush crop had already been harvested, the tubers obtained were small in size and few (per individual plant) in number. It is probable, however, that the absence of readily available tubers caused the collectors to search more diligently and to find some of the little known or used types of Dioscorea trifida which might

otherwise have remained unnoticed.

Each tuber collection, supposedly from a single cush-cush plant, was packaged separately. On its arrival at Central Experiment Station, it was given an accession number and its characteristics in respect of flesh colour and tuber shape were noted (Appendix V). Forty-one accessions were collected in Trinidad. Two more were received from overseas, one from British Guiana (now Guyana) and the other from Jamaica, through courtesies extended by the Ministries of Agriculture in those countries. A sample of tubers received from the Department of Agriculture in Antigua proved to be Dioscorea esculenta and not D. trifida.

The accessions were numbered consecutively from 1 to 44 with the digits 6 and 3 appended to each number to indicate 1963, the year in which collection was made. Thus, accessions 1/63 to 41/63 were collected in Trinidad, 42/63 came from Guyana, and 44/63 was received from Jamaica. 43/63 which came from Antigua was not cush-cush and was removed from the collection. Subsequently, after the tubers had been planted and aerial growth was sufficient, the identification of all the accessions was confirmed by reference to botanical descriptions of Dioscorea trifida by Grisebach (1864) and Britton and Wilson (1924). Further confirmation was obtained by comparison with cush-cush specimens in the Herbarium of the University of the West Indies, St. Augustine, Trinidad.

Tubers to be used as source material for agronomic experiments were purchased in local food markets. This material comprised 3 varieties which are known by the names White cush-cush, Purple cush-cush and Boucan.

The venders in the markets maintained that white cush-cush is imported annually from Guyana, and it is interesting to note that the cush-cush tubers (accession 42/63) were identical with many of the white cush-cush tubers purchased.

2. Plant Description - Observation and Measurements

Establishment of Observation Plots. The observation plots were located on Las Lomas Sands soil type (Appendix II). The land was ploughed in May, 1963 and formed into ridges 1 ft. high and 3 ft. apart. The furrows between the ridges were filled with partially rotted pen manure and then the ridges were split lengthwise to cover the pen manure and so form new manure-filled ridges.

The tubers of the 43 accessions were cut into 4 oz. "seed" pieces and these were planted about 2" deep in the tops of the ridges and 48 inches apart along the length of each ridge. A stout bamboo pole about 7 ft. long was firmly planted near to each "seed" piece. Planting date was 11 May, 1963. (This wide row spacing is unusual for yams but was intended to avoid intertwining of the vines of adjacent plants which would make the recognition and measurement of individual plant characters difficult.) The number of plants established in observation plots is shown in Table 2.

Observations and Measurements. The stages in the morphological development of the plants in the observation plots were noted and in many instances photographic records were made. In addition, characters of stem leaf and tuber were measured. Wherever possible a complete set

TABLE 2.

Number of plants of *Dioscorea trifida* established in observation plots 1963-1964.

Accession No.	No. of plants established	Accession No.	No. of plants established	Accession No.	No. of plants established
1/63	4	16/63	10	31/63	0
2/63	5	17/63	3	32/63	5
3/63	2	18/63	3	33/63	1
4/63	0	19/63	4	34/63	0
5/63	3	20/63	1	35/63	4
6/63	5	21/63	3	36/63	2
7/63	0	22/63	3	37/63	7
8/63	0	23/63	7	38/63	1
9/63	6	24/63	2	39/63	4
10/63	5	25/63	5	40/63	7
11/63	5	26/63	2	41/63	2
12/63	10	27/63	8	42/63	13
13/63	3	28/63	5	43/63	0
14/63	1	29/63	3	44/63	39
15/63	15	30/63	4		

of measurements were taken for at least one plant in each accession. If the variation between plants in a single accession was unusually pronounced, "seed" mixture was suspected and aberrant as well as normal types were noted and measured. The accessions from which measurements of stem, leaf and tuber characters were taken are listed in Table 3. Details of the measurements are given below. All characters were measured on fully-grown, adult plant organs.

(a) Stem Characters (Measured on 4 plants selected at random in each accession).

1. Number of wings. Counts taken at first, third, fifth and tenth internode above the surface of the ground.
2. Stem thickness: as represented by the diameter of the fifth internode above ground. The measurement refers only to the thickness of the body of the stem. The wings are excluded.
3. Length of internode: as represented by the length of the fifth internode above ground.
4. Number of branches per stem: at 2.5 ft. above ground.
5. Stem colour. Appraisal carried out in the basal portion of the stem.

(b) Leaf Characters (Measured on 15 randomly selected adult leaves per plant. The number of plants involved in each accession varied from 1 to 5).

1. Length of petiole
2. Length of lamina lobes: from top of petiole to tip of lobe.
3. Number of lobes per leaf.

TABLE 3.

Accessions from which measurements of stem, leaf and tuber characters were taken.

Accessions	Stem Characters	Leaf Characters	Tuber Characters
1/63	+	+	+
2/63	+	+	+
3/63	+	-	+
5/63	+	+	+
6/63	+	+	+
9/63	-	+	+
10/63	+	+	+
12/63	+	+	+
13/63	+	-	+
15/63	+	+	+
16/63	+	+	+
18/63	+	-	+
20/63	+	-	+
23/63	+	+	+
27/63	+	+	+
29/63	+	+	+
33/63	-	+	+
35/63	+	+	+
36/63	-	+	+
37/63	+	+	+
38/63	-	+	+
39/63	-	+	+
40/63	+	+	+
41/63	+	-	+
42/63	+	+	+
44/63	+	+	+

(c) Tuber Characters (by visual evaluation).

1. Cluster habit. An assessment of whether the tubers are densely packed in the cluster or loosely attached.
2. Tuber shape: Whether round, ovoid, filiform, cylindrical, fan-shaped or variously lobed.

Floral characters were also measured. These measurements were restricted to fewer accessions since all accessions did not flower. The following characters were measured:

1. Number of axes per inflorescence.
2. Number of flowers per axis.
3. Length of axes.
4. Length of flower (from base of pedicel to topmost extremity of anthers - in male flowers - , and stigmas - in female flowers).
5. Width of flower (span of perianth whorl).

Finally, the measurements and estimates listed above were supplemented by photographs illustrating the characteristics of stem, leaf, flower and tuber.

Preliminary observation on flower induction. In Trinidad, the 21st to 29th June are the longest days in the year and the duration of daylight on these days is 12 hours and 43 minutes. The shortest days (11 hours and 32 minutes) are 17th to 25th December. Cush-cush normally starts to flower in the shortening days of October and continues flowering until the end of January. By this time the dry season has

started and the plant soon matures and dies. In the long days of June, July and August the plant is normally in its phase of greatest vegetative growth. It is commonly believed in Trinidad that flowering in Dioscorea trifida is photoperiodically controlled and only takes place during short days. An investigation of this matter was initiated at Central Experiment Station in this programme when 10 seedling plants, about 6 months old, were subjected to short-day conditions. This was accomplished in the following manner. The seedlings were grown in large pots standing on a low (12" high) moveable, platform set on low casters. Low trellises were built on the platform to provide support for the cush-cush vines. The platform was wheeled every night (after the sun had set) into a shed specially built to receive it. The shed was painted black on the inside and there was a black curtain over the doorway completely preventing the entry of light. By removing the plants from the shed each morning at 8.00 hours, a long night, not less than 13 hours, was ensured. High temperatures built up during the day were avoided by waiting until the shed had cooled at night before moving the plants in.

3. Germination and the Seedling - Observations and Germination Tests

Observations. Observations on the germination process itself were made in the course of several germination tests. Germinating seeds were dissected and examined at regular intervals before and after emergence of the primary root to determine the sequence of events leading to normal germination. Some of the major characteristics of seed structure were noted.

Observations on seedling growth and development were made

on more than 50 seedlings from time of emergence of the primary root until the aerial shoots assumed adult characteristics and began to twine. It was noted early in these studies that the growth rate of young seedlings exposed to normal light intensity is very slow and seedling mortality is high. When these slow-growing plants are transferred to shaded conditions, the rate of growth increases and mortality is reduced. It was decided therefore to give some shade to most of the seedlings grown at Central Experiment Station. This was achieved by constructing wooden frames about 10 ft. high and covering the tops with saran netting. Approximately 50% reduction in normal light intensity was obtained in this manner.

Germination Tests. Germination tests were started in May, 1963 and continued, with but few interruptions, until April, 1967. These experiments were initiated to determine the nature and rate of germination of cush-cush seeds. Standard tests on filter paper in Petri dishes were conducted from May to July, 1963. It soon became evident that germination in Dioscorea trifida is lengthy and irregular, and it was decided to carry out the following testing programme aimed at finding methods of accelerating the process:

(a) Date of Seeding Experiment. Six germination tests were performed successively in March, April, May, June, July and October, 1964. The seed samples used in all the tests were drawn from a batch of open-pollinated seed harvested from a single female parent, 16/63/8 in January, 1964, about 6 weeks before the commencement of the first test. The aim of this work was to find out whether a dormancy period affected the

length of time required for germination. All tests were carried out in soil and there were 200 seeds per test. (Ripeness of seed was assumed when the capsules dehisced and the seed was dry, brown and brittle.)

(b) Seed Treatment Experiment I. In this experiment a random sample of open-pollinated seed was pretreated in 5 different ways and set to germinate under two regimes of light. The following treatments were used:

(i) Exposure to low temperature (5°C) for 12 hours.

(ii) Exposure to low temperature (5°C) for 24 hours.

(iii) Exposure to high temperature (52°C) for 12 hours.

(iv) Exposure to high temperature (52°C) for 24 hours.

(v) No treatment (control).

Germination was carried out on filter paper in Petri dishes on a bench in the laboratory. There were 25 seeds per Petri dish and 8 dishes (i.e. 200 seeds) per pretreatment. Four of the dishes with seeds from each treatment were set to germinate under conditions of continuous darkness achieved by covering the dishes with a heavy black cloth. The remainder of the seeds were allowed to germinate under the normal conditions of daylight and night in the laboratory. The objective of the experiment was to find out whether the germination rate and/or percentage could be improved by any of these treatments. The test was started on 14th March, 1964.

(c) Seed Treatment Experiment II. This test also involved the pretreatment of open-pollinated seed before germination. The seed sample used was harvested from a single female

clone (2/63/9). The treatments were as follows:

(i) Removal of wings.

(ii) Removal of wings and exposure to high temperature (52°C) for 24 hours.

(iii) Removal of seed coats.

(iv) Removal of seed coats and exposure to high temperature (52°C) for 24 hours.

(v) Exposure to 52°C for 24 hours.

(vi) No treatment (control).

Germination was carried out on filter paper in Petri dishes. There were 200 seeds per treatment. The purpose of the experiment was to find out whether germination rate and percentage were influenced by high temperatures and the presence or absence of the testa and outer tissues. The test was started on 19th May, 1966.

(d) Open-pollinated Seed Test. This was designed to test and compare the germination rate and percentage of open-pollinated seeds of 7 female clones of Dioscorea trifida. The clones were selected from 7 accessions, viz., 2/63, 5/63, 9/63, 10/63, 15/63, 23/63 and 26/63. Germination was carried out on filter paper in Petri dishes. There were 100 seeds per clone. The experiment was started on 23rd April, 1965.

4. Studies on Sex Expression

The data presented on sex ratios in Dioscorea trifida were obtained, for the most part, from experiments which involved the growing of 7 seedling populations under both field and reduced light conditions

during 1964-1965, and 7 clonal populations under field conditions in 1965-1966. The planting material (tubers or tuber pieces) used in establishing the field of cush-cush in 1965-1966 was produced by the seedling plants grown in 1964-1965.

The seedling populations (1964-1965) were grown from open-pollinated seeds collected from 7 female clonal plants belonging to the following 6 accessions: 1/63, 2/63 (2 plants), 12/63, 15/63, 16/63 and 35/63. The selection of these clones as seed parents was largely based on the fact that they had each produced the large quantities of seed needed to establish sizable plant populations. In addition, however, the 6 accessions exemplified much of the variation in the cush-cush material under study.

The size of each seedling population established is shown in Table 4. Establishment was an involved process. Nearly 3000 seeds (i.e. over 400 seeds from each clone) were sown in flats in the greenhouse 15th May, 1964. On germination, the seedlings were transplanted individually in small plastic pots (about 8 in. tall and 8 in. in diameter) and placed in 50% shade, under saran netting. (While some shade appeared from previous observations to be essential for seedling growth, the performance of plants grown past the seedling stage under open field conditions was yet unknown.) In an effort to ensure adequate growing conditions for at least some of the plants, half of the seedlings under saran netting were transferred to shaded field conditions as soon as they had entered the adult phase of growth, i.e. adult leaves were being produced and stems had begun to twine. The remaining seedlings were transferred to open field conditions at the same time.

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TABLE 4.

Number of seedling plants established in shaded and unshaded plots for sex expression studies 1964-1965.

Female Parent	Shaded Plots	Unshaded Plots
1/63/5	107	112
2/63/6	117	131
2/63/9	111	136
12/63/6	117	100
15/63/6	126	66
16/63/8	132	100
35/63/1	92	83
Totals	803	728

The shaded field was in fact a light stand of young pine (Pinus hondurensis Loock) already well established on Piarco Fine Sand (see Appendix III). These relatively tall, slender trees were spaced about 18 x 18 ft. apart and reduced normal light intensity by about 50%. Each cush-cush seedling was planted in a mound 18 in. high and about 24 in. in diameter. The mounds were 9 x 9 ft. apart and a stout bamboo pole about 7 ft. long was driven firmly into the ground near each mound to provide support for the twining cush-cush vines.

The unshaded field of cush-cush was also sited on Piarco Fine Sand. The seedlings were spaced 9 ft. apart on ridges 15 in. high and 3 ft. apart. The planting distances on each ridge were so arranged that each plant appeared to be located midway between two plants on adjacent ridges. The purpose of the wide spacing in shaded and unshaded plots was to avoid intertwining of vines of adjacent plants so as to facilitate the identification of the sexes. Staking was done in the normal way, one stake per plant.

The fertilizer programme in both plots consisted of an initial application of 100 lb. of sulphate of ammonia (20-21 % N) per acre to the seedlings as soon as growth was resumed after transplanting; and a complete dressing of 600 lb. of fertilizer (of the composition listed below) per acre applied 4 weeks after the first dressing:

Sulphate of Ammonia (20-21 % N)	= 200 lb.
Superphosphate (16-20 % available P_2O_5)	= 250 lb.
Muriate of Potash (50-55 % K_2O)	= 150 lb.

Growth was more vigorous in the shaded plot than in the unshaded plot. Daily inspections to observe flower emergence commenced

early in October, 1964 and continued until the end of March, 1965.

At harvest, the tubers from each plant in both shaded and unshaded plots were collected separately. Tuber weights for each shaded plant were recorded. On the other hand, the tubers from the unshaded plot were so small and poorly formed that weighing them seemed unwarranted. However, all tubers from both plots were stored in paper bags, one bag to each plant harvested, for use as planting material in the following season.

In May, 1965 two unshaded plots, each with clonal representatives of all the plants in the 7 populations grown in 1964-1965, were established; one plot (Plot A) by means of tubers from the shaded source, and the other (Plot B) with tubers from the unshaded source. Because of the poor yield of tubers from the unshaded source, seed pieces used for planting Plot B weighed 2 oz. or less. Those planted in Plot A were at least 4 oz. in weight. Land preparation, planting distances and staking were the same as those used in the unshaded plot in the previous year. The rates of fertilizer were also similar but, in both Plot A and Plot B, the nitrogenous fertilizer was applied at the time of sprout emergence from the soil, while the complete fertilizer was put on about 6 weeks later.

Throughout the growing season the plants in Plot B were much less vigorous than those in Plot A. Regular inspections to observe flower emergence commenced in October, 1965 and continued until March, 1966.

At harvest, tuber weights per individual plants were recorded.

5. Agronomic Studies.

In the 1963-1964 growing season agronomic studies were restricted to observations of field performance and measurement of yield on an individual plant basis. One hundred and thirty-six plants were established in a small variety plot on a heavy clay loam (Cunupia Clay Loam-Appendix IV). These plants comprised the following 3 commercial varieties:

White cush-cush - 53 plants

Purple cush-cush - 41 plants

Boucan - 42 plants

It was evident from an examination of the tubers before planting that each of these so-called varieties were in fact mixtures of several types. For example, the flesh colour of tubers belonging to the purple variety ranged from deep purple through pink to white. All the varieties contained tubers of various shapes, although the tubers of White cush-cush were predominantly ovoid and those of Boucan predominantly fan-shaped and lobed.

The "seed" pieces were planted in well-manured ridges in the variety plot. The ridges were 4 ft. apart and the spacing distance along the ridge was 18 in. Staking was done with bamboo poles which were so placed that the vines of two adjacent plants could be supported by a single stake. Growth was vigorous. At harvest, the tubers produced by each plant were weighed and classified according to habit and shape (Appendix VI). The tubers of 8 plants, identified by the accession numbers C/67/63, C/69/63, C/88/63, C/90/63, C/92/63, C/131/63 and C/134/63, were selected on the basis of high yield per plant, uniform tuber shape, and ease of harvesting, as planting material for a yield

trial to be conducted the following season. The remaining tubers were bulked according to varieties and stored as planting material for use in further agronomic studies.

The following field trials were conducted from May, 1964 to March, 1966:

1. Cush-cush clonal evaluation experiment, 1964-1965 (referred to hereinafter as Clonal Experiment (1964-1965).
2. Cush-cush clonal evaluation experiment, 1965-1966 (referred to hereinafter as Clonal Experiment (1965-1966).
3. Cush-cush planting distance and seed weight experiment, 1965-1966 (referred to hereinafter as Spacing Experiment).
4. Yam Variety Trial, 1965-1966.

1. Clonal Experiment (1964-1965). This trial was designed to provide a preliminary evaluation of the yield potential of some of the cush-cush material available. The clones tested were selected from tubers of the White cush-cush and Boucan varieties. Specifications of the experiment were as follows:

(a) Layout: randomized block design.

(b) Clones tested: C/67/63, C/69/63, C/88/63, C/90/63, C/92/63, C/109/63, C/131/63, C/134/63.

(c) Number of replications: 3.

(d) Weight of "seed" piece: 4 oz.

(e) Plot size: 12 x 3 ft. (4 ridges, each 3 ft. long and 3 ft. apart).

(f) Spacing between "seed" pieces in the ridge: 1 ft.

(g) Number of plants per plot: 12.

(h) Soil type: Las Lomas Sand.

(i) Land preparation: as performed in the preparation of observation plots, described on page 44 .

(j) Staking: done with bamboo poles so placed that the vines of two adjacent plants could be trained onto one pole.

(k) Fertilizers applied:

(i) 100 lb. sulphate of ammonia per acre, applied as soon as young shoots had emerged.

(ii) 600 lb. per acre of the following mixture, applied 6 weeks after previous dressing:

Sulphate of ammonia (20-21 % N)	- 200 lb.
Superphosphate (16-20 % available P_2O_5)	- 250 lb.
Muriate of Potash (50-55 % K_2O)	- 150 lb.

(l) Date of planting: 29 May, 1964.

(m) Date of harvesting: 10 March, 1965.

2. Clonal Experiment (1965-1966). This experiment was carried out as part of the continuing process of evaluating yield potential in cush-cush. It was similar to the clonal experiment conducted in 1964-1965 and differed from it only in respect of plot size, number of replications and location. This experiment was conducted on Piarco Fine Sand. It was planted on 5th June, 1965 and harvested on 2nd March, 1966. There were 4 replications in the randomized block design used, and plots measured 12 x 6 ft. with 24 plants per plot.

3. Spacing Experiment. The objectives in carrying out this experiment were to compare the effects of different row spacings on yield in cush-cush

and to determine whether these effects are dependent on the weight of "seed" piece. Other specifications of the experiment were as follows:

(a) Layout: split-plot design.

(b) Main plots:

(i) treatments: "seed" weights - 2 oz., 4 oz., 8 oz.

(ii) plot size: 12 x 96 ft. (4 ridges, each 96 ft. long and 3 ft. apart).

(iii) number of replications: 4.

(c) Sub-plots:

(i) treatments: planting distances - 9 in., 12 in., 18 in., and 24 in., apart along the ridge.

(ii) plot size: 12 x 24 ft. (4 ridges each 24 ft. long and 3 ft. apart).

(iii) number of plants per plot:

at 9 in. spacing = 128

at 12 in. spacing = 96

at 18 in. spacing = 64

at 24 in. spacing = 48

(d) Soil type: Las Lomas Sand.

(e) Land preparation: as described for the preparation of observation plots on page 44.

(f) Staking: Vines were supported on strings tied to overhead wires stretching the length of the ridges and elevated 6 ft. above the ground by means of stout poles firmly planted at each end of the ridges. One overhead wire served to support the plants growing in 2 ridges. The vines climbed on twine tied at one end to the plant and, at the other end, to the

overhead wire.

(g) Fertilizers applied: same rate and method of application as reported for Clonal Experiment (1964-1965) on page 59.

(h) Date of planting: 3 June, 1965.

(i) Date of harvesting: 14 March, 1966.

4. Yam Variety Trial. In this experiment the yielding ability of 2 well-known varieties of Dioscorea alata, viz., Lisbon and Oriental, was compared with that of the cush-cush variety Boucan. Lisbon and Oriental are two of the most commonly cultivated yams in the West Indies and are considered to be among the highest yielders. The specifications of the experiment were as follows:

(a) Layout: randomized block design.

(b) Varieties: 3 - Lisbon, Oriental, Boucan.

(c) Number of replications: 4.

(d) Weight of "seed" pieces: 4 oz.

(e) Plot size: 16 x 24 ft. (4 ridges, each 24 ft. long and 4 ft. apart).

(f) Spacing between "seed" pieces in the ridge: 1 ft.

(g) Number of plants per plot: 96.

(h) Soil type: Cunupia clay loam.

(i) Land preparation: as performed in the preparation of observation plots, described on page 44.

(j) Staking: as described for the staking done in the spacing experiment (page 60)

(k) Fertilizers applied: same rate and method of application as used in Clonal Experiment (1964-1965), described on page 59.

(l) Date of planting: 8 June, 1965.

(m) Date of harvesting: 28 February, 1966.

6. Cytological Investigations

Most of the studies on chromosome numbers were carried out on root tip material from plants originating from the accessions 1/63, 2/63, 12/63 and 39/63. Open-pollinated seeds of female plants in these accessions were grown in 1964-1965 and the tubers of the male, female and hermaphrodite segregates have since been maintained vegetatively. In January 1967, tubers from male and female plants of 1/63, 2/63, 12/63, 39/63 and hermaphrodite plants of 1/63 were brought to Macdonald College where they were sprouted in a specially heated "seed" box. Some open-pollinated seeds were also germinated here at Macdonald College and the seedlings used as sources of root tip material for chromosome studies.

Collection of root tips. The root tips from both tuber sprouts and seedlings were usually collected in the early afternoon and best results were obtained if there had been sunshine in the morning previous to collection.

Pretreatment of root tips. Low temperature (24 hours at 1°C), colchicine (0.01% for 12 hours), and 8-hydroxy-quinoline (0.002 M. for 12 hours) were tried as methods of contracting, and thereby, separating the chromosomes at metaphase. 8-hydroxy-quinoline proved to be satisfactory for this purpose.

Fixation. Fixation in 6:3:1 (alcohol:acetic acid:chloroform) gave best results and was the method used in the preparation of most of the squashes studied. It is believed that the chloroform in 6:3:1 aids in removing some of the oil globules (storage products) which normally obscure the chromosomes in root tip preparations of Dioscorea trifida.

Staining. After fixation the root tips were treated in 50% HCl for 20 minutes, washed, and stained in leuco-basic fuchsin for 30 minutes. They were then treated with 5% pectinase for 8-12 hours and transferred to a drop of aceto-carmine on a clean slide where about 2 mm. of the apex of the tip was prepared for squashing.

Squashing. Satisfactory squashing was accomplished by first teasing out the root tip tissue into very small pieces. This was most readily done with the aid of a dissecting microscope and two fine dissecting needles. Three or four pieces of tissue were left on the first slide and the other pieces, in groups of 3 or 4, were transferred to drops of aceto-carmine on fresh slides. The root tip material was allowed to remain in the aceto-carmine for 5-10 minutes after which the pieces of tissue were finally separated from each other and the cover slip applied. Squashing was done by placing the slide on a firm, level part of the laboratory bench holding the cover slip in place with the aid of a rubber-tipped pencil in one hand and tapping quite firmly with the other hand with the wooden end of a dissecting needle.

Sealing the cover slip. After squashing, the slide was passed quickly 4 or 5 times over the flame of a spirit lamp, the excess aceto-carmine was blotted off, and the cover slip sealed temporarily. The temporary

sealing of the cover slip was particularly important, since despite fixation in 6:3:1, the accumulation of oil globules in freshly-made squashes frequently made it impossible to see the chromosomes. However, it was observed that the oil droplets tend to move and coalesce exposing by this action groups of cells. Thus, from this point of view, the preparations improve with time. Sealing to delay desiccation therefore facilitates the cytological work.

OBSERVATIONS AND RESULTS

1. A description of the vegetative planting material collected for this research programme is given in Appendix V. The seeds used are described in "Materials and Methods".

2. Plant Description - Observations and Measurements.

The Seed. The seed of Dioscorea trifida is flat, thin, and roughly triangular in shape with a slightly notched base opposite the micropylar end or apex. Both flat surfaces are covered with thin membranous tissue which projects on all sides beyond the periphery of the seed to form a flat, encircling, slightly wavy wing. The wing projections are greater on the two sides of the seed than on either the base or the apex and the resulting organ is elongated and appears somewhat kidney-shaped (Figure 1).

The results of seed-size investigations conducted in this programme are summarized in Table 5.

The dry wing tissue is smooth, light and fragile. It is light brown in colour. Despite its seemingly delicate nature, it adheres quite firmly to the seed and must be scraped away to expose the seedcoat beneath. The seedcoat is shiny, dark brown to almost black in colour, and usually marked on one side by a shallow but distinct groove extending in a curved line from the base of the seed to the apex. The seedcoat is hard and brittle when dry and becomes leathery and tough when soaked. It is intimately and firmly attached to the flat, white, opaque endosperm which it overlies. It is very difficult to separate

Figure 1. Cush-cush seeds.
Seeds with wings removed (above).
Winged seeds (below).
Squares 1 cm. x 1 cm.

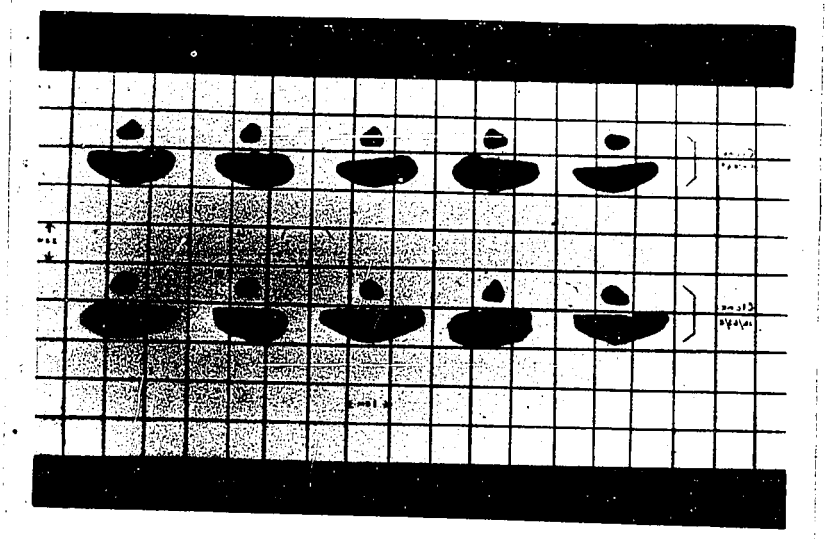

Figure 1. Cush-cush seeds.
Seeds with wings removed (above).
Winged seeds (below).
Squares 1 cm. x 1 cm.

TABLE 5

Dimensions of some seed of Dioscorea trifida. Measurements taken on open pollinated seeds from 3 accessions.

Accessions	Winged Seeds		Seeds per Gram		Weight of wings per seed (percent)
	Length[M] mm.	Breadth[M] mm.	With wings	Without wings	
1/63	19.13	7.89	91	127	28.25
2/63	19.92	8.32	72	91	20.78
16/63	21.08	8.12	78	101	21.52

[M] Each measurement based on 200 determinations.

endosperm from seedcoat even in germinating seeds. The endosperm is pocket-like and appears to consist of two thin walls of endosperm tissue sealed together along the edges except for a small region in the vicinity of the apex. In this way it encloses a large, flat cavity in which lies a very small embryo (Figure 2). The embryo of Dioscorea trifida is pear-shaped with a short conical column at its apical end merging backwards into a broader, progressively flattened, foliaceous cotyledon. It is found in the apical region of the endosperm cavity and is so oriented that its conical end points toward the opening in the cavity wall.

The Root System. The adult cush-cush plant has a fibrous root system (Figure 3). Sturdy adventitious roots measuring 2-5 mm. in thickness arise from the sides of the central corm at the base of the stem - usually axillary to emerging tubers. The roots radiate outwards and branch progressively forming a mat of fibrous roots in the surface soil around the stem. Few roots grow directly downwards in the soil. Some straight unbranched adventitious roots may be observed overlying the main fibrous root system. These are young roots which may branch distally in time, replacing old and non-functional roots. The developing tubers also bear roots, but these are thinly scattered, sparingly branched, and short-lived. The root system of Dioscorea trifida is not extensive. Shoot-root ratios computed on the dry weights of 5 well-grown plants, about 6 months old, varied from 1.58 to 3.40.

The Stem. Previous reports that the stem of Dioscorea trifida is angular, winged, and twines to the left were amply verified by observations at Central Experiment Station (Figure 4). Moreover, the

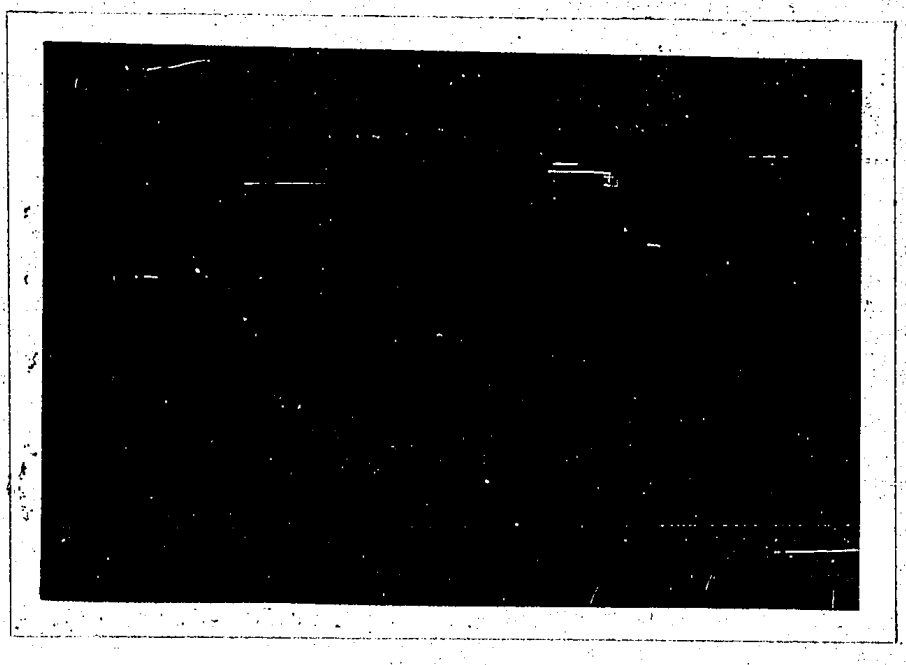

Figure 2. Embryo in apex of endosperm cavity.

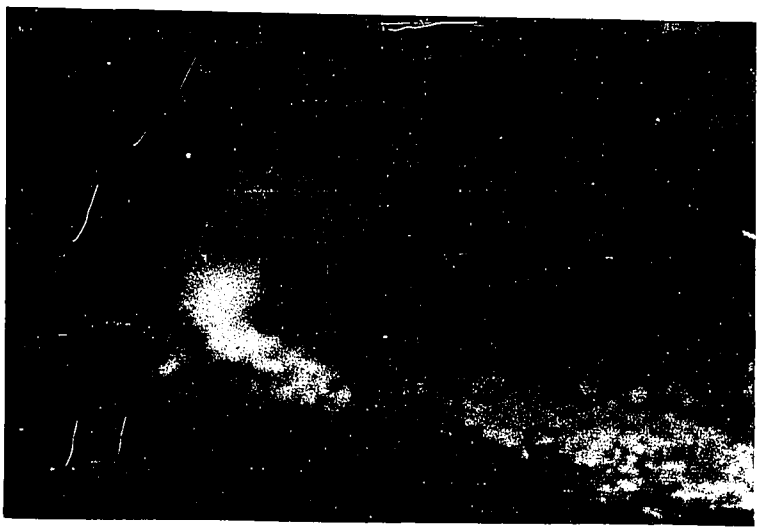

Figure 2. Embryo in apex of endosperm cavity.

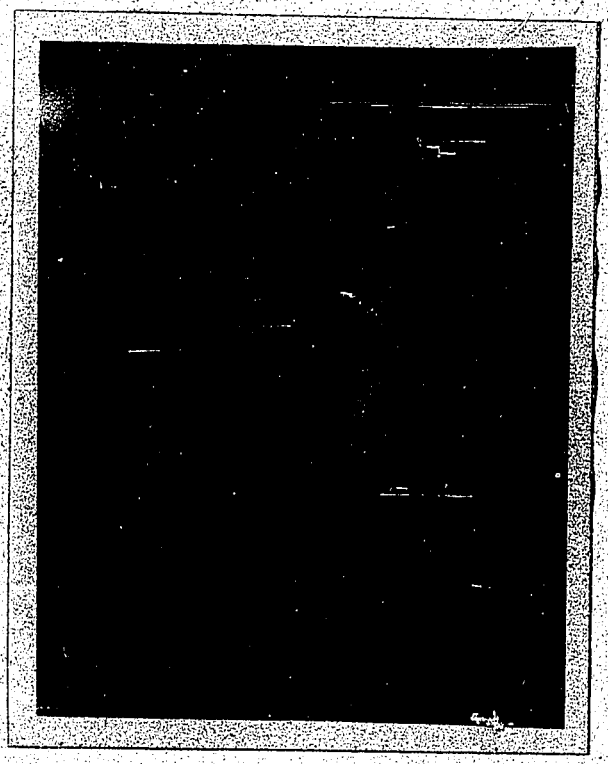

Figure 3. Fibrous root system of adult plant.

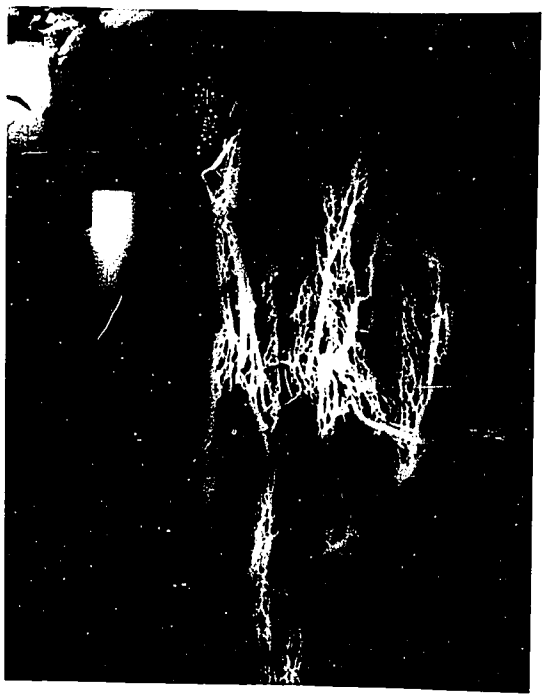

Figure 3. Fibrous root system of adult plant.

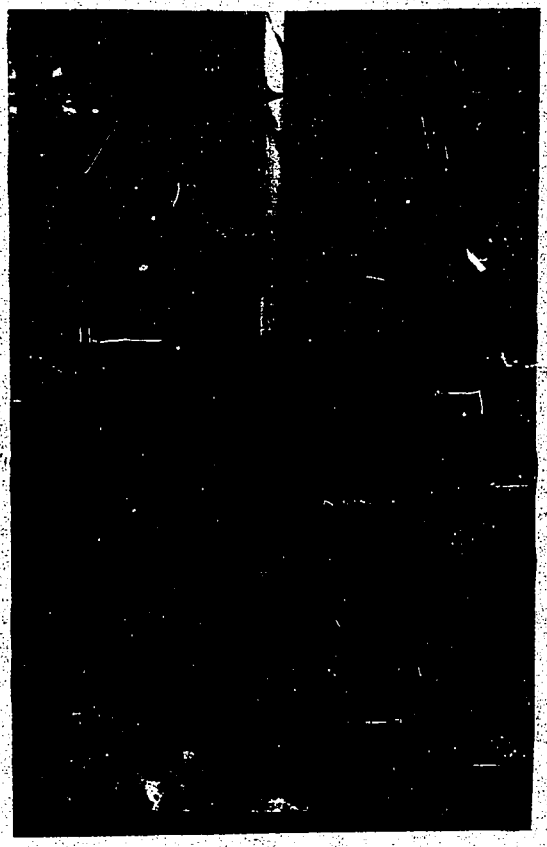

Figure 4. Stem twining to the left.

Figure 4. Stem twining to the left.

stem itself is frequently twisted, screw-like, in a clockwise direction whether it is twined about a support or not (Figure 5). The impulse to climb upwards is strong and unsupported stems or branches will grow outwards almost horizontally until they touch some object around which they may twine and ascend. The stem readily adapts itself to the thickness of its support forming small close-fitting spirals when on slender props of wire or string, and big spirals when the support is a thick bamboo pole or branch of a tree.

The adult stems of Dioscorea trifida are invariably winged but the number of wings per stem is by no means constant within the species. Transverse sections of stems having 2, 3, 4, 5 and 6 wings are shown in Figures 6 to 10. This character was examined in all of the clones in the observation plots and the data shown in Table 6 was collected from plants selected at random from amongst this population. Plants with 4 and 2 wings predominate, and 4 wings are more common than 2. Variations in wing number on a single plant are not uncommon. Sometimes the stems in a plant are 2- or 4-winged except for small areas near the base where several wings are found. This virtual ring of wings is buttress-like in appearance and may be involved in the strength and rigidity of the stem before circumnutation commences. Occasionally, there is an abrupt transition from 4 wings to 2 wings in the stems of some clones. The reason for this sudden change is not known but, since it is usually from a higher to a lower wing number, it may also be associated with decreasing dependence of the stem on its own strength as it twines more securely about its support. Odd numbers of wings are infrequent.

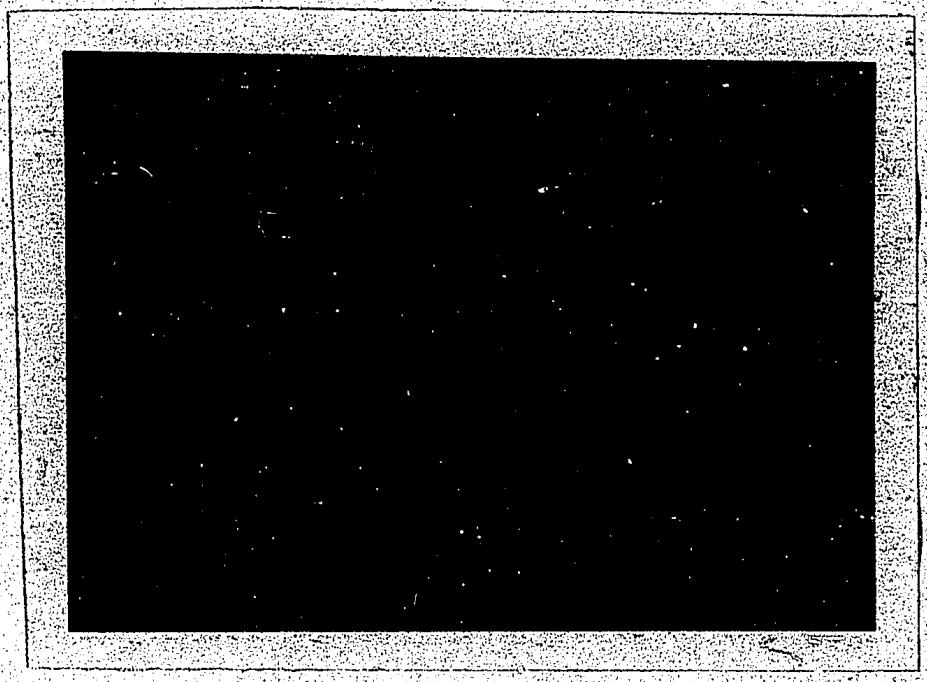

Figure 5. Stem showing characteristic twist to the left (clockwise).

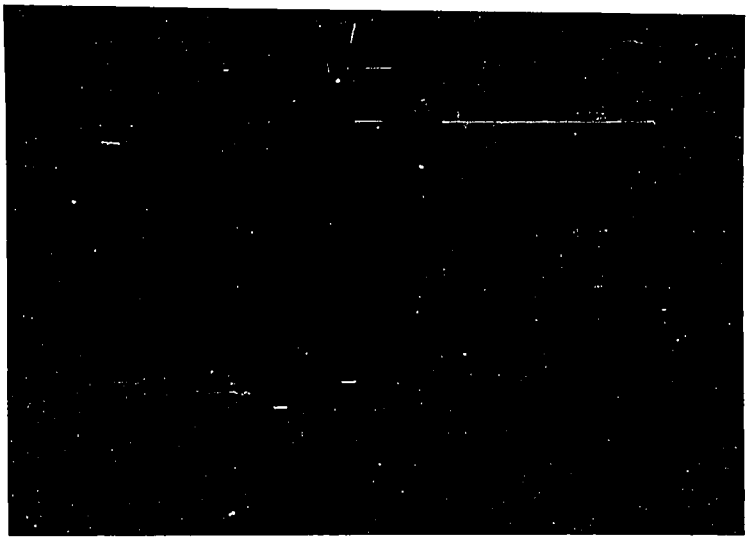

Figure 5. Stem showing characteristic twist to the left (clockwise).

Figure 6. Transverse section of stem with 2 wings.

Figure 7. Transverse section of stem with 3 wings.

Figure 6. Transverse section of stem with 2 wings.

Figure 7. Transverse section of stem with 3 wings.

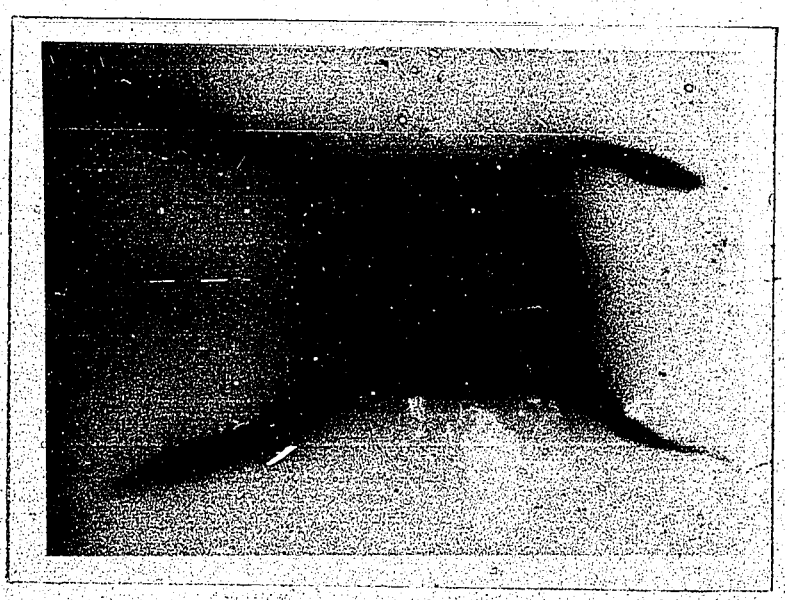

Figure 8. Transverse section of stem with 4 wings.

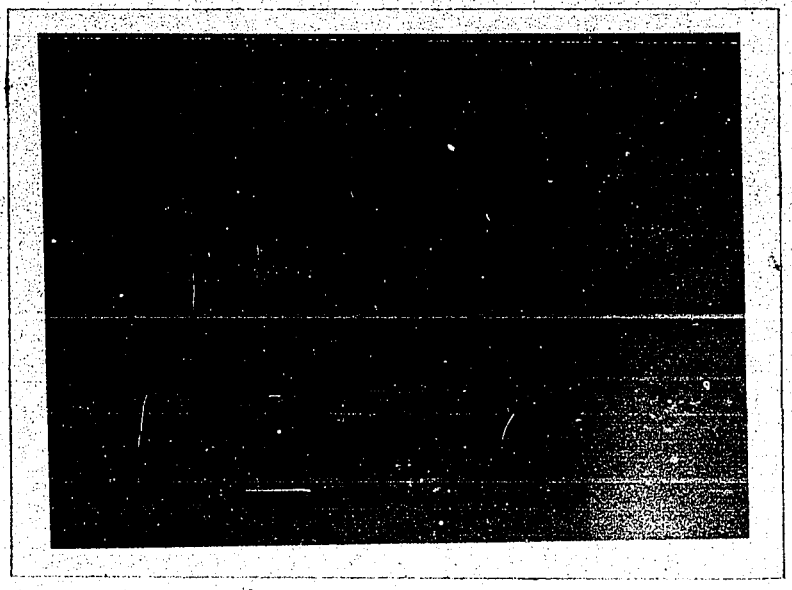

Figure 9. Transverse section of stem with 5 wings.

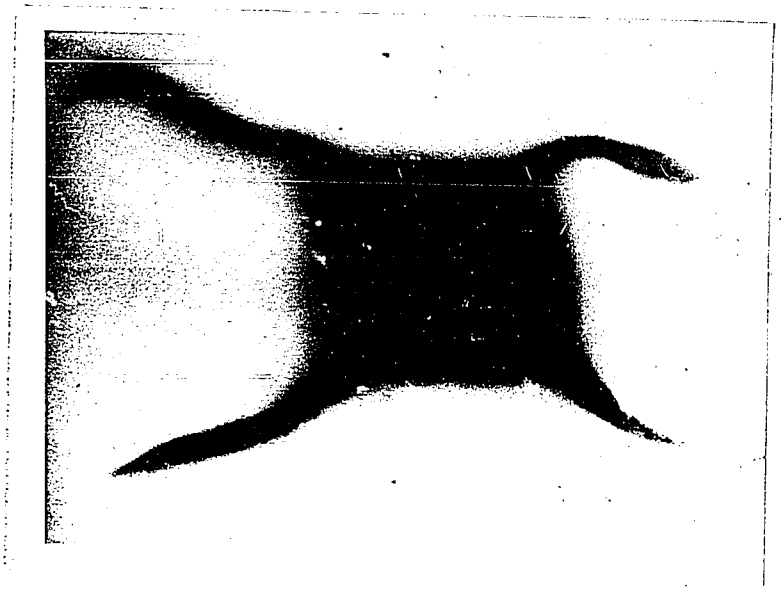

Figure 8. Transverse section of stem with 4 wings.

Figure 9. Transverse section of stem with 5 wings.

Figure 10. Transverse section of stem with 6 wings.

Figure 10. Transverse section of stem with 6 wings.

TABLE 6.

Number of wings per stem in 21 clones counted at stem internodes numbers 1, 3, 5 and 10 above ground surface.

Clones	Internodes			
	No. 1	No. 3	No. 5	No. 10
1/63/3	5	4	4	4
2/63/2	4	4	4	4
3/63/1	2	2	2	2
5/63/2	4	4	4	2
6/63/2	2	2	2	2
10/63/1	6	6	4	4
12/63/2	4	4	4	4
13/63/3	2	2	2	2
15/63/1	4	4	4	4
16/63/1	4	4	4	4
18/63/2	4	4	4	4
20/63/1	4	4	4	4
23/63/3	4	4	4	4
27/63/1	4	4	4	4
29/63/	3	2	2	2
35/63/3	4	4	4	4
37/63/	4	4	4	4
40/63/2	6	5	4	4
41/63/3	5	4	4	3
42/63/2	7	5	4	4
44/63/1	2	2	2	2

The cush-cush stem, if 4-winged, appears rectangular in cross section with a wing at each corner. Similarly, a 5-winged stem appears pentagonal in cross section, and so on.

Some dimensions of stems are summarized in Table 7. (The original data are recorded in Appendix VII). Stem thickness ranges from 2.00 mm. in the smallest adult stem examined to 8.00 mm. in the largest. Internode length also varies considerably and measurements of 74.00 mm. and 300 mm. were recorded. It is worth noting that variations within accessions are greater with respect to internode length than to stem thickness. Also, there is a tendency for longer internodes to be associated with thicker stems. The regression of internode length on stem thickness is significant at the 5% point (Table 8), and the trend is evident in the regression graph shown in Figure 10.

Transverse sections of the cush-cush stem reveal that the vascular bundles are arranged in two fairly distinct rings (Figures 12 to 15). Thick stems have larger numbers of bundles per ring (both cauline and common) than thin stems, and wings invariably overlie bundles. The endodermis is pronounced and the cortex relatively thin.

Leaves are borne alternately on the adult cush-cush stem and there is a bud in each leaf axil. Branching of the stem takes place when one or other of these axillary buds grow out, but this happens infrequently, and it seems, only when the apical growing region of the main stem encounters adverse conditions, or when its vigour is reduced because of approaching maturity and the reproductive phase. Usually 5-12 stems arise successively from the central corm below ground. Each of these tend to develop unbranched throughout most of its life; and

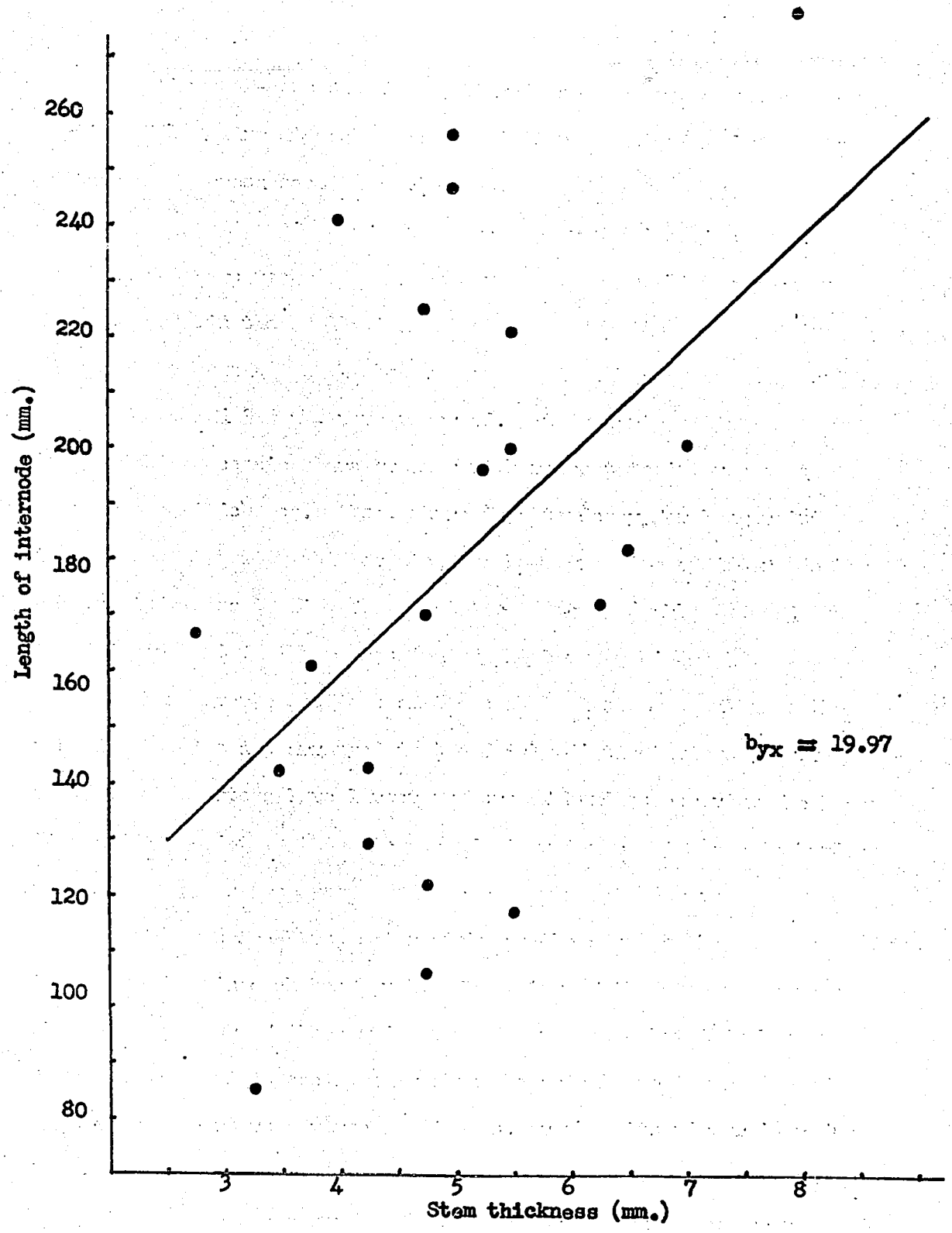

Figure 11. Regression of length of internode on stem thickness.

TABLE 7.

Dimensions of cush-cush stems. Measurements taken on 4 plants per accession at the fifth internode of the stem.

Accessions	Internode Length		Internode thickness (diameter)	
	Range mm.	Mean mm.	Range mm.	Mean mm.
1/63	165.00 - 213.00	196.25	5.00 - 6.00	5.25
2/63	100.00 - 160.00	129.25	3.00 - 5.00	4.25
3/63	150.00 - 180.00	166.00	2.00 - 3.00	2.75
5/63	93.00 - 145.00	121.50	4.00 - 5.00	4.75
6/63	146.00 - 270.00	199.75	5.00 - 6.00	5.50
10/63	250.00 - 300.00	278.50	8.00	8.00
12/63	200.00 - 298.00	247.00	5.00	5.00
13/63	205.00 - 275.00	241.25	4.00	4.00
15/63	65.00 - 115.00	85.25	3.00 - 4.00	3.50
16/63	145.00 - 192.00	172.25	5.00 - 7.00	6.25
18/63	150.00 - 272.00	224.75	4.00 - 6.00	4.75
20/63	145.00 - 185.00	169.50	4.00 - 5.00	4.75
23/63	190.00 - 270.00	220.75	5.00 - 6.00	5.50
27/63	139.00 - 175.00	160.75	3.00 - 4.00	3.75
29/63	234.00 - 272.00	257.00	5.00	5.00
35/63	74.00 - 160.00	106.00	4.00 - 7.00	4.75
37/63	145.00 - 227.00	181.75	6.00 - 7.00	6.50
39/63	100.00 - 120.00	116.50	5.00 - 6.00	5.50
40/63	100.00 - 235.00	201.00	6.00 - 9.00	7.00
42/63	106.00 - 165.00	142.75	3.00 - 6.00	4.25
44/63	126.00 - 149.00	142.00	3.00 - 4.00	3.50

TABLE 8.

Regression analysis of internode length on stem thickness.

Analysis of Variance

Source	SS	DF	MS	F	F values 5%	1%
Regression	12412.03	1	12412.03	5.33	4.38	8.18
Error	44253.63	19	2329.14			
Total	56665.66	20				

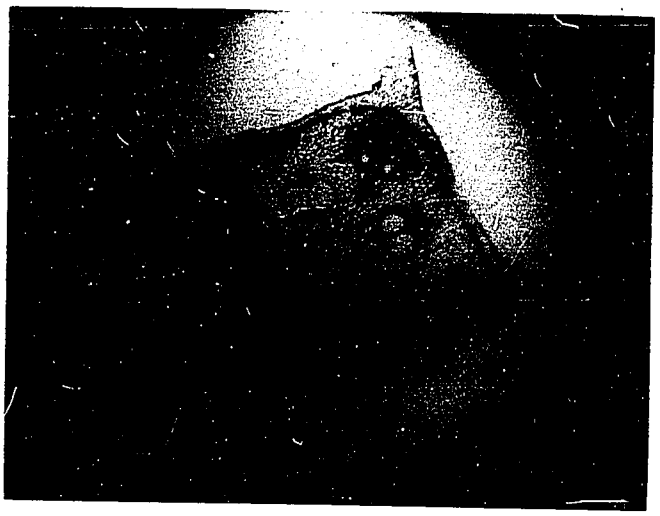

Figure 12. Transverse section of stem showing 8 vascular bundles arranged in 2 rows.

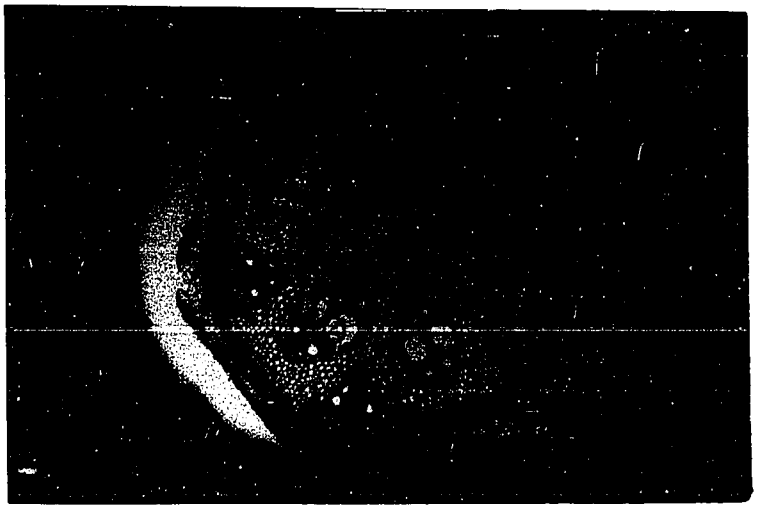

Figure 13. Transverse section of stem showing 11 vascular bundles arranged in 2 rows.

Figure 12. Transverse section of stem showing 8 vascular bundles arranged in 2 rows.

Figure 13. Transverse section of stem showing 11 vascular bundles arranged in 2 rows.

Figure 14. Transverse section of stem showing 12 vascular bundles arranged in 2 rows.

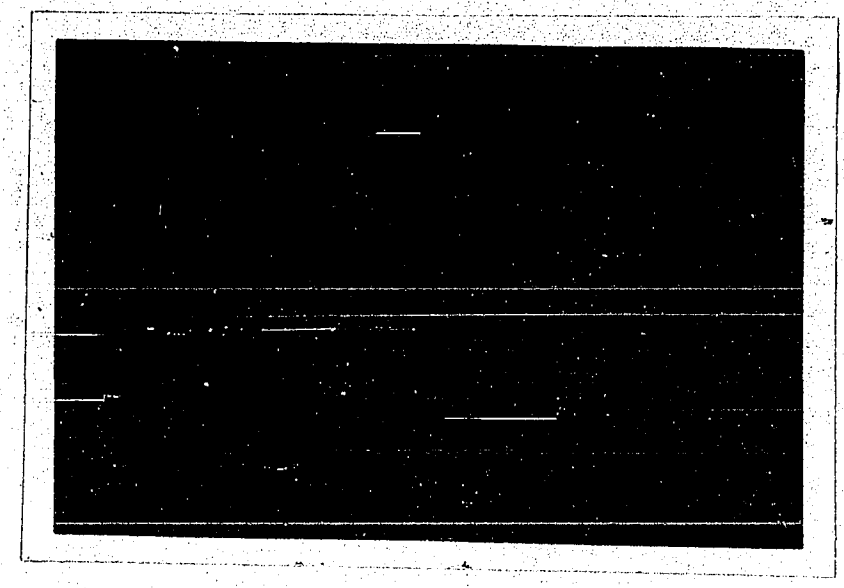

Figure 15. Transverse section of stem showing 18 vascular bundles arranged in 2 rows.

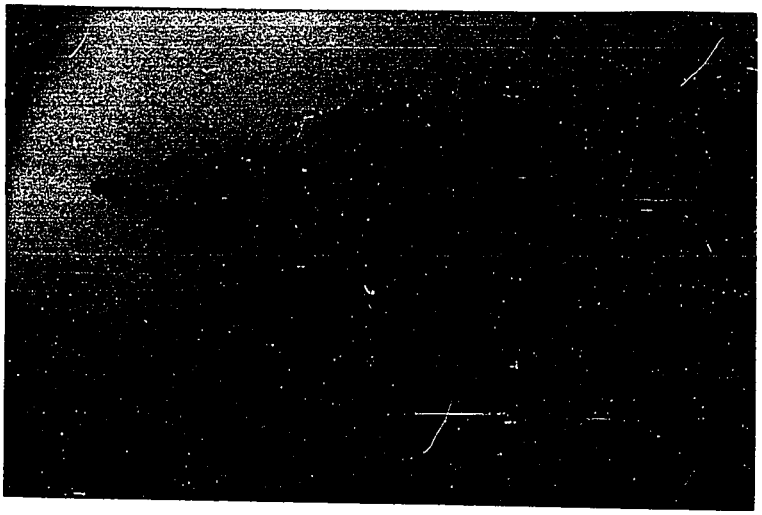

Figure 14. Transverse section of stem showing 12 vascular bundles arranged in 2 rows.

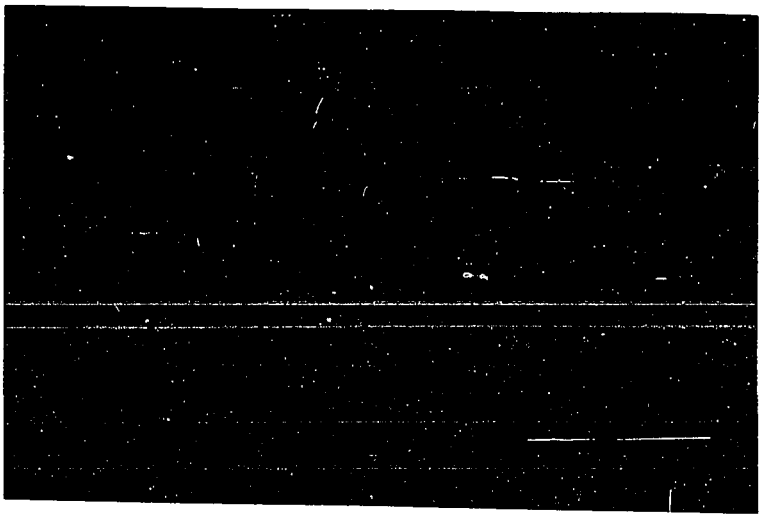

Figure 15. Transverse section of stem showing 18 vascular bundles arranged in 2 rows.

axillary branches, when they are formed, occur in the later stages of development. The results of studies carried out on branching in 21 accessions are presented in Table 9. They tend to substantiate the observation that branching increases toward the extremities of the stem as maturity approaches (Figure 16). Despite its meagre branching habits, the cush-cush stem possesses remarkable powers of survival and continues growth from dormant axillary buds whenever actively growing shoots are damaged or destroyed. This is a striking characteristic of the plant and is evident from the earliest stages of seedling growth.

The aerial parts of the cush-cush plant are relatively short-lived and, in Trinidad, normally die within 10 months after emergence from the ground. In that country, cush-cush sprouts with the early rains in May and the foliage dies back as the dry season intensifies in February. Any new shoots appearing subsequently originate as sprouts from tubers underground.

Green is the dominant colour in the cush-cush stem but it is frequently spotted or blended with some shade of purple. In a well-grown plant, colour development is most pronounced in the basal or older parts of the stem and, in these areas, the following colours or colour combinations are easily recognizable: (1) uniformly green, (2) green flecked with purple, (3) greenish purple, (4) purple. The purple colour is usually most conspicuous in the wings. The body of the stem in the growing regions is normally green while the wings may be green or variously flecked with purple. The classification of 25 accessions on the basis of stem colour in the basal regions is shown in Table 10. Colour appraisal was carried out on 4 randomly selected

TABLE 9.

Number of branches per stem in the clonal plants selected from 21 accessions. Counts taken at 2.5 ft. and 5 ft. above the ground.

Accessions	Branches at 2.5 ft.	Branches at 5.0 ft.
1/63	2	3
2/63	2	3
3/63	0	0
5/63	1	2
6/63	2	3
10/63	1	4
12/63	4	6
13/63	0	0
15/63	0	0
16/63	1	3
18/63	2	4
20/63	2	4
23/63	2	3
27/63	2	4
29/63	0	0
35/63	2	4
37/63	3	5
40/63	5	9
41/63	5	8
42/63	1	2
44/63	0	0

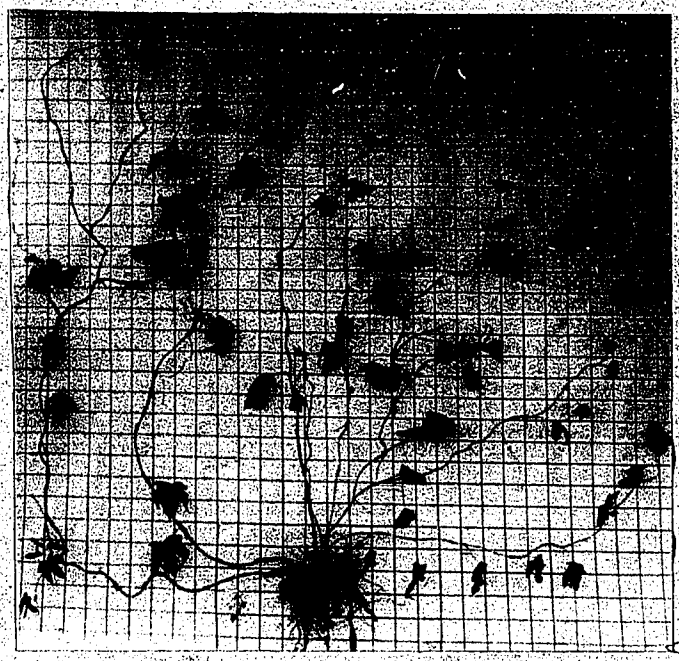

Figure 16. Single cocklebur seedling plant, typical of its stage of growth. Squares 1 in. x 1 in.

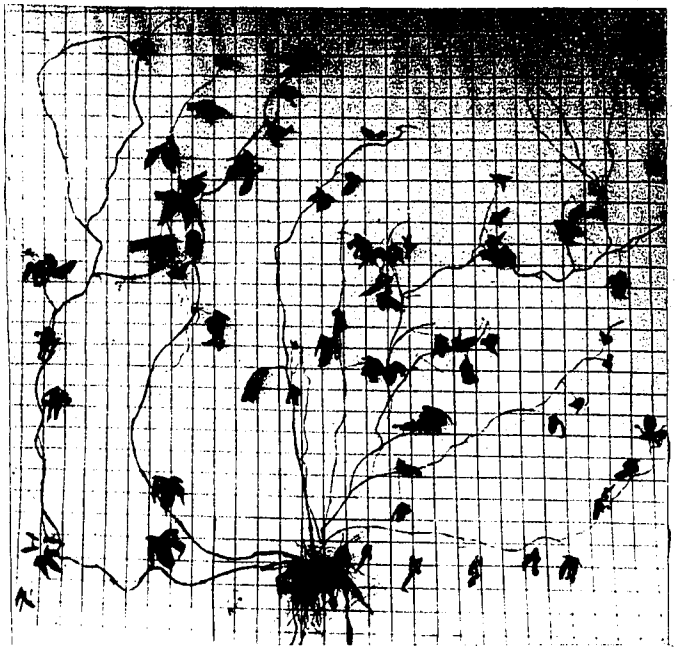

Figure 16. Single cush-cush seedling plant.
Spread out to show branching of stems.
Squares 3 in. x 3 in.

TABLE 10.

Stem colour in 25 accessions of Dioscorea trifida. Colour appraisal was conducted on the basal portions (approx. 2.5 ft.) of the stems of 4 plants in each accession.

Accession	Green	Green flecked with purple	Greenish purple	Purple
1/63		+		
2/63	+			
3/63	+			
5/63			+	
6/63		+		
10/63		+		
12/63		+		
13/63		+		
15/63		+		
16/63		+		
18/63				+
20/63			+	
23/63			+	
27/63		+		
29/63		+		
35/63	+			
37/63			+	
40/63		+		
41/63		+		
42/63			+	
44/63	+			
Total	4	11	5	1

plants per accession.

The Leaf. The adult leaf of Dioscorea trifida consists of a long winged petiole and a broad, glabrous, palmate lamina.

There is a pulvinus at each end of the petiole; the one at the base is large and prominent, and the other at the top end is small and inconspicuous. Together, they cause the leaf to be highly motile. The petiole varies in length from 6 cm. to 18 cm. (Appendix VIII). It is usually semi-terete in cross section with the flattened or ventral surface fringed with wings (Figure 18). On the rounded dorsal surface a central ridge normally extends along the whole length of the petiole. This ridge is frequently winged. The body of the petiole is usually the same colour as the stem to which it is attached. The wings, on the other hand, are nearly always green flecked with purple, or purple.

The characteristic feature of the adult cush-cush leaf blade is the fact that it is deeply lobed. Variations in the length and breadth of lobes and the angles which they bear toward each other have resulted in a profusion of shapes. However, certain common features are readily discernible in various leaf forms permitting classification into groups. The following groups can be distinguished in the material at Central Experiment Station:

A. Leaves 5-lobed.

(a) Base of leaf deeply cordate.

1. Basal lobes overlap. Figure 19

2. Basal lobes discrete.

(i) Central lobe distinctly longer than adjacent lateral lobes. Figure 20

(ii) Central lobe not distinctly longer than adjacent lateral lobes. Figure 21

Figure 18. Transverse section of petiole.

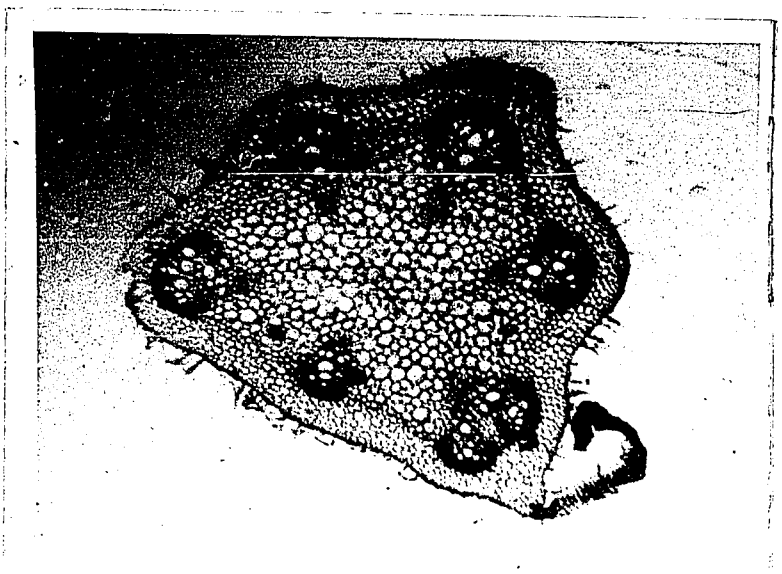

Figure 18. Transverse section of petiole.

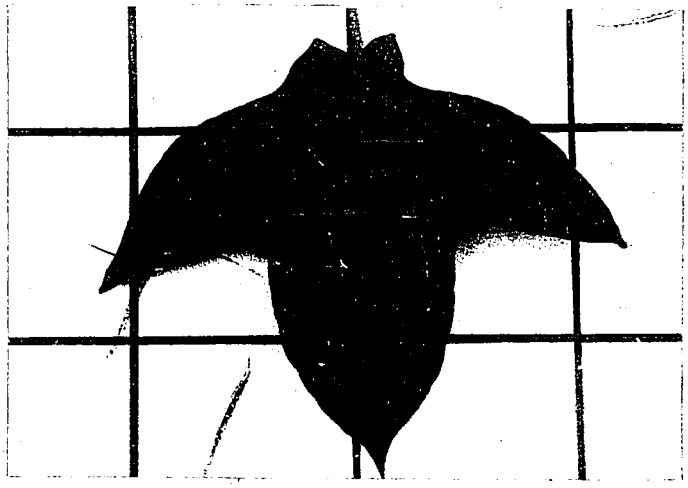

Figure 19. Cush-cush leaf.
Squares 3 in. x 3 in.

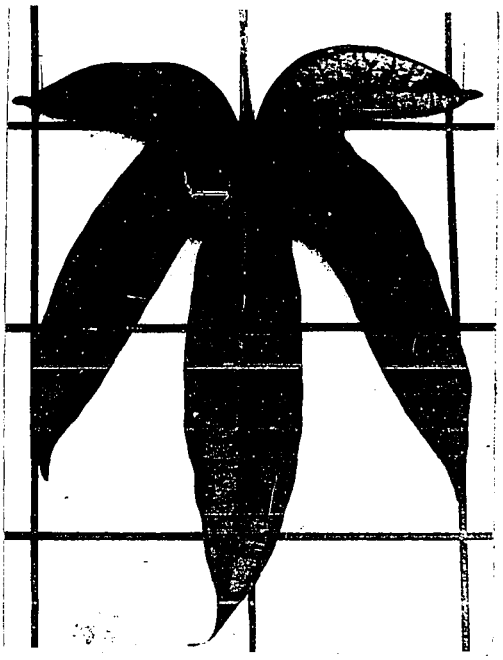

Figure 20. Cush-cush leaf.
Squares 3 in. x 3 in.

(b) Base of leaf subcordate.

1. Central lobe distinctly longer than adjacent lateral lobes. Figure 22

2. Central lobe not distinctly longer than adjacent lobes. Figure 23

B. Leaves 3-lobed.

Base of leaf deeply cordate.

1. Basal lobes overlap. Figure 24

2. Basal lobes discrete. Figure 25

Some cush-cush plants have only 5-lobed leaves while others are exclusively 3-lobed. There are also plants with both 3- and 5-lobed leaves. The lobing characteristics of some of the clonal plants grown at Central Experiment Station were examined and some of the data collected has been summarized in Table 11. No completely 3-lobed individuals are recorded although these were observed to occur not infrequently among seedling populations.

The veins in the cush-cush lamina are unusually protuberant on the dorsal side. There are 11 nerves extending from the apex of the petiole to the tips of the lobes in the 5-lobed leaf; 3 of them in the central lobe and 2 each in the lateral lobes. The intermediate venation is retioulate.

The lamina is generally green in colour although there may be a small purple spot where it joins the petiole. Also, the prominent leaf tip (on the central lobe) is usually darker green and frequently is flecked with pruple. This leaf tip develops before the other parts of the lamina and is a conspicuous feature of the developing leaf (Figure 27).

TABLE 11.

Percentages of 5-lobed and 3-lobed leaves in 16 clonal plants selected from 16 accessions.

Accessions	Percentage of leaves with 5 lobes	Percentage of leaves with 3 lobes
1/63	100.00	-
2/63	93.33	6.67
5/63	86.67	13.33
6/63	40.00	60.00
10/63	93.33	6.67
12/63	46.67	53.33
15/63	93.33	6.67
16/63	73.33	26.67
23/63	100.00	-
27/63	86.67	13.33
29/63	73.33	26.67
35/63	80.00	20.00
37/63	66.67	33.33
39/63	92.31	7.69
40/63	93.33	6.67
42/63	93.33	6.67
44/63	26.67	73.33

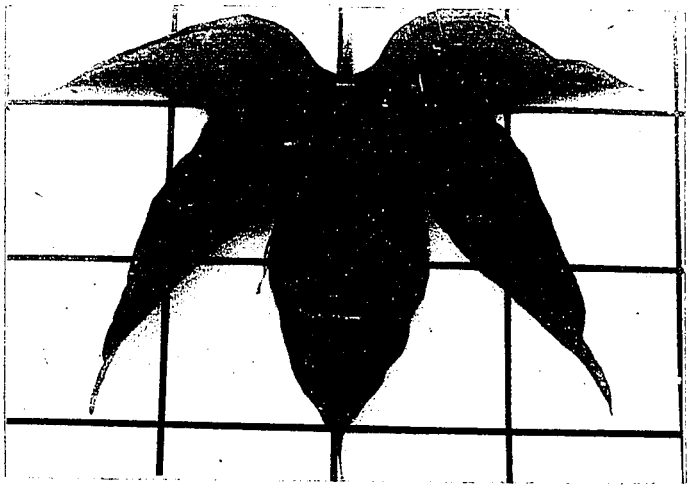

Figure 21. Cush-cush leaf.
Squares 3 in. x 3 in.

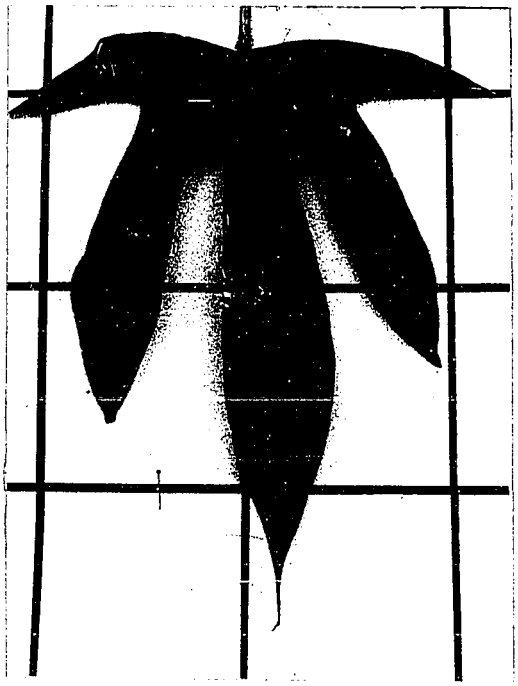

Figure 22. Cush-cush leaf.
Squares 3 in. x 3 in.

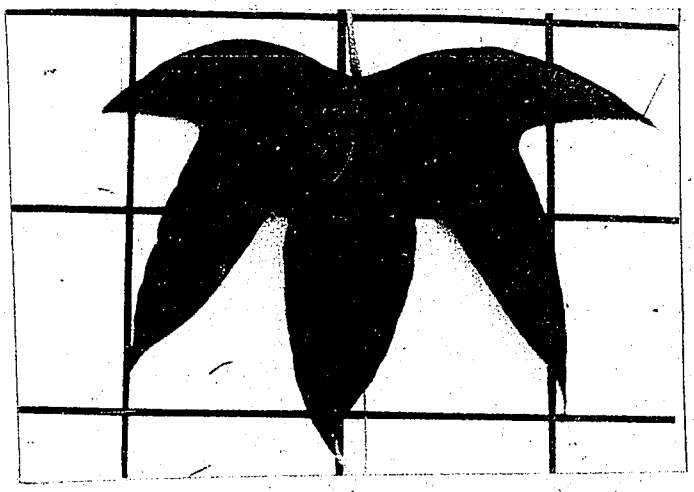

Figure 23. Cush-cush leaf.
Squares 3 in. x 3 in.

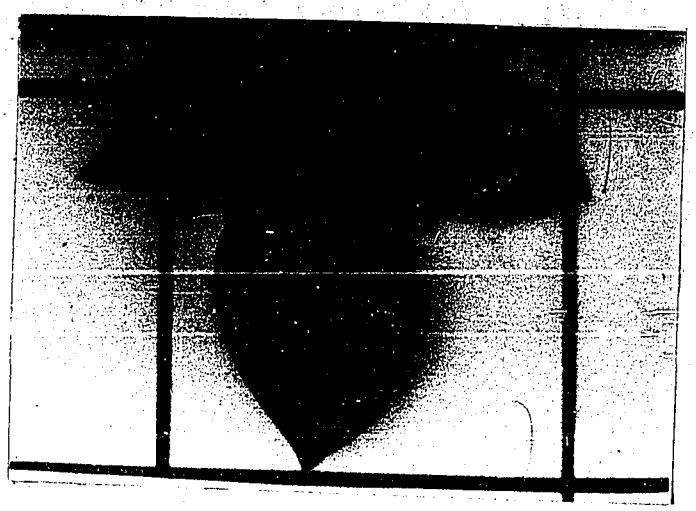

Figure 24. Cush-cush leaf.
Squares 3 in. x 3 in.

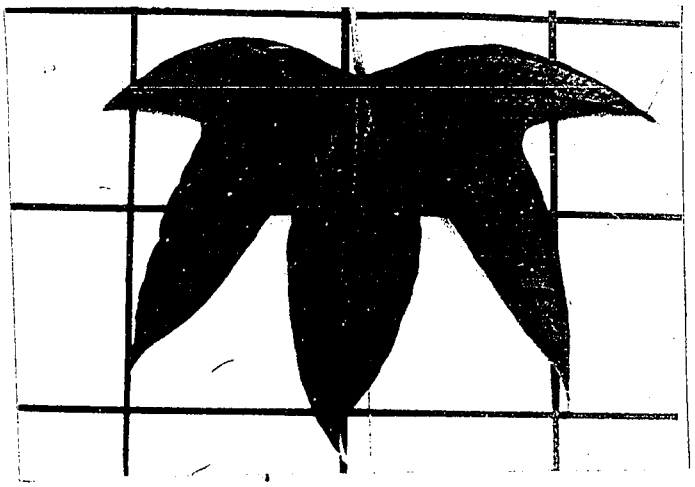

Figure 23. Cush-cush leaf.
Squares 3 in. x 3 in.

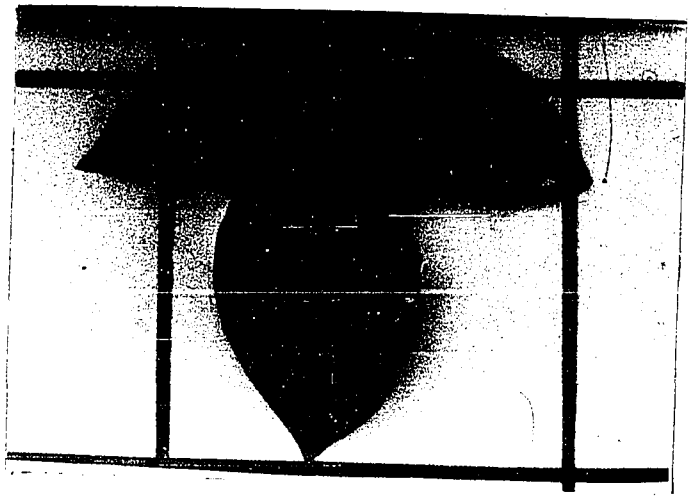

Figure 24. Cush-cush leaf.
Squares 3 in. x 3 in.

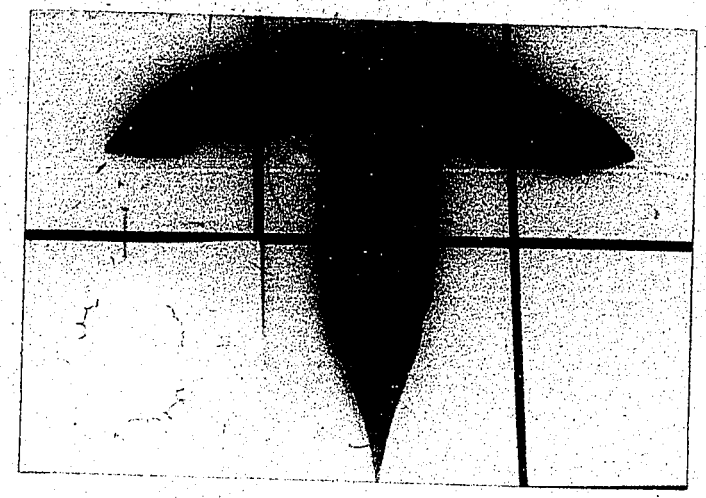

Figure 25. Cush-cush leaf.
Squares 3 in x 3 in.

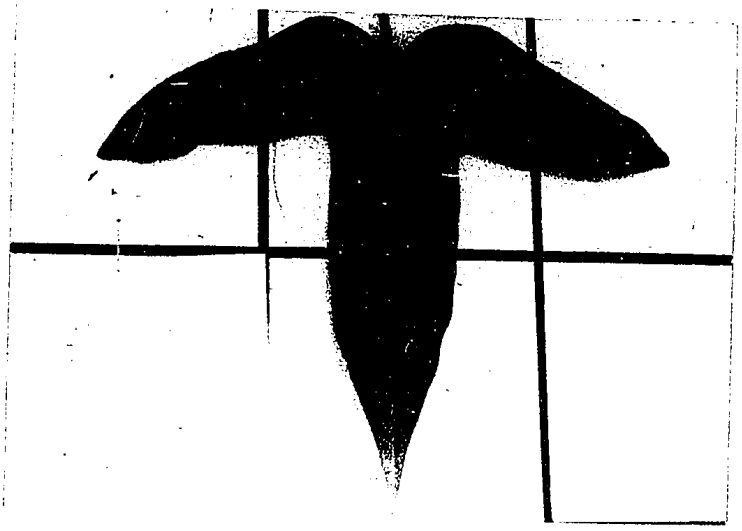

Figure 25. Cush-cush leaf.
Squares 3 in x 3 in.

Figure 27. Prominent leaf tip in developing leaf.

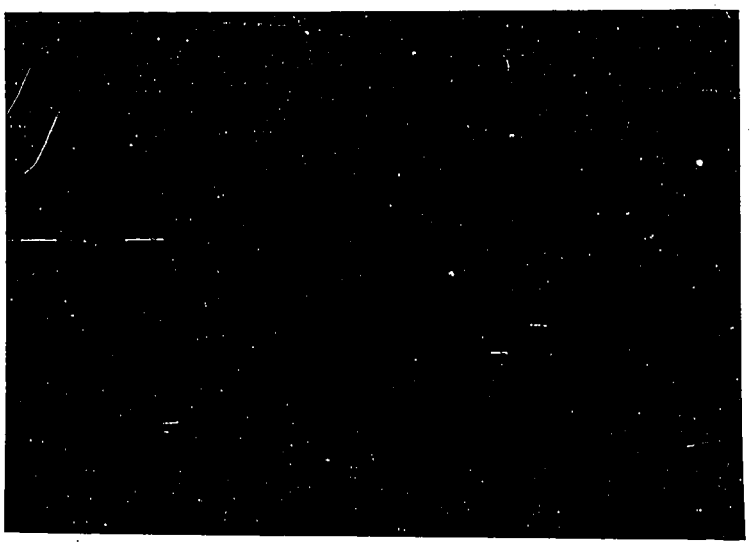

Figure 27. Prominent leaf tip in developing leaf.

The leaf measurements taken in this study are recorded in Appendix VIII. Some of the data is summarized in Table 12. The regression of lamina length on petiole length based on data in Table 12 is significant at the 5% point (Table 13) suggesting some dependence of the one character on the other. This suggestion is apparent in the regression graph in Figure 28.

Attention is directed to the fact that a leaf length to leaf width ratio commonly computed for leaves with entire margins would have little meaning if calculated for the cush-cush leaf since in most cases the widest part of the lamina is in fact a function of the spread of two lateral lobes and does not indicate the breadth of tissue in the leaf.

The Inflorescence. Cush-cush inflorescences are borne in leaf axils and are normally found in the upper regions of the stems and branches. Plants which bear flowers in the axils of leaves in all parts of the vines have also been observed.

The species is predominantly dioecious. Data on male and female inflorescences are recorded in Appendix IX and the more important aspects have been summarized in Tables 14 to 19.

The male inflorescence varies greatly. Sometimes it consists of a single raceme-like axis on which the flowers develop in acropetal order. More frequently it is irregularly branched with accessory axes arising from odd places on the main axis and several axes originating in the same leaf axil. Whatever its origin however, the ultimate branches of the inflorescence are raceme-like. The male axes tend to be somewhat rigid and jut out obliquely from the stems of the plant (Figure 29). In this respect they differ from the floral axes of the female plant

TABLE 12.

Leaf measurements: Means* of petiole length and leaf length in 16 plants from 16 accessions.

Accession	Length of Petiole (cm.)	Length of Lamina Lobes (cm.) 1	2	3 (central)	4	5
1/63	12.65	12.43	17.46	18.41	16.61	12.00
2/63	11.34	9.72	13.39	14.95	13.81	9.16
5/63	11.33	9.76	13.58	14.06	13.22	9.28
6/63	10.99	8.87	11.65	14.01	11.35	8.74
10/63	13.29	9.03	13.21	14.86	13.47	19.16
12/63	10.45	9.41	11.79	14.65	11.69	9.57
15/63	11.66	10.40	15.84	19.33	15.97	10.12
16/63	13.75	11.77	16.99	20.48	17.06	11.17
23/63	11.85	11.75	16.65	18.03	16.43	11.48
27/63	12.05	11.16	16.03	18.43	15.51	10.88
29/63	9.54	8.40	11.75	13.51	11.74	8.27
35/63	10.80	7.68	12.62	14.10	12.69	8.12
37/63	12.27	9.63	16.97	19.39	17.14	9.17
39/63	9.20	8.52	12.63	14.22	12.81	8.32
40/63	11.71	10.79	15.68	16.75	15.69	11.10
42/63	11.91	7.30	12.45	14.18	12.20	7.54
44/63	9.62	7.15	11.69	14.58	11.55	6.80

* Means based on the measurements taken from 15 leaves.

TABLE 13.

Regression analysis of lamina length on petiole length.

Analysis of Variance

Source	SS	DF	MS	F	F values 5%	1%
Regression	31.99	1	31.99	8.40	4.54	8.68
Error	57.09	15	3.81			
Total	89.08	16				

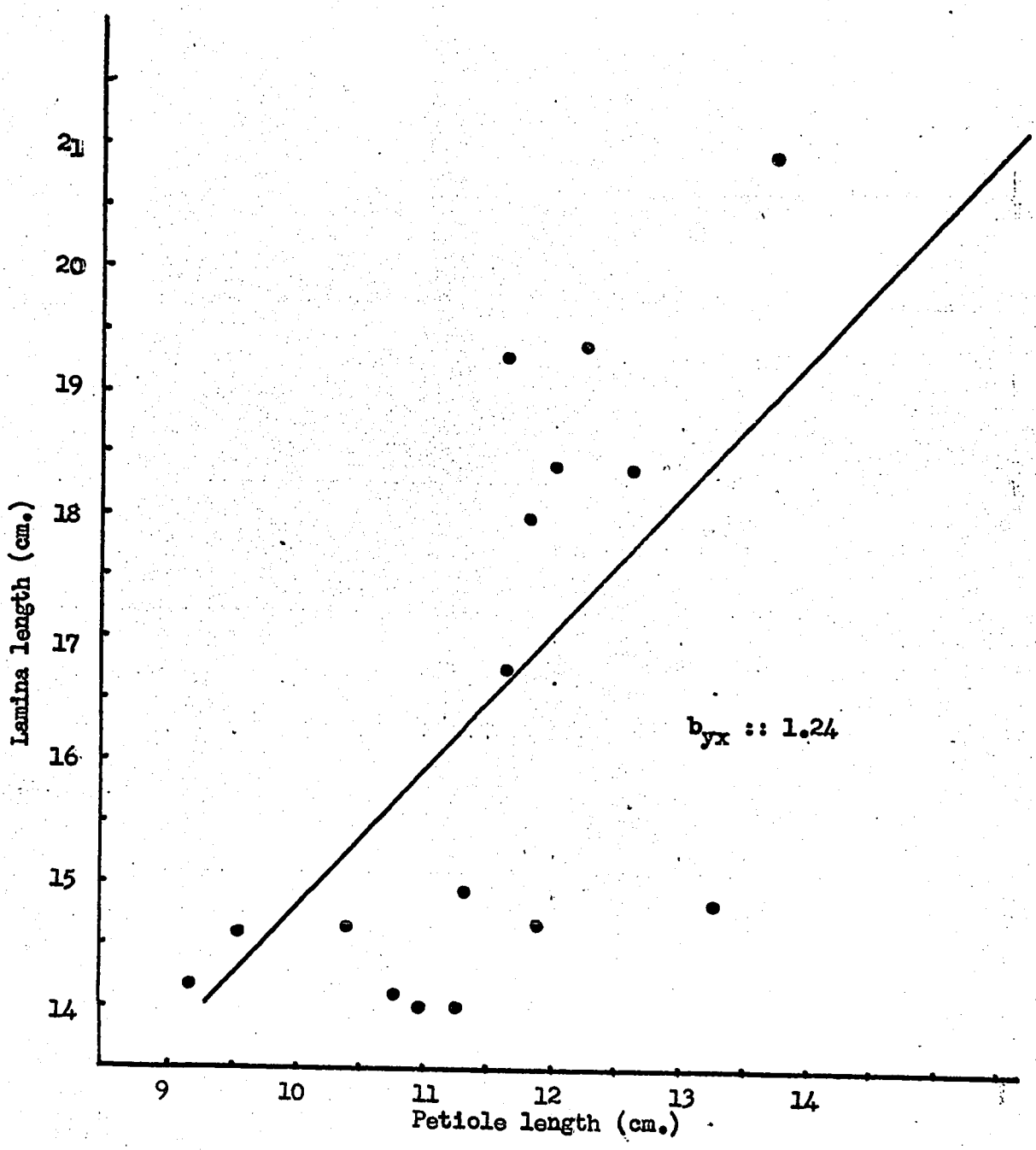

Figure 28. Regression of lamina length on petiole length.

TABLE 14.

Summary of the measurements of fifteen male inflorescences taken from a clonal plant belonging to the accession 12/63.

Inflorescence No.	Number of branches	Number of flowers per branch		Length of branch (cm.)		Mean number of flowers per cm.
		Range	Mean	Range	Mean	
1	3	5 - 19	10.67	1.91-6.38	4.04	2.64
2	2	13 - 15	14.00	5.10-6.38	5.74	2.44
3	3	24 - 29	26.00	8.93-11.48	10.20	2.55
4	4	10 - 29	21.00	4.46-12.75	9.25	2.27
5	4	11 - 28	22.00	3.83-14.03	10.04	2.19
6	3	14 - 27	20.33	5.74-12.75	9.56	2.13
7	3	16 - 21	19.33	8.29-10.20	9.14	2.11
8	5	14 - 37	23.60	7.65-15.30	11.99	1.97
9	3	21 - 36	27.33	8.93-14.66	11.48	2.38
10	3	20 - 31	25.67	7.01-11.48	9.78	2.62
11	2	23 - 26	24.50	9.56-10.20	9.89	2.48
12	2	14 - 20	17.00	5.74-8.93	7.33	2.32
13	14	3 - 29	18.43	1.28-10.84	7.42	2.48
14	2	12 - 13	12.50	5.74-7.65	6.19	2.02
15	4	14 - 32	22.75	5.10-12.11	9.09	2.50

TABLE 15.

Summary of the measurements of fifteen male inflorescences taken from a clonal plant belonging to the accession 13/63.

Inflorescence No.	Number of branches	Number of flowers per branch		Length of branch (cm.)		Mean number of flowers per cm.
		Range	Mean	Range	Mean	
1	5	9 - 43	26.80	1.91-11.48	7.65	3.50
2	5	6 - 42	23.40	1.28-9.56	5.61	4.17
3	22	6 - 27	15.14	1.28-5.10	3.10	4.88
4	5	10 - 37	24.20	1.28-8.93	5.36	4.51
5	2	21 - 26	23.50	5.10-6.38	5.74	4.09
6	3	10 - 28	18.00	2.55-7.65	5.10	3.53
7	2	4 - 18	11.00	1.28-3.83	2.50	4.40
8	10	6 - 44	21.00	1.28-10.20	4.72	4.45
9	4	18 - 34	28.00	4.46-7.65	6.22	4.50
10	4	33 - 47	35.00	7.01-10.20	8.21	4.26
11	10	5 - 21	12.00	1.28-4.46	2.74	4.38
12	5	4 - 22	16.00	1.28-5.10	3.19	5.02
13	3	21 - 23	22.00	3.19-5.10	4.46	4.93
14	4	11 - 62	36.25	1.28-1.48	7.49	4.84
15	5	8 - 21	13.60	1.91-4.46	2.87	4.74

TABLE 16.

Summary of the measurements of fifteen male inflorescences taken from a clonal plant belonging to the accession 44/63.

Inflorescence No.	Number of branches	Number of flowers per branch		Length of branch (cm.)		Mean number of flowers per cm.
		Range	Mean	Range	Mean	
1	1	29	29.00	15.30	15.30	1.90
2	1	24	24.00	12.75	12.75	1.88
3	2	19 - 24	21.50	8.29-9.56	8.93	2.41
4	3	28 - 34	31.67	14.03-16.58	15.73	2.01
5	2	32	32.00	16.58-17.85	17.21	1.86
6	2	8 - 16	12.00	3.83-8.29	6.02	1.98
7	3	22 - 28	25.00	12.11-14.03	12.75	1.96
8	3	5 - 26	17.33	3.83-13.39	9.56	1.81
9	3	22 - 33	26.00	11.48-15.30	12.96	2.01
10	2	21 - 29	25.00	11.48-14.03	12.75	1.96
11	2	15 - 20	17.50	8.29-9.56	8.98	1.95
12	1	28	28.00	14.03	14.03	2.00
13	2	17 - 20	18.50	6.38-9.56	7.97	2.32
14	2	22 - 28	25.00	10.20-14.66	12.43	2.01
15	1	21	21.00	9.56	9.56	2.20

TABLE 17.

Summary of the measurements of fifteen female inflorescences taken from a clonal plant belonging to the accession 15/63.

Inflorescence No.	Number of branches	Number of flowers per branch		Length of branch (cm.)		Mean number of flowers per cm.
		Range	Mean	Range	Mean	
1	2	10 - 20	15.00	7.65-12.75	10.20	1.47
2	1	14	14.00	10.20	10.20	1.37
3	2	18 - 25	21.50	12.11-15.30	13.71	1.57
4	1	18	18.00	10.84	10.84	1.66
5	1	21	21.00	11.48	11.48	1.83
6	2	17 - 25	21.00	8.93-11.48	10.20	2.06
7	1	28	28.00	19.13	19.13	1.46
8	3	8 - 18	12.00	5.10-12.75	8.71	1.38
9	2	10 - 21	15.50	8.29-13.39	10.84	1.43
10	2	10 - 16	13.00	8.29-10.84	9.56	1.36
11	3	14 - 33	24.67	8.93-16.58	12.96	1.90
12	2	17 - 26	21.50	9.56-12.14	10.84	1.98
13	2	26 - 32	29.00	15.30	15.30	1.90
14	2	14 - 22	18.00	8.93-11.48	10.20	1.76
15	2	21 - 24	22.50	16.58-18.49	17.53	1.28

TABLE 18.

Summary of the measurements of fifteen female inflorescences taken from a clonal plant belonging to the accession 16/63.

Inflorescence No.	Number of branches	Number of flowers per branch		Length of branch (cm.)		Mean number of flowers per cm.
		Range	Mean	Range	Mean	
1	3	13 - 26	20.33	5.74-12.75	9.99	2.04
2	2	28 - 31	29.50	19.13-21.68	20.40	1.45
3	2	16 - 22	19.00	11.48-17.85	14.66	1.30
4	2	12 - 18	15.00	10.20-11.48	10.84	1.38
5	2	18	18.00	12.75-14.66	13.71	1.31
6	2	18 - 24	21.00	12.75-17.85	15.30	1.37
7	3	12 - 19	15.00	11.48-15.30	13.60	1.10
8	2	16 - 17	16.50	14.03	14.03	1.18
9	1	18	18.00	15.94	15.94	1.13
10	3	16 - 30	24.00	12.11-21.04	17.85	1.34
11	1	26	26.00	21.68	21.68	1.20
12	1	9	9.00	9.56	9.56	0.94
13	2	14 - 22	18.00	11.48-17.85	14.66	0.95
14	2	21 - 28	24.50	16.58-21.04	18.81	1.30
15	2	11 - 25	18.00	8.29-14.03	11.16	1.61

TABLE 19.

Summary of the measurements of fifteen female inflorescences taken from a clonal plant belonging to accession 39/63.

Inflorescence No.	Number of branches	Number of flowers per branch		Length of branch (cm.)		Mean number of flowers per cm.
		Range	Mean	Range	Mean	
1	2	20 - 26	23.00	12.75-17.85	15.30	1.50
2	3	14 - 24	19.00	10.20-14.03	12.33	1.54
3	2	6 - 18	12.00	7.65-10.84	9.24	1.30
4	2	9 - 10	9.50	7.65	7.65	1.24
5	2	10 - 16	13.00	8.29-11.48	9.88	1.32
6	3	13 - 23	17.00	10.20-14.03	11.48	1.48
7	3	4 - 12	14.00	5.10-9.56	8.08	1.73
8	3	7 - 18	12.00	7.01-12.75	9.56	1.26
9	3	5 - 19	11.67	6.38-11.48	8.93	1.31
10	2	17 - 19	18.00	11.48-13.39	12.43	1.45
11	2	11 - 17	14.00	7.65-10.20	8.93	1.57
12	4	12 - 31	21.50	5.10-15.94	11.48	1.83
13	3	13 - 23	17.00	8.93-14.66	11.26	1.51
14	3	11 - 18	13.67	8.93-12.75	10.20	1.34
15	1	10	10.00	8.93	8.93	1.12

which are pliant and hang straight down from their points of attachment to the plant. The female inflorescence branches sparingly and occurs as 1 to 3 simple, slender, pendant racemes originating in a single leaf axil (Figure 30). The axes of both male and female inflorescences are hairy.

On the basis of counts taken at Central Experiment Station, male plants produce at least 50% more flowers than female plants so that there is usually adequate quantities of pollen available for pollination at time of flowering.

The Flower. Cush-cush flowers, male and female, are small, green in colour and individually inconspicuous. However, the mass effect of many flowers per plant renders them quite noticeable in the field. Both male and female flowers have very short pedicels and are subtended by acuminate bracts, 2 to each flower. The male flower is shorter than the female flower (Table 20 - see Appendix X for original data), and appears wheel-shaped when the perianth segments are fully expanded. The perianth consists of 6 oblong-lanceolate segments arranged in 2 whorls and united at the base. There are 6 fertile stamens with anthers borne about 1 mm. above the perianth by erect filaments inserted at the base of the perianth segments. The anthers are curved, oblong and introrse. The style is rudimentary and consists of a roughly triangular pillar made up of 3 fused but distinct segments. It measures about 0.5 mm. in height and thickness. (Figure 30a).

The perianth of the female flower is similar to that of the male. Six short, inconspicuous, tuft-like staminodes are inserted at the base of the perianth segments. A prominent inferior hairy ovary

Figure 29. Male inflorescences.

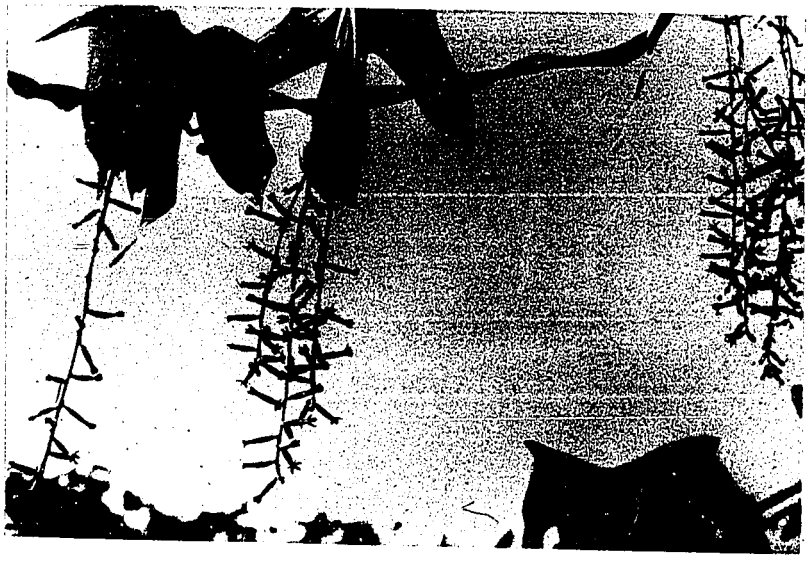

Figure 30. Female inflorescences.

Figure 30a. Cush-cush flowers. (Approx. x5)
Left: Female flower.
Centre: Bisexual flower. (Note well-developed anthers and inferior ovary).
Right: Male flower.

Figure 29. Male inflorescences.

Figure 30. Female inflorescences.

Figure 30a. Cush-cush flowers. (Approx. x5)
Left: Female flower.
Centre: Bisexual flower. (Note well-developed anthers and inferior ovary).
Right: Male flower.

TABLE 20.

Dimensions of flowers. Mean length and width[*] of the flowers of 10 clonal plants belonging to 10 accessions.

Accession	Sex	Length (mm.)[**] Mean	Length (mm.)[**] Standard Deviation	Width (mm.)[***] Mean	Width (mm.)[***] Standard Deviation
12/63	Male	6.56	.822	6.69	1.105
13/63	Male	4.54	.933	6.53	1.015
17/63	Male	5.53	.803	7.05	.779
41/63	Male	5.91	.369	7.11	.811
44/63	Male	5.09	.660	7.87	.351
1/63	Female	11.94	.973	6.38	.000
16/63	Female	14.32	1.503	8.95	.569
23/63	Female	11.13	.737	5.72	.792
42/63	Female	12.74	.730	7.32	.789
41/63	Hermaphrodite	10.62	.979	7.43	.764

[*] Based on 20 determinations.

[**] Measured from point of attachment to axis of inflorescence to top of anthers.

[***] Measured across the diameter of the whorl of expanded perianth segments.

is prolonged into a conical style which terminates in 3 reflexed, tube-like stigmas. (Figure 30a).

A few hermaphrodite plants were found amongst the cush-cush populations at Central Experiment Station (Sex Expression Studies - Tables 29-31), and there were also some predominantly male inflorescences which bore some bisexual flowers. These flowers are always similar in form to the female flowers but with slightly smaller ovaries and greatly modified stigmas. In many instances the stigmas are reduced to small knobs or may be completely absent. (Figure 30a).

In the preliminary study on flower induction carried out in this programme (Materials and Methods, p.48), 2 out of 10 plants subjected to short-day conditions on 22nd June flowered on 26th July, i.e. when the days are normally long. None of the control plants flowered during the course of the experiment which lasted until 30th September. The significance of this result is difficult to evaluate. Only 2 plants out of 10 subjected to short days flowered; but a flowering frequency of 20% among cush-cush seedlings grown under normal conditions is not unusual. The fact is that the experimental control was too limited to permit precise evaluation. Available facilities did not extend to the control of other environmental factors such as temperature and humidity, both of which might have been influential in the result. Only photoperiod was controlled. Further experimentation involving more critical methods must be carried out before the mode of flower induction in Dioscorea trifida can be determined.

Anthesis occurs 10-30 days after the appearance of the flower buds, the actual length of time depending on the vigour of the plants.

A large number of insect species are capable of effecting pollination in Dioscorea trifida. In the fully-opened flowers, both stamens and styles are readily accessible to flying and crawling insects, and individuals belonging to the following orders have been observed regularly moving from flower to flower in the cush-cush plots:

Orders	Families
Hymenoptera	- Formicidae (ants)
	- Vespidae (social wasps)
	- Chalcididae (chalcid wasps)
Coleoptera	- Curculionidae (weevils)
	- Lamprydae (fire flies)
	- Chrysomelidae (leaf beetles)
Diptera	- Muscidae (house flies)
	- Tachinidae (Tachina flies)
	- (a few other identified species)

Insect activity among the flowers is greatest between 9 a.m. and 2 p.m. daily.

The proportion of female flowers which eventually set fruit after pollination varies from flowering branch to flowering branch on the same plant and also from plant to plant. Estimates based on the measurement of 20 randomly selected inflorescence branches in 6 accessions are shown in Table 21.

Artificial pollination was not examined critically in this research programme but some hand pollinations were tried with encouraging results. The method used involved the following:

(a) bagging the female inflorescence in a finely-meshed muslin bag prior to flower opening to exclude insects.

TABLE 21.

Estimates of fruit set per inflorescence in six plants taken from six accessions; based on the measurement of 20 randomly selected inflorescence branches per plant.

Accession	Number of Flowers	Number of Fruit Set	Fruit Set Percentage
1/63	365	246	67.39
2/63	301	226	75.08
5/63	239	208	87.03
10/63	412	270	65.53
15/63	279	166	59.50
23/63	550	279	50.72

(b) removal of bag to effect transfer of pollen from male to female flower when the latter is fully opened.

(c) replacement of bag until evidence of successful fertilization is indicated by swelling of the ovary.

Transfer of pollen is effected by removing a fully dehisced male flower from its parent plant and rubbing its pollen-laden anthers onto the stigmas of the female flower.

Fruit set after pollination by this method was found to be nearly as successful as that following natural pollination and the seeds which resulted germinated normally. Bisexual flowers when self- or cross-pollinated in this manner failed to set fruit.

The Fruit. The fruit of Dioscorea trifida is a tri-locular, reflexed capsule (Figure 31). It is somewhat elongated, bulges a little in the middle and is rounded at both ends. It may be slightly broader toward the base than at the apex. In cross section the capsule is 3-cornered with concave sides and appears stellate in configuration. Dehiscence is septicidal and there may be 1 or 2 seeds per locule. Data on capsule length and number of seeds per capsule are shown in Table 22. The capsule is green and succulent during growth. At maturity it dries and becomes brown and papery.

The Tuber. One of the most interesting and important characteristics of Dioscorea trifida is the fact that a single plant produces clusters of relatively small shallow rooted tubers. These tubers are easy to harvest, handle and transport. In a growing season of 7-10 months a single cush-cush plant can produce a tuber cluster weighing

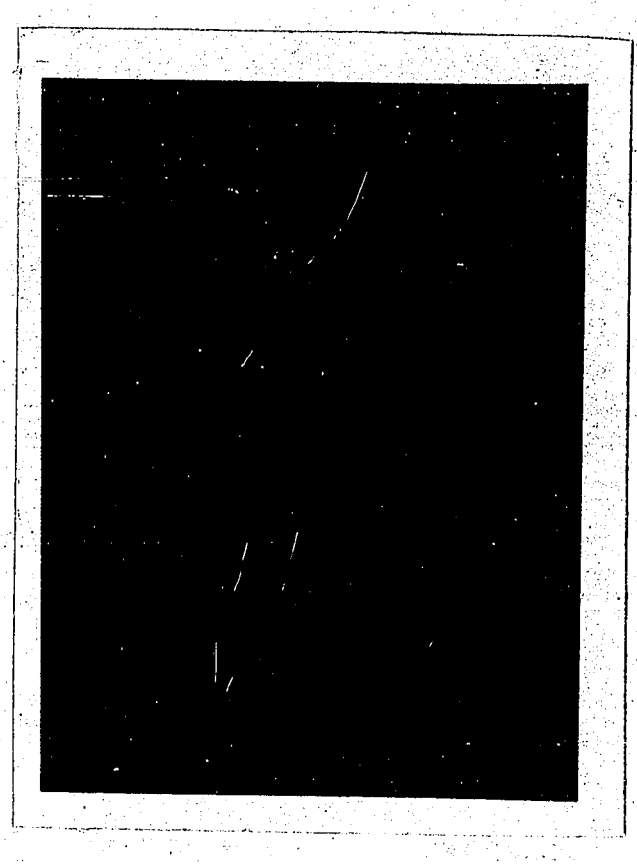

Figure 31. Reflexed capsules.

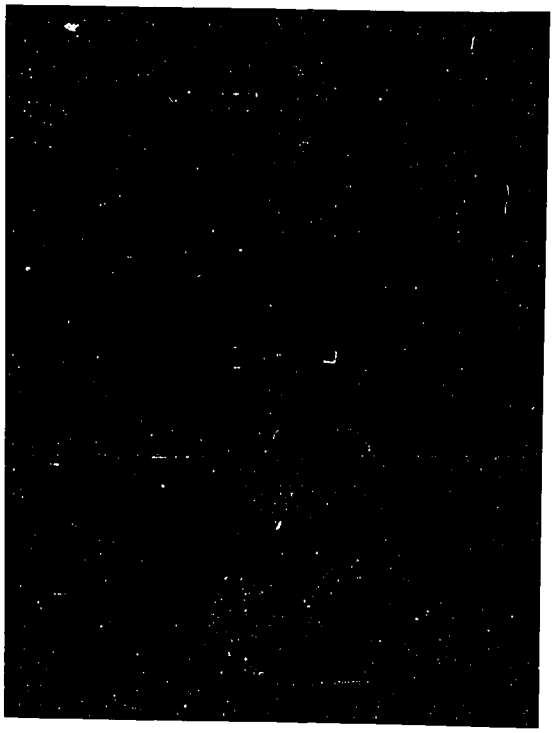

Figure 31. Reflexed capsules.

TABLE 22.

Mean length[M] of capsules and number of seeds[M] per capsule. Measured on 4 clonal plants from 4 accessions.

Accession	Mean Length of Capsule (cm.)	Number of Seed per Capsule
1/63	2.25	3.73
2/63	2.27	4.57
15/63	2.69	3.60
39/63	2.41	3.35

[M] Based on the measurement of 100 seeds per plant.

up to 15 lb. and containing 15 marketable tubers.

The tuber cluster is a composite of large and progressively smaller tubers. The larger tubers are older and are generally found in the centre of the cluster. They frequently extend below the shorter younger tubers. Successive rings of progressively smaller tubers radiate outwards from the central corm above the older tubers until finally the smallest tubers are found at the top of the cluster (Figure 32). Fibrous roots are usually scattered throughout the cluster but most of them tend to be concentrated at the base of the stem (or stems) immediately above the cluster.

The disposition of the tubers, or tuber habit, varies from one cultivar to another. The clusters of some types contain a few large tubers and many small unmarketable ones. Others have a relatively large number of small well-formed marketable tubers. Some tubers have long necks and the clusters are loose, open and spread over a relatively large area of ground; other tubers have short necks and form compact non-spreading clusters. The latter are easy to harvest. Some of the shapes of individual tubers are illustrated in Appendix XI.

The skin or periderm of the mature cush-cush tuber is dull brown in colour and coarse in texture. Tiny, elongated cracks in the corky surface may make it seem streaked and roughened. The outer cortical layers immediately below the periderm may be light green, cream, white or purple. The flesh varies from white to purple and although the gradations in colour are numerous, 4 colours are readily recognizable, viz., white, light purple, purple, and deep purple.

The tubers are of course the normal propagating units of

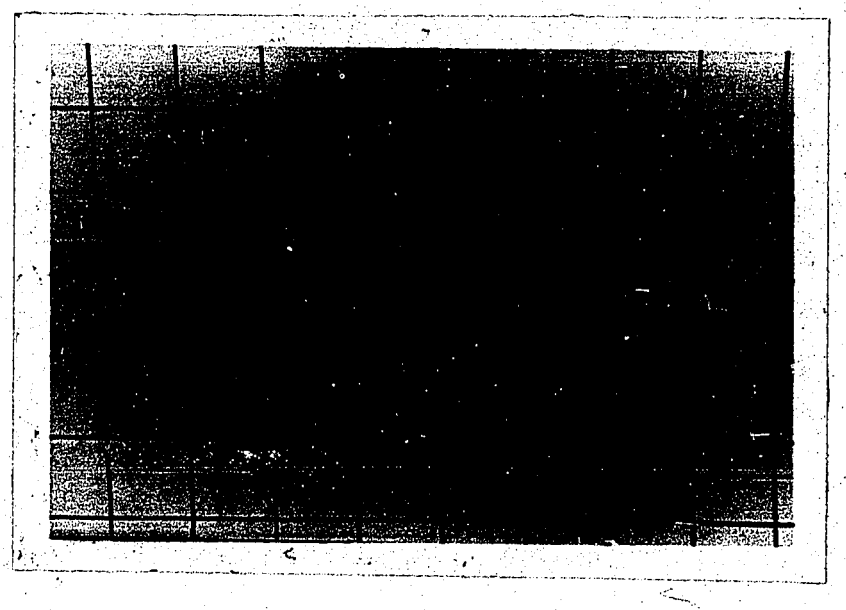

Figure 32. Tuber cluster with successive layers of tubers.

Figure 32. Tuber cluster with successive layers of tubers.

Dioscorea trifida. Observations indicate that any part of the mature tuber will grow if placed in suitable growing conditions. However, when whole tubers are set to sprout, the buds at the top end (i.e. near to the original point of attachment to the plant) emerge more quickly and in greater numbers than those at the distal end.

Association of Plant Characters. Some of the data previously cited were assembled in Table 23 and a multiple scatter diagram was plotted (Figure 32) to determine whether the association of simple characters can be used in the classification of the variation found in Dioscorea trifida. In this preliminary attempt emphasis was laid in the choice of characters on obvious features of plant form used commonly to separate varieties and cultivars in other species, viz., the leaves, stems and tubers. The disposition of individual glyphs on the graph suggests the occurrence of two major groups, viz., a group with short leaf blades and a group with long leaf blades. (There is also a suggestion of a minor, intermediate group, but since it only contains 2 individuals it may be premature to regard it as such.) Assuming two major groups, subgroups based on stem thickness, tuber shape and petiole length are clearly indicated as follows:

A. Lamina short. Group I

(a) Tuber cluster compact.

(i) Tubers fan-shaped. Immature tubers club-shaped. Stems thin. Petioles short. Sub-group 1.
44/63/13
44/63/31
44/63/41

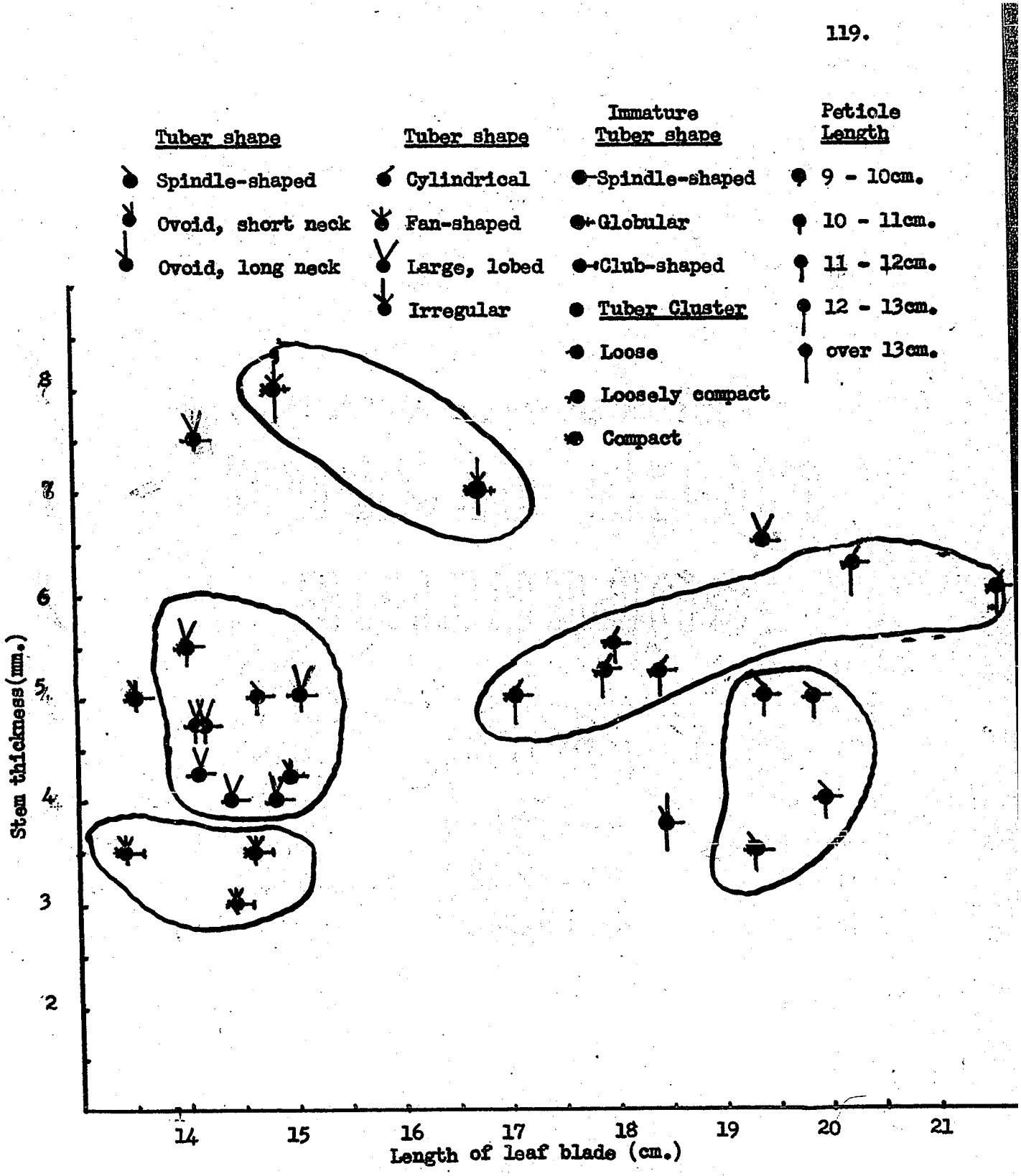

Figure 32a. Pictorialized scatter diagram showing 28 individuals (clones) simultaneously diagrammed for 7 characters.

TABLE 23.

Characters measured in 28 individual clonal plants from 16 accessions.

	Clones	Lamina Length cm.	Petiole Length cm.	Stem Thickness mm.	Shape of Immature Tubers	Tuber Shape
1.	1/63/4	18.41	12.65	5.25	Spindle	Spindle
2.	1/63/5	17.87	13.71	5.25	Spindle	Spindle
3.	1/63/6	17.03	12.84	5.00	Spindle	Spindle
4.	2/63/7	14.95	11.34	4.25	Spindle	Large, lobed
5.	2/63/8	14.42	9.73	4.00	Spindle	Large, lobed
6.	2/63/10	15.06	10.65	5.00	Spindle	Large, lobed
7.	5/63/6	14.06	11.33	4.75	Spindle	Large, lobed
8.	6/63/7	14.01	10.99	5.50	Spindle	Large, lobed
9.	10/63/7	14.86	13.29	8.00	Globular	Irregular
10.	12/63/6	14.65	10.45	5.00	Spindle	Spindle
11.	12/63/8	19.37	11.59	5.00	Spindle	Spindle
12.	12/63/9	19.84	12.89	5.00	Spindle	Spindle
13.	15/63/6	19.99	13.28	4.00	Spindle	Spindle
14.	15/63/9	19.33	11.66	3.50	Spindle	Spindle
15.	16/63/7	21.59	12.10	6.00	Spindle	Cylindrical, curved
16.	16/63/8	20.48	13.75	6.25	Spindle	Cylindrical, curved
17.	23/63/5	18.03	11.85	5.50	Spindle	Cylindrical, curved
18.	27/63/7	18.43	12.05	3.75	Spindle	Ovoid, long neck
19.	29/63/4	13.51	9.54	5.00	Spindle	Ovoid
20.	35/63/4	14.10	10.80	4.75	Spindle	Large, lobed
21.	37/63/7	19.39	12.27	6.50	Spindle	Large, lobed
22.	39/63/5	14.22	9.20	7.50	Spindle	Large, lobed
23.	40/63/6	16.75	11.71	7.00	Globular	Irregular
24.	42/63/6	14.81	11.35	4.00	Spindle	Large, lobed
25.	42/63/7	14.18	11.91	4.25	Spindle	Large, lobed
26.	44/63/13	14.45	8.75	3.00	Fan	Club
27.	44/63/31	13.41	8.53	3.50	Fan	Club
28.	44/63/41	14.58	9.62	3.50	Fan	Club

(ii) Tubers irregular, ovoid, fusiform or lobed. Immature tubers globular. Stems thick. Petioles long.

Sub-group 2.
10/63/7
40/63/6

(b) Tuber cluster loose, open.

(i) Tubers large, lobed. Immature tubers spindle-shaped. Stems medium. Petioles medium.

Sub-group 3.
2/63/7
2/63/8
2/63/10
5/63/6
6/63/7
35/63/4
42/63/6
42/63/7
12/63/6

B. Lamina long. Group II

(a) Tuber cluster loosely compact.

(i) Tubers cylindrical, variously curved. Immature tubers spindle-shaped. Stems thick. Petioles long.

Sub-group 4.
1/63/4
1/63/5
1/63/6
16/63/7
16/63/8
23/63/5

(ii) Tubers spindle-shaped. Immature tubers spindle-shaped. Stems medium-sized to thin. Petioles medium-sized.

Sub-group 5.
12/63/8
12/63/9
15/63/6
15/63/9

A few individuals did not fall appropriately into the suggested sub-groups.

3. Germination and the Seedling - Observations and Germination Tests.

Observations. Many cush-cush seeds swell with moisture when placed on a moist medium. Some of the swelling is gradual and occurs in the endosperm and seed coats making these tissues less brittle and flinty. Sudden and dramatic swelling takes place when seeds imbibe water directly into their endosperm cavities causing the middle regions to bulge prominently. The immediate effect of this kind of imbibition on embryo growth has not been determined but the seeds in which it occurs often fail to germinate and endosperm and embryo soon decompose. Some seeds do not swell when set to germinate in moist conditions and may remain unchanged in these conditions for several months. This long exposure to controlled high moisture levels apparently does no harm and the seeds may finally germinate. Frequently, the embryos of seeds which fail to germinate after 5-6 months appear perfectly normal and healthy.

The first obvious sign that germination has commenced is the appearance of the radicle as it bursts through the seed coat at the apex of the seed. Before this occurs however, the cotyledon which remains in the seed expands until it fills, or almost fills, the endosperm cavity pushing the cone of the embryo toward the micropyle (Figures 33 and 34). After emergence the radicle or primary root elongates unbranched at the rate of 2-3 mm. per day. When it is about 10 mm. long a pronounced swelling in the proximal region marks the emergence of the primary bud in association with the cotyledonary sheath. The sheath is unfolded at the time of emergence and appears in the form of two interlocking bracts in the centre of which lies the developing first functional leaf. The growing point of the first functional leaf is conical in shape and

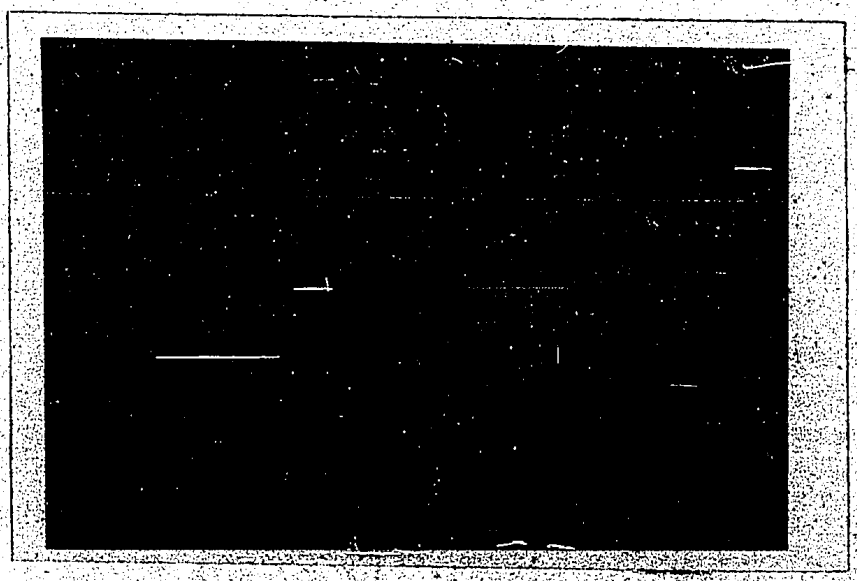

Figure 33. Embryos. Dormant embryo on left and growing embryo on the right with fully expanded cotyledon.

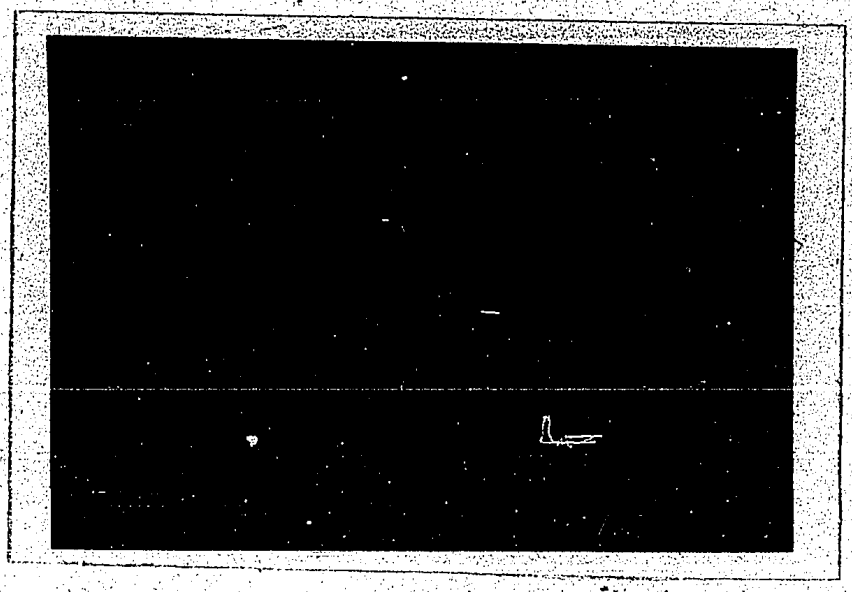

Figure 34. Stages in early seedling growth.
Left : radicles has started to emerge.
Right : radicles is relatively elongated. Slight swelling may be observed at its proximal end.
Centre: emerging first functional leaf and its associated sheath can be seen.

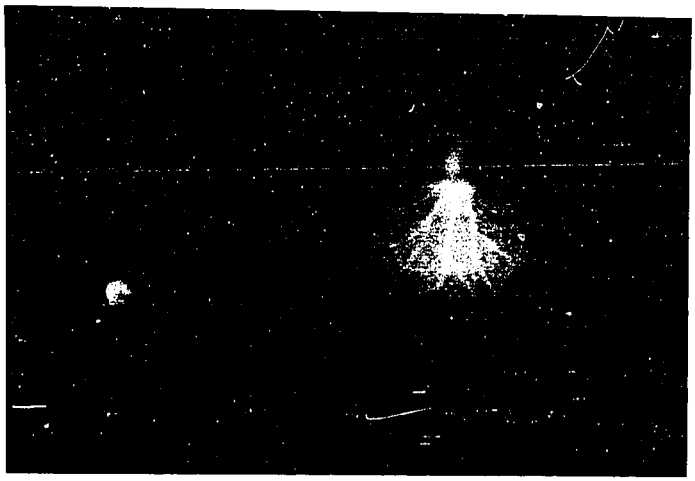

Figure 33. Embryos. Dormant embryo on left and growing embryo on the right with fully expanded cotyledon.

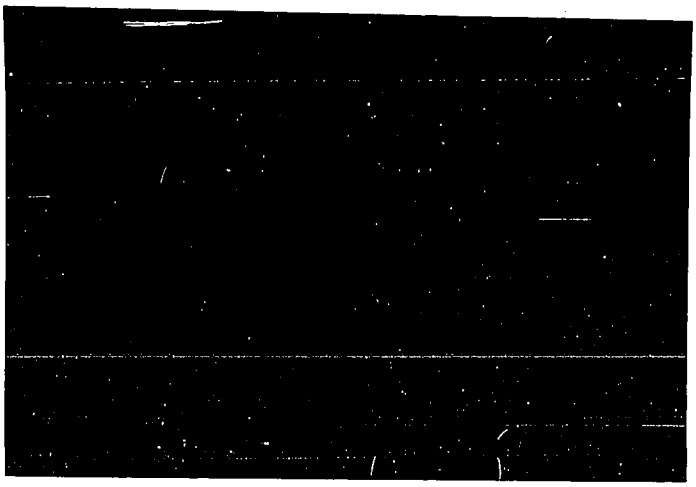

Figure 34. Stages in early seedling growth.
Left : radicles has started to emerge.
Right : radicles is relatively elongated. Slight swelling may be observed at its proximal end.
Centre: emerging first functional leaf and its associated sheath can be seen.

erect as it pushes through the sheath but as soon as this is accomplished it curves over and downwards developing into a tiny but well-formed leaf blade having its ventral surface facing the rapidly elongating petiole (Figure 35). The leaf remains bent over, like a shepherd's staff, until it is well above ground at which time it gradually becomes erect and the lamina orients toward the light (Figure 36). It takes 14-30 days from the time of emergence of the radicle for the first leaf to become erect and, if in soil, to appear above ground.

It becomes apparent 7-14 days after its emergence that the first functional leaf is in fact the first functional shoot. As the first leaf blade expands a minute leaf bud becomes noticeable on what had seemed to be the petiole of the first leaf. The new leaf bud develops in due course into another leaf having at the base of its petiole yet another leaf bud (Figure 37). In this manner 5 or 6 leaves may be produced on the first functional shoot.

While the primary shoot is developing the swelling first observed at the proximal end of the radicle increases in size on the side opposite the shoot, i.e. on the lower side. This is the beginning of plagiotropic lobing in the hypocotyl and results eventually in the formation of the tubers. Adventitious roots are quickly produced on the new tuberous growth and these soon become the principal root system of the young plant, the primary root being lost or indistinguishable from the other roots. Meanwhile the seed coat is still evident and may persist throughout the seedling phase. In Dioscorea trifida the bulge in the hypocotyl develops very slowly. It forms a corm-like axis and appears capable of producing a succession of aerial shoots each arising

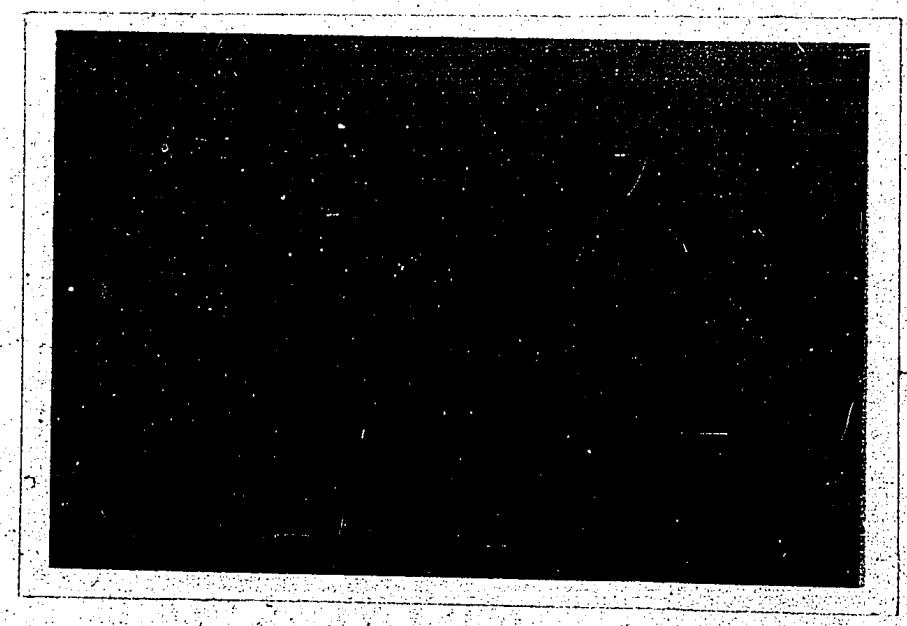

Figure 35. Young seedling with first functional leaf still bent over and downwards. Small squares 0.1 in. x 0.1 in.

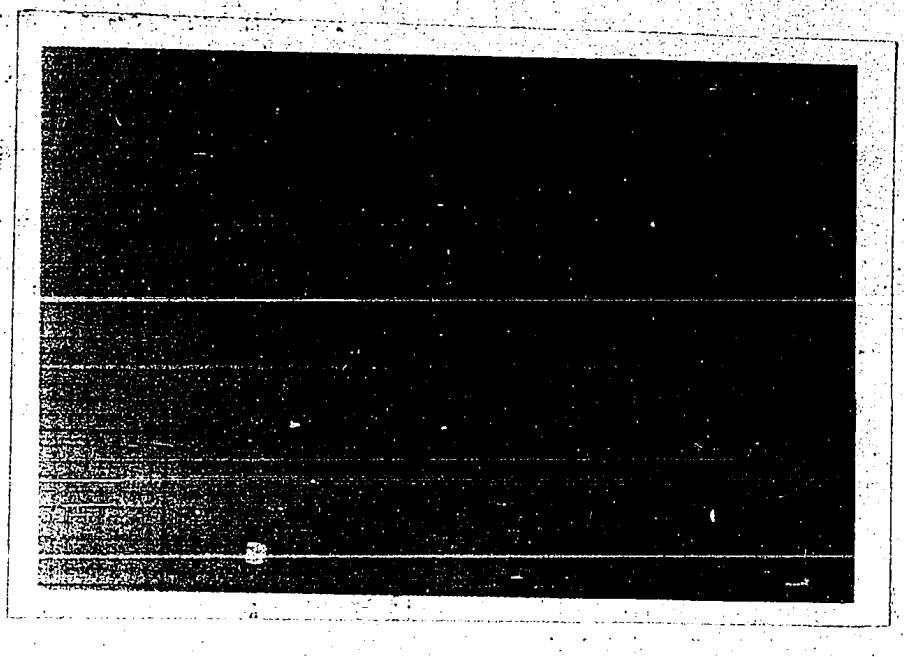

Figure 36. Young seedling with first functional leaf becoming erect. Small squares 0.1 in. x 0.1 in.

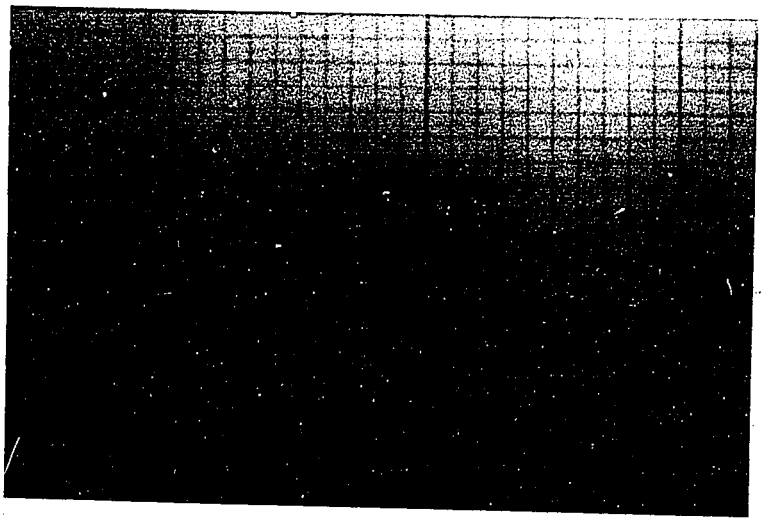

Figure 35. Young seedling with first functional leaf still bent over and downwards. Small squares 0.1 in. x o.1 in.

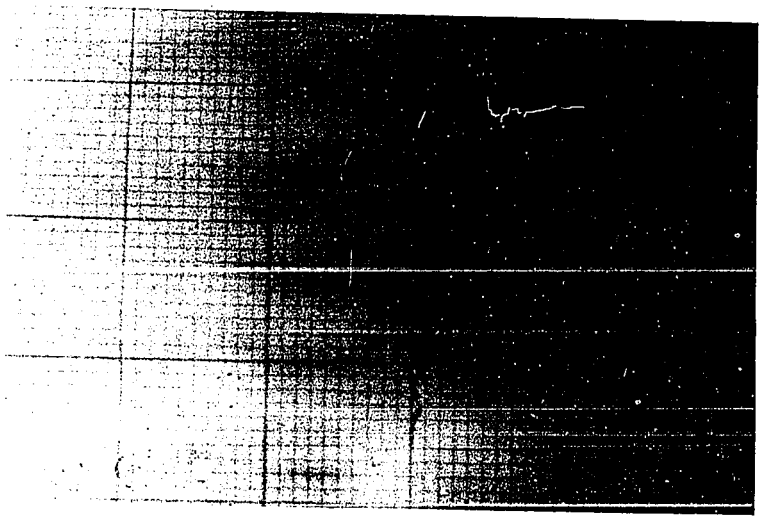

Figure 36. Young seedling with first functional leaf becoming erect. Small squares 0.1 in. x 0.1 in.

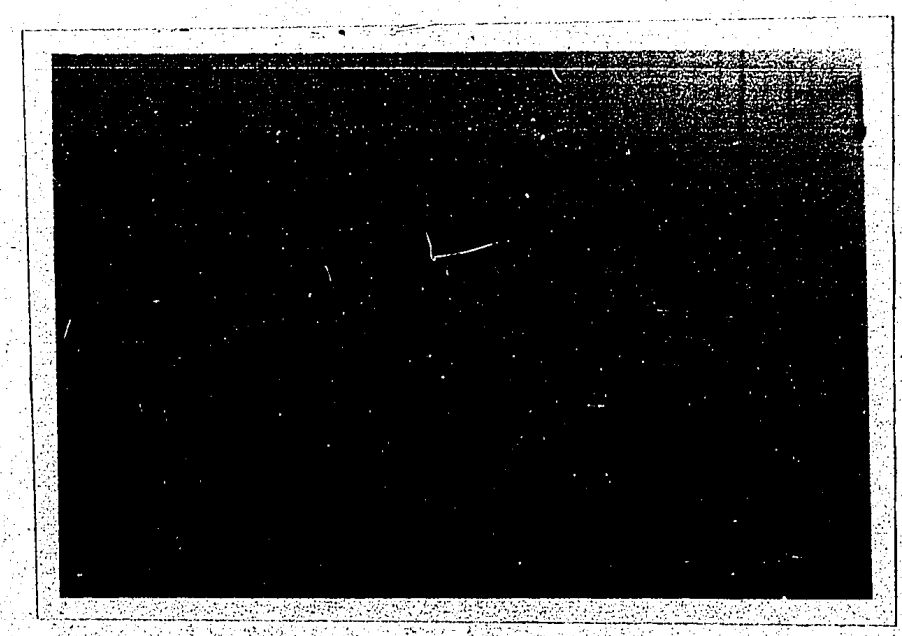

Figure 37. Young seedling with second leaf emerging. Small squares 0.1 in. x 0.1 in.

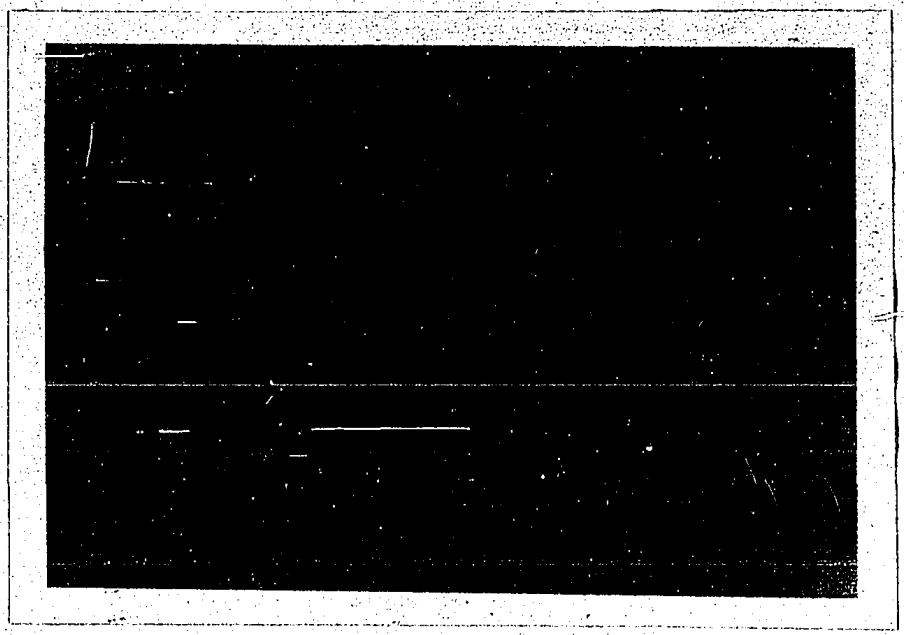

Figure 38. Seedling with expanding leaf blades and elongating petioles. Secondary shoot has emerged from bulge of the base of first shoot. Small squares 0.1 in. x o.1 in.

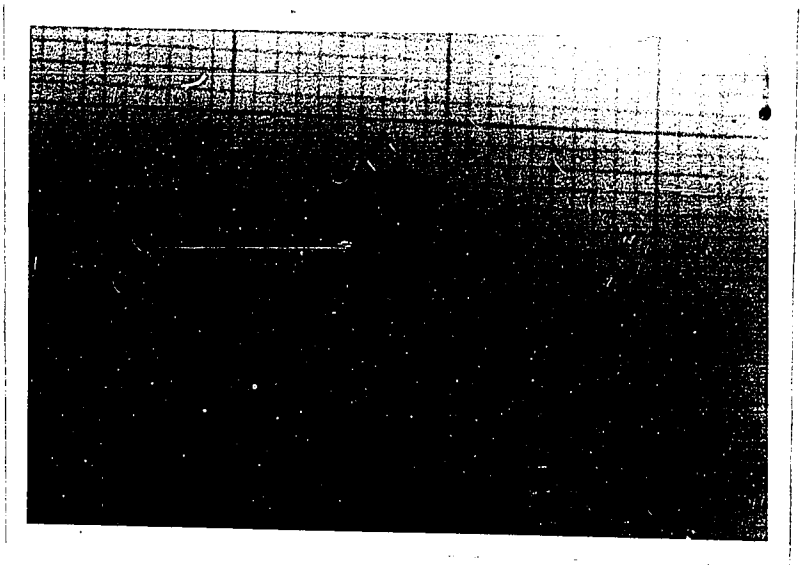

Figure 37. Young seedling with second leaf emerging. Small squares 0.1 in. x 0.1 in.

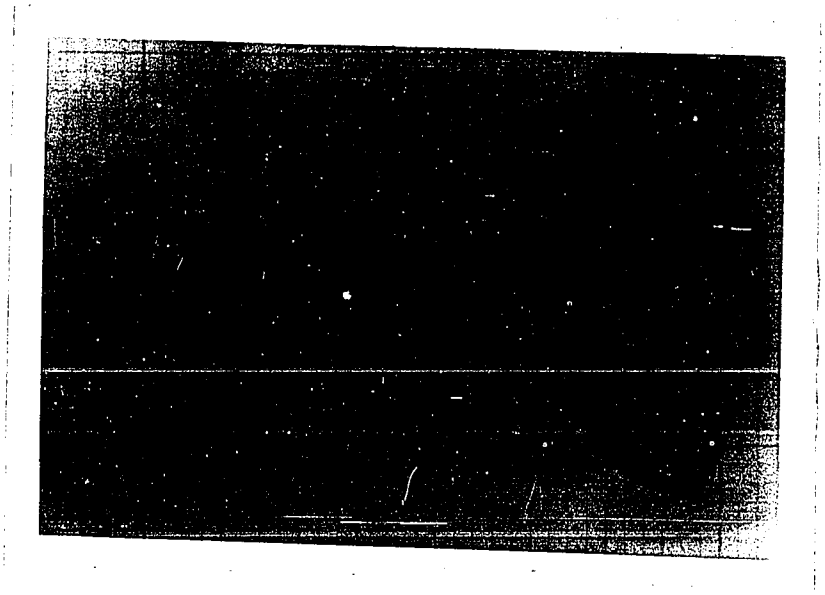

Figure 38. Seedling with expanding leaf blades and elongating petioles. Secondary shoot has emerged from bulge of the base of first shoot. Small squares 0.1 in. x o.1 in.

from a new increment in the bulge. No significant tuber formation takes place until vigorous and abundant foliage growth is achieved.

A new shoot usually emerges before the first shoot has completed its development. It is usually more vigorous than the first shoot and its leaves are larger and more numerous. Otherwise its development is similar to that described for the first shoot. Three to six shoots may arise successively in this manner.

The leaves of the primary shoot of the cush-cush seedling unlike those of the adult plant are entire, small and heart-shaped. The stem is erect and wingless unlike the winged, twining adult stem. The foliage of Dioscorea trifida is in fact heteroblastic and entire leaves and erect stems characterize the juvenile phase in development. In this phase also, the dominant feature of growth is petiole elongation and lamina expansion. Relatively little stem elongation occurs and as a consequence seedling shoots are at first rosette-like in appearance (Figure 38). The change from juvenile to adult phase is gradual and each succeeding shoot has a slightly longer stem and larger and increasingly more indented leaves than its predecessor. Wings then begin to appear on stems and petioles. The rate of stem elongation finally exceeds that of petiole elongation in the fifth or sixth shoot. The stem becomes long and pliant and tends to twine around any object with which it comes into contact and the characteristically lobed adult leaves are produced (Figure 39). The older juvenile shoots may persist for several months, but they eventually die. It takes 2 to 3 months for a seedling to commence twining after germination.

Figure 39. Seedling undergoing transition from juvenile to adult phase. A shoot with twining stem and lobed leaves has developed.

Figure 39. Seedling undergoing transition from juvenile to adult phase. A shoot with twining stem and lobed leaves has developed.

Germination Tests.

(a) Date of Seeding Experiment. The results of this series of germination tests which were carried out over a 7-month period in 1964 are recorded in Table 24. It is evident that the seed material tested has high germinability if seeded when fresh. The decreasing germination percentages as the seed got older suggest fairly rapid loss of viability. The long period required to complete germination in each test is worth noting. This is a common phenomenon in Dioscorea trifida. The fact that the commencement of germination was delayed longer in the March test than in any other is also of interest and may indicate a period of dormancy through which the seed was passing when it was set to germinate and which had to be completed before the germination process could begin. In the subsequent tests the seed was older and such a dormancy period could have been avoided by the later seeding.

(b) Seed Treatment Experiment I. The germination percentages obtained in this experiment were generally good (Table 25). The seed treatments tested seem to have had little effect and the untreated seeds germinated as well as the majority of those treated. It should be noted that this experiment was started in March, which also proved to be a successful planting time in the Date of Seeding Experiment. The length of time needed to complete germination in this experiment should also be noted.

(c) Seed Treatment Experiment II. It is evident from these results (Table 26) that removal of the seed coats was deleterious to successful germination. It was observed that seeds with this treatment

TABLE 24.

Germination Tests[*]. Date of Seeding Experiment. Carried out in soil with open-pollinated seed from female clonal plant 16/63/8.

Date of Seeding per Test	Germination %	No. of days to commencement of germination	No. of days to completion of test	Germination period (days)
18th March 1964	96.0	40	67	27
23rd April 1964	84.0	31	58	27
15th May 1964	70.5	27	59	32
15th June 1964	72.5	27	86	59
23rd July 1964	50.0	22	45	23
5th October 1964	16.5	25	62	35

[*] Based on 200 seeds per test.

TABLE 25.

Germination Tests[*]. Seed Treatment Experiment I. Carried out on filter paper in Petri dishes with open-pollinated seed.[**]

Seed Treatment	Continuous Darkness			Normal light and dark		
	Germination %	No. of days to germination beginning[+]	end[++]	Germination %	No. of days to germination beginning	end
5°C for 12 hrs.	88.0	21	49	80.0	19	45
5°C for 24 hrs.	80.0	21	37	76.0	17	35
52°C for 12 hrs.	84.0	17	37	92.0	17	26
52°C for 24 hrs.	88.0	23	47	84.0	19	38
Control	44.0	23	35	84.0	17	33

[*] Based on 200 seeds per treatment.

[**] Seeded 14th March 1964.

[+] Germination of first seed.

[++] Germination of last seed or termination of experiment.

TABLE 26.

Germination Tests[*]. Seed Treatment Experiment II. Carried out on filter paper in Petri dishes with open-pollinated seed from female clonal plant 2/63/9.[**]

Seed Treatment	Germination %	No. of days to commencement of germination	No. of days to completion of test[***]	Germination period days
(a) Wings removed	68	14	37	23
(b) Wings removed and seeds preheated (52°C) for 24 hours	66	16	37	21
(c) Seedcoats removed	28	14	37	23
(d) Seedcoats removed and seeds preheated (52°C) for 24 hours	11	19	37	18
(e) Seeds preheated (52°C) for 24 hours	78	20	37	17
(f) Control	70	17	37	20

[*] Based on 200 seeds per treatment.

[**] Seeded 19th May 1966.

[***] Experiment terminated due to the rotting of ungerminated seeds.

were rapidly invaded by molds; and decomposition of the invaded tissue soon followed. Embryo mortality may also have been increased by the exposure of these naked seeds to high temperatures. Apparently no harm is done to the germinating seed by removing its wings and exposing it to temperatures of 52°C provided the seed coat is intact. On the other hand, these treatments do not appear to be very beneficial in increasing germination percentage or the speed with which germination takes place.

Open-pollinated Seed Test. The results of this test (Table 27) indicate differential germinability of the seeds tested. Further testing is required to confirm this result.

4. Studies on Sex Expression.

The first observations on sex ratios in Dioscorea trifida were made on two populations grown in 1963/1964 at Central Experiment Station. One population consisted of 137 plants grown from randomly selected commercial tubers, and the other comprised about 150 plants grown from tubers of 38 accessions collected randomly from wild, semi-wild and cultivated sources. The results are shown in Table 28.

The preponderance of males, especially in the commercial plants is remarkable. Of the 96 plants which flowered among the commercial cultivars, 93.8% were male and 6.2% female. The difference between males and females was less pronounced in the non-commercial material - 56.3% males and 37.5% females among the flowering plants. The occurrence of a relatively large number of hermaphrodites (6.2%) in this variable population is also noted.

TABLE 27.

Germination Tests[M]. Open-Pollinated Seed Test. Carried out in Petri dishes on open-pollinated seeds from 7 female plants belonging to 7 accessions.

Clones	Germination %	Days to commencement of germination	Days to completion of germination	Period of germination (days)
2/63	84	21	35	14
5/63	88	16	42	26
9/63	72	16	42	26
10/63	64	21	33	12
15/63	52	16	41	25
23/63	63	17	40	23
26/63	71	19	38	19

[M] Based on 200 seeds per female parent.

TABLE 28.

Male and female plants in commercial cush-cush and random collections.

Sex	Commercial Plants Number of plants	%	Random Collections Number of accessions	%
Males	90	65.7	9	23.7
Females	6	4.4	6	15.8
Hermaphrodites	0	0.0	1	2.6
Did not flower	41	29.9	22	57.9
	137		38	

Experiments were conducted in 1964/1966 to examine sex expression in Dioscorea trifida more critically (Materials and Methods, Sex Expression). Data on sex ratios collected in these trials are summarized in Tables 29 to 31. Perusal of these data reveals the following important results:

(1) Relatively few plants flowered in the two seedling populations; only 15.44% in the shaded plots (Table 29), and 34.07% in the unshaded plots (Table 30).

(2) Of the seedling plants which flowered males were 76.6%, females were 12.9%, and hermaphrodites were 10.5% in the shaded plots, and 76.6%, 16.5% and 6.9% in the unshaded plots. The male to female ratio was about 5 to 1 (Tables 29 and 30).

(3) More plants flowered in the unshaded plots than in the shaded plots (Tables 29 and 30).

(4) The flowering percentage increased to 62.25 when the seedlings were re-grown as clonal plants in 1965/1966 (Table 31).

(5) Improved flowering was accompanied by more even distribution of male and female plants among those which flowered. The percentage of hermaphrodite plants decreased somewhat. Chi-square tests on the male and female data confirmed that in each of the 7 populations tested, the sex ratio does not deviate significantly from a 1:1 expectation (Table 32).

Some predominantly male plants bearing a few bisexual flowers were observed from time to time.

An attempt was made to determine what relationship, if any, existed between sex and yield of tubers per plant. The yields of male

TABLE 29.

Sex expression in open-pollinated progeny of 7 seedling female individuals. Shaded plots 1964-1965.

Female Parent Accession No.	Male	Female	Hermaph-rodite	Did not flower	Total	Flowering No.	Flowering %
1/63/5	13	2	8	84	107	23	21.50
2/63/6	18	0	4	95	117	22	18.80
2/63/9	9	2	0	100	111	11	9.91
12/63/6	11	9	0	97	117	20	17.09
15/63/6	20	1	1	104	126	22	17.46
16/63/8	19	1	0	113	133	20	15.04
35/63/1	5	1	0	86	92	6	6.52
	95	16	13	679	803	124	15.44
% of flowering plants	76.61	12.91	10.48				

TABLE 30.

Sex expression in open-pollinated progeny of 7 seedling female individuals.

Unshaded plots 1964-1965.

Female Parent Accession No.	Male	Female	Hermaph-rodite	Did not flower	Total	Flowering No.	Flowering %
1/63/5	31	16	8	57	112	55	49.11
2/63/6	37	7	4	83	131	48	36.64
2/63/9	37	6	4	89	136	47	34.56
12/63/6	22	2	0	76	100	24	24.00
15/63/6	15	1	1	49	66	17	25.76
16/63/8	36	7	0	57	100	43	43.00
35/63/1	12	2	0	69	83	14	16.87
	190	41	17	480	728	248	34.07
% of flowering plants	76.61	16.54	6.85				

TABLE 31.

Sex expression in open-pollinated progeny of 7 clonal female individuals. Unshaded plots 1965-1966. (Each plant a clone of one seedling plant from the 1964-1965 sex expression trials.)

Female Parent Accession No.	Male	Female	Hermaph-rodite	Did not flower	Total	Flowering No.	Flowering %
1/63/5	71	65	13	70	219	149	68.04
2/63/6	81	78	11	78	248	170	68.55
2/63/9	90	79	6	72	247	175	70.85
12/63/6	62	64	3	88	217	129	59.45
15/63/6	68	47	2	75	192	117	60.94
16/63/8	70	61	2	100	233	133	57.08
35/63/1	42	35	3	95	175	80	45.71
	484	429	40	578	1531	953	62.25
% of flowering plants	50.79	45.02	4.19				

TABLE 32.

Sex ratios among progenies of open-pollinated clones of *Dioscorea trifida*.[x]

Accession No. of Female Parent	Males	Females	Total	Ratios Male/Female	χ^2 1 : 1
1/63/5	71	65	136	1.09	0.27
2/63/6	81	78	159	1.04	.057
2/63/9	90	79	169	1.14	0.72
12/63/6	62	64	126	0.97	0.03
15/63/6	68	47	115	1.45	3.83
16/63/8	70	61	131	1.15	0.62
35/63/1	42	35	77	1.20	0.64
Totals	484	429	913	1.13	
χ^2_p				3.31	
χ_h				2.86	

P .05 = 3.84

P .01 = 6.63

and female plants in the studies on sex expression are recorded in Appendix XII and summarized in Tables 33 and 34. A single female clone (2/63/6) in Plot B yielded significantly better (at the 5% point) than its male counterpart. Otherwise there was no significant difference between the tuber yields of male and female segregates. The generally low yields in Plot B as compared with those in Plot A are interesting especially when it is recalled that the "seed" pieces used to establish the plot (Plot B) were 2 oz. in weight or less.

No sex-linked morphological characters which could be used for field identification of the sexes before the occurrence of flowering were observed.

5. Agronomic Studies.

1. Clonal Experiment (1964-1965). The data collected from this experiment are recorded in Table 35. The analysis of variance is shown in Table 36. There was no significant difference between the yields of the clones tested. The average yield per plant over the whole experimental area was 4.39 lb.

2. Clonal Experiment (1965-1966). In this re-examination of yielding ability of the clones tested the year before, highly significant yield differences were obtained. The results and analysis of variance are shown in Tables 37 and 38 respectively. Duncan's multiple-range test was used to compare the clone means. The results of this test are given in Table 39. The average yield per plant in this experiment was 1.52 lb., much lower than the yields obtained in 1964-1965.

TABLE 33.

Mean tuber weight per male and female plant. Clonal plants derived from shaded seedling parents.

Plot A (1965-1966)

Female Parent Accession No.	Yields of Male oz.	Yields of Female oz.	t^1	Probability
1/63/5	47.523	48.421	.119	.905
2/63/6	50.520	51.421	.094	.925
2/63/9	50.426	59.914	1.304	.196
12/63/6	68.632	73.576	.438	.662
15/63/6	59.066	60.083	.108	.913
16/63/8	55.433	66.847	1.200	.234
35/63/1	45.538	55.157	.765	.447

t^1 = t calculated for unpaired variates.

TABLE 34.

Mean tuber weight per male and female plant. Clonal plants derived from unshaded seedling parents.

Plot B (1965-1966)

Female Parent Accession No.	Yields of Male oz.	Yields of Female oz.	t^1	Probability
1/63/5	27.340	34.078	.760	.450
2/63/6	14.460	24.466	2.218	.030[x]
2/63/9	18.813	19.728	.234	.815
12/63/6	15.196	18.750	.851	.398
15/63/6	12.676	17.083	.765	.450
16/63/8	21.500	27.000	.756	.453
35/63/1	16.466	24.766	1.237	.226

t^1 = t calculated for unpaired variates.

[x] Significant at the 5% point.

TABLE 35.

Clonal Experiment (1964-1965).

Yields of Eight Clonal Plants.

Clones	Block I lb.	Block II lb.	Block III lb.	Totals lb.	Means lb.
C/67/63	69.06	83.25	66.49	218.80	72.93
C/131/63	72.94	67.69	62.19	202.82	67.61
C/92/63	61.00	71.49	67.19	199.68	66.56
C/134/63	80.38	40.94	48.19	169.51	56.50
C/69/63	31.13	69.88	34.63	135.64	45.21
C/109/63	37.25	49.50	29.25	116.00	38.67
C/88/63	47.19	28.88	36.50	112.57	37.52
C/90/63	23.94	20.75	64.56	109.25	36.42
Totals	422.89	432.38	409.00	1264.27	

TABLE 36.

Clonal Experiment (1964-1965).

Analysis of Variance.

Source	SS	DF	MS	F	F tabulated 5%	F tabulated 1%
Blocks	34.57	2	17.29			
Clones	4759.86	7	680.00	2.63	2.77	4.28
Error	3612.41	14	258.03			
	8406.84	23				

TABLE 37.

Clonal Experiment (1965-1966).

Yields of Eight Clonal Plants.

Clones	Block I lb.	Block II lb.	Block III lb.	Block IV lb.	Totals lb.	Means lb.	lb. per plant
C/92/63	66.78	61.72	39.92	64.90	233.32	58.33	2.4
C/109/63	64.10	36.36	54.32	44.00	198.78	49.70	2.1
C/131/63	26.02	33.60	39.18	73.72	172.52	43.13	1.8
C/67/63	33.92	35.34	44.00	52.42	165.68	41.42	1.7
C/90/63	31.40	31.20	49.52	29.68	141.80	35.45	1.5
C/134/63	30.58	26.32	47.12	16.74	120.76	30.19	1.3
C/69/63	21.56	15.14	24.00	26.00	86.70	21.68	0.9
C/88/63	11.64	17.64	9.22	7.20	45.70	11.43	0.5
Totals	286.00	257.32	307.28	314.66	1165.26		

TABLE 38.

Clonal Experiment (1965-1966)

Analysis of Variance.

Source	SS	DF	MS	F	F tabulated 5%	F tabulated 1%
Blocks	247.98	3	82.67			
Clones	6432.87	7	918.98	5.86	2.49	3.65
Error	3288.55	21	156.60			
	9969.40	31				

TABLE 39.

Clonal Experiment (1965-1966).

Comparison of Means.

Clones	Means lb.	Duncan's Range
C/92/63	58.33	a
C/109/63	49.70	a b
C/131/63	43.13	b c
C/67/63	41.42	b c d
C/90/63	35.45	b c d e
C/134/63	30.19	b c d e f
C/69/63	21.68	d e f
C/88/63	11.43	f

3. Spacing Experiment. The results of this trial are shown in Table 40. The analysis of variance is presented in Table 41. The means of the "seed" weight classes were not significantly different. Highly significant differences in yield performance were obtained between spacing classes and in the interaction between spacing classes and "seed" weights. These results are graphically represented in Figure 40. Yields (on the Y-axis) of each spacing class are plotted against seed weight classes (on the X-axis) on the graph. Yields of spacing classes 9" and 12" were determined by Duncan's multiple-range test (Table 42) to be significantly (at the 1% point) better than yields of spacing classes 18" and 24". These differences are clearly shown in the graph. Attention is directed to the high peaks in yield shown in the 9" and 12" spacing classes at the 4 oz. "seed" weight, and the relatively shallow dips at the same seed weight in the 18" and 24" classes.

4. Yam Variety Trial. The differences in yield between the "varieties" tested in this experiment were significant at the 5% point (Tables 43 and 44). It was determined by Duncan's multiple-range test (Table 45) that there was no significant difference between the yields of cush-cush and oriental variety. Lisbon yam was significantly higher yielding than cush-cush but did not differ significantly from Oriental in this character. The highly significant differences between Blocks were noted.

6. Cytological Investigations.

The chromosome numbers determined in the present study are

TABLE 40.

Spacing Experiment.

Yields of Cush-cush in a Split-Plot Experiment.

Seed Weights	Within-row spacings	Replicates 1	2	3	4	Totals	Row Spacing Means
2 oz.	9"	12.72	110.04	244.63	109.74	477.13	119.28
	12"	10.96	74.62	130.01	211.94	427.53	106.88
	18"	78.93	69.82	69.36	98.41	316.52	79.13
	24"	35.06	82.22	67.68	44.02	228.98	57.25
Totals 1st Wt. Class		137.67	336.70	511.68	464.11	1450.16	
4 oz.	9"	112.35	147.18	301.76	18.86	580.15	145.04
	12"	124.32	118.76	100.43	203.62	547.13	136.78
	18"	78.98	73.28	62.63	77.71	292.60	73.15
	24"	40.19	51.48	34.88	82.22	208.77	52.19
Totals 2nd Wt. Class		355.84	390.70	499.70	382.41	1628.65	
8 oz.	9"	176.01	136.78	103.77	137.97	554.53	138.63
	12"	168.93	99.34	92.96	132.46	493.69	123.42
	18"	109.54	65.97	91.92	90.95	358.38	89.60
	24"	70.29	84.09	108.10	75.91	338.39	84.60
Totals 3rd Wt. Class		524.77	386.18	396.75	437.29	1744.99	
Grand Totals		1018.28	1113.58	1408.13	1283.81	4823.80	

TABLE 41.

Spacing Experiment.

Analysis of Variance.

Source	SS	DF	MS	F	F tabulated 5%	F tabulated 1%
Replicates	7557.60	3	2519.20			
Seed Weight Classes	2756.63	2	1378.32	N.S.	5.14	10.92
Error (a)	19387.01	6	3231.17			
Spacing Classes	39597.60	3	13199.20	9.11**	2.96	4.60
Seed Wt. x Spacing	45816.69	6	7636.12	5.27**	2.46	3.56
Error (b)	39121.69	27	1448.95			
Total	154237.22	47				

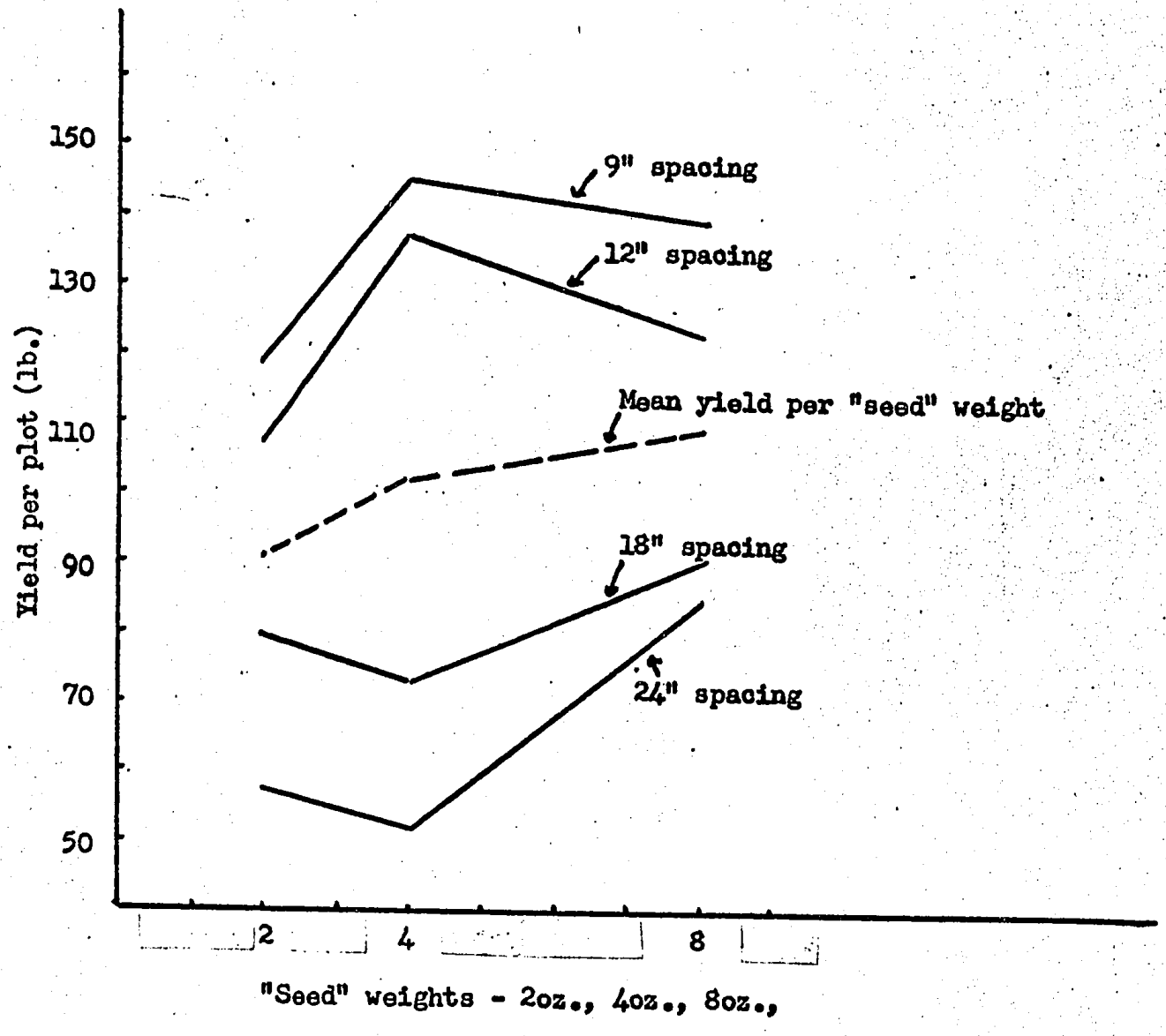

Figure 40. Yield per plot at each within-spacing treatment per "seed" weight.

TABLE 42.

Spacing Experiment.

Comparison of Means.

Row Spacings	Means lb.	Duncan's Range
9"	134.32	a
12"	122.36	a
18"	80.63	b
24"	64.68	b

TABLE 43.

Yam Variety Trial.

Yields of two varieties of Dioscorea alata and one cush-cush variety compared.

Varieties	Block I lb.	Block II lb.	Block III lb.	Block IV lb.	Totals lb.	Means lb.
Lisbon Yam	305.76	101.73	102.56	162.06	672.11	168.03
Oriental Yam	210.32	83.39	101.38	135.50	530.59	132.64
Cush-cush	191.94	77.92	72.40	89.31	431.57	107.89
Totals	708.02	263.04	276.34	386.87	1634.27	

TABLE 44.

Yam Variety Trial.

Analysis of Variance.

Source	SS	DF	MS	F	F tabulated 5%	F tabulated 1%
Blocks	42934.98	3	14311.66	22.81**	4.76	9.78
Varieties	7307.70	2	3653.85	5.82*	5.14	10.92
Error	3764.69	6	627.45			
	54007.37	11				

TABLE 45.

Yam Variety Trial.

Comparison of Means.

Varieties	Means lb.	Duncan's Range
Lisbon	168.03	a
Oriental	132.64	a b
Cush-cush	107.89	b

summarized in Table 46. The chromosome complement in male and female segregates of 3 accessions was 2n = 72; that in the male segregate of a fourth accession was also 2n = 72; and, the complement in the single hermaphrodite plant studied was 2n = 81 chromosomes. An unsexed seedling plant had 2n = 54 chromosomes. Photomicrographs and photodrawings of cells of male, female and hermaphrodite plants showing the somatic chromosomes in metaphase are given in Figures 41 to 46. A photomicrograph of a cell with 2n = 54 chromosomes is shown in Figure 47. And, a photomicrograph and a camera lucida drawing of a metaphase plate with 2n = 81 chromosomes are given in Figures 48 and 49.

Prominent prochromosomes were observed in resting nuclei of most root tips. Sometimes they were large, few in number and well-formed. At other times, they appeared to be small, indefinite in shape and numerous. They seemed to be peripheral within the nuclear membrane.

Mitosis was normal in all of the squashes examined. The photographs in Figures 50 and 51 show typical prophase, anaphase and telophase cells.

The chromosomes of Dioscorea trifida are small and numerous. They vary in size and shape and it is difficult to prepare squashes sufficiently thin and well-spread for all the chromosomes to be in microscopic focus at the same time. Accurate chromosome counts can only be achieved in many instances by focussing the microscope up and down repeatedly. This technique must also be used to discover the shape and structure of individual chromosomes. Some chromosomal structures can be observed in the late prophase shown in Figure 47. In this preparation the nuclear membrane and nucleolus have not yet disappeared and primary

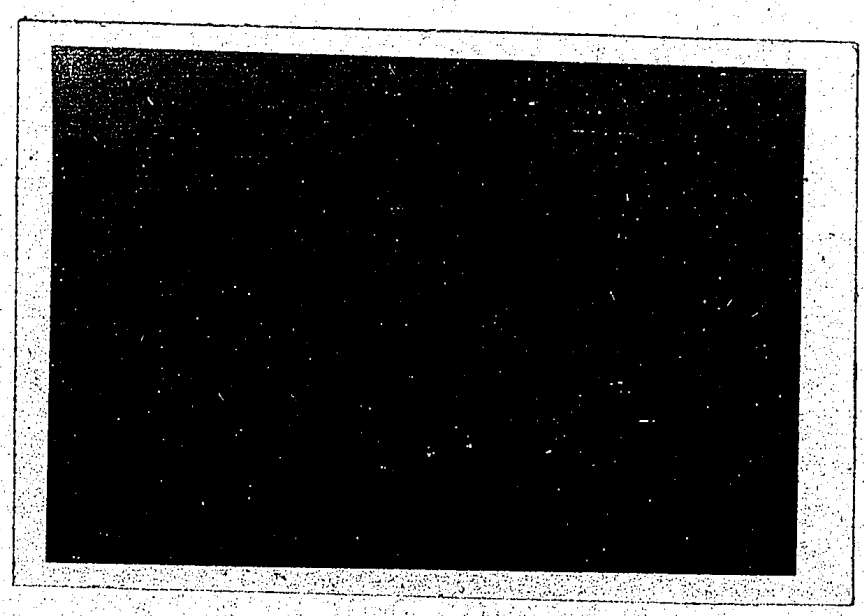

Figure 41. Photomicrograph of cell with 2n ≃ 72 chromosomes (male clone). x 6615

Figure 42. Photo drawing of same cell. x 6615.

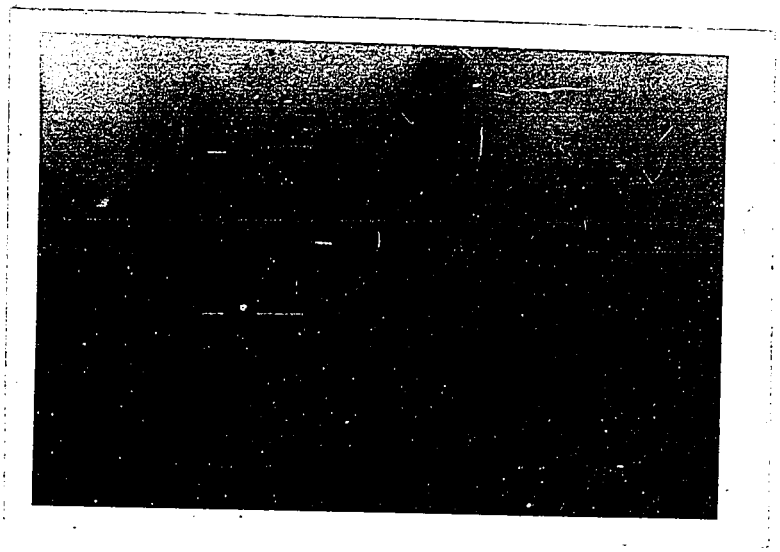

Figure 41. Photomicrograph of cell with 2n = 72 chromosomes (male clone). x 6615

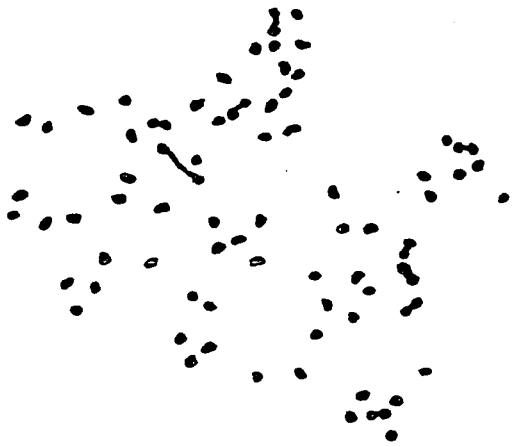

Figure 42. Photo drawing of same cell. x 6615.

Figure 43. Photomicrograph of cell with 2n = 72 chromosomes (female clone) x 8788

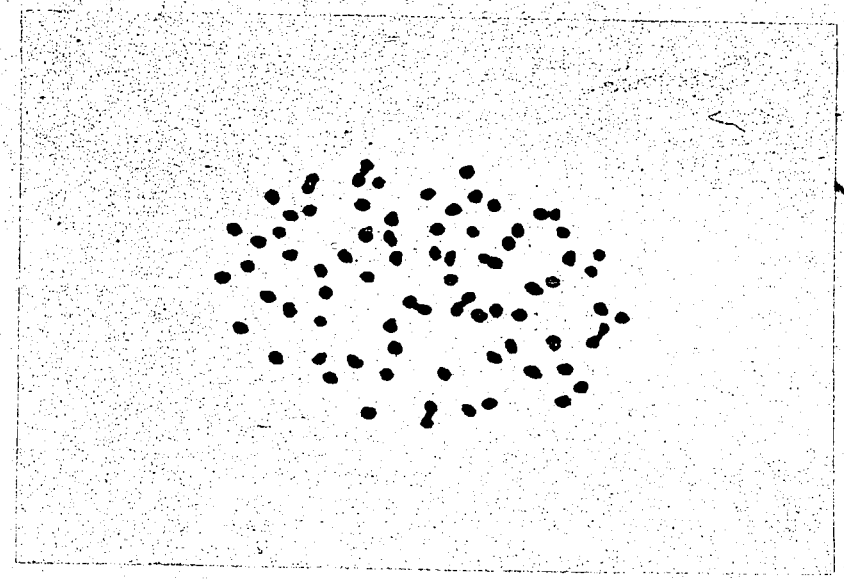

Figure 44. Photodrawing of same cell. x 8788

Figure 43. Photomicrograph of cell with 2n = 72 chromosomes (female clone) x 8788

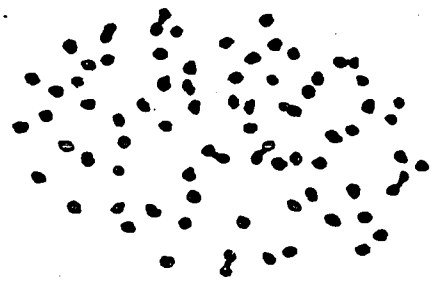

Figure 44. Photodrawing of same cell. x 8788

Figure 45. Photomicrograph of cell with 2n=81 chromosomes (hermaphrodite clone).
x 12045

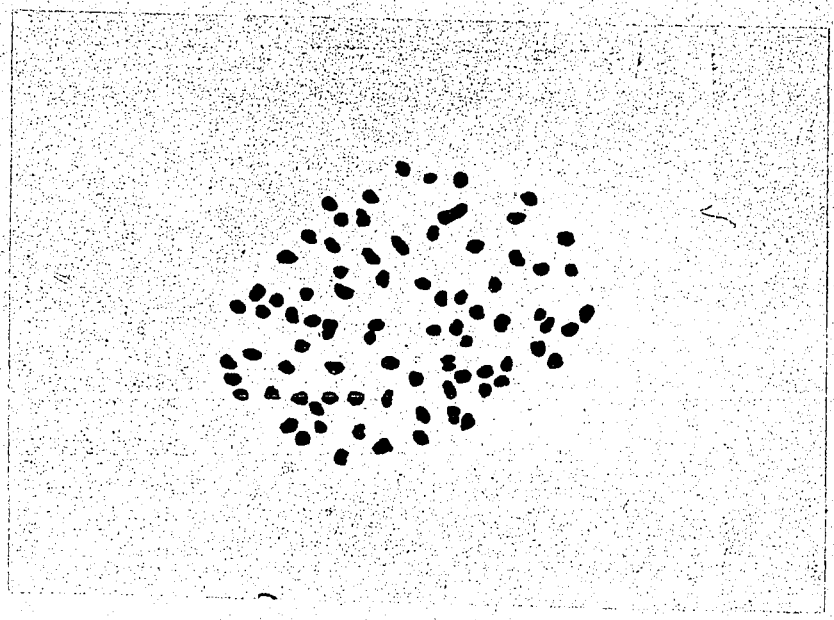

Figure 46. Photodrawing of same cell.
x 12045

Figure 45. Photomicrograph of cell with 2n=81 chromosomes (hermaphrodite clone).
x 12045

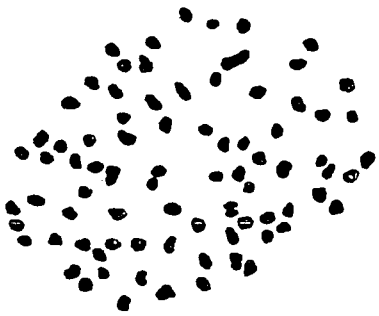

Figure 46. Photodrawing of same cell.
x 12045

Figure 47. Photomicrograph of cell with 2n = 54 chromosomes (seedling) x 2677

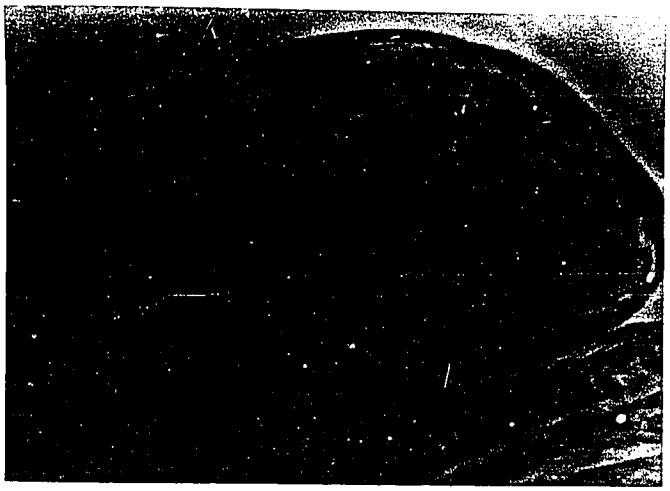

Figure 47. Photomicrograph of cell with 2n = 54 chromosomes (seedling) x 2677

TABLE 46.

Chromosome numbers in *Dioscorea trifida*.

Accession No. of Open-pollinated Seed Parent	Male Segregate 2n	Female Segregate 2n	Hermaphrodite Segregate 2n	Sex Unknown 2n
1/63	72	72	81	-
2/63	72	72	-	-
12/63	72	72	-	-
39/63	72	-	-	-
16/63[x]	-	-	-	54

[x] Seedling, sex unknown.

constrictions in the chromosomes are clearly visible. Primary median constrictions were observed in many of the chromosomes studied and a few satellites were also seen (Figure 49). In the chromosome complement of each male plant examined, one chromosome was larger than any of the others. This large chromosome was also observed in the chromosome complement of the hermaphrodite plant.

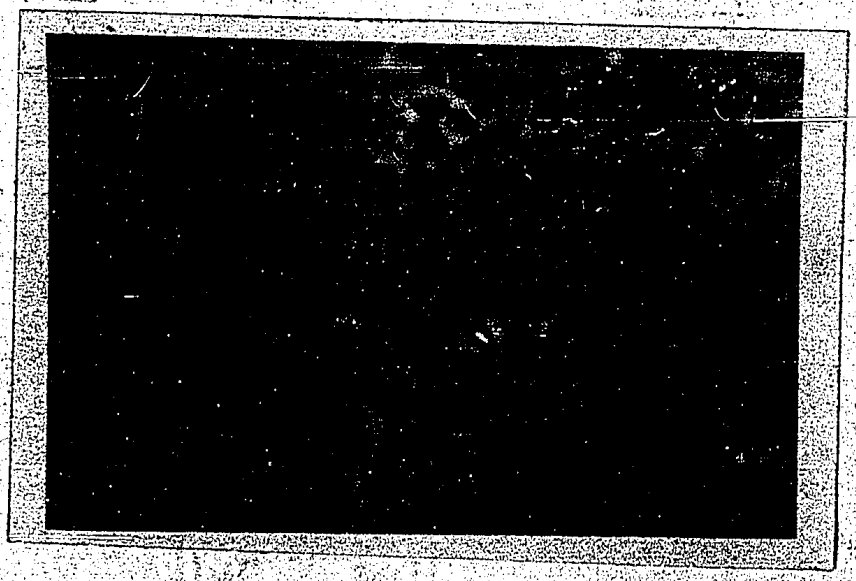

Figure 48. Photomicrograph of cell with 2n = 81 chromosomes. x 5846

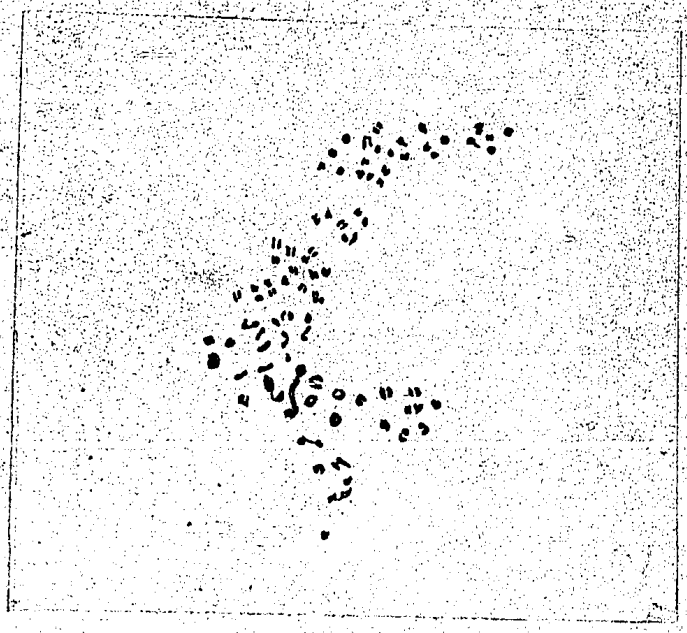

Figure 49. Camera lucida of same cell with 2n::81 chromosomes. x 5846.

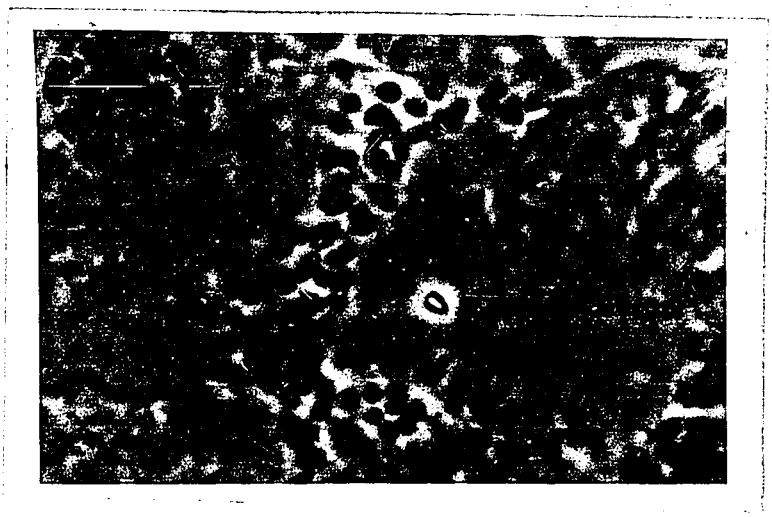

Figure 48. Photomicrograph of cell with 2n = 81 chromosomes. x 5846

Figure 49. Camera lucida of same cell with 2n::81 chromosomes. x 5846.

Figure 50. Cells showing late prophase.
x 4284

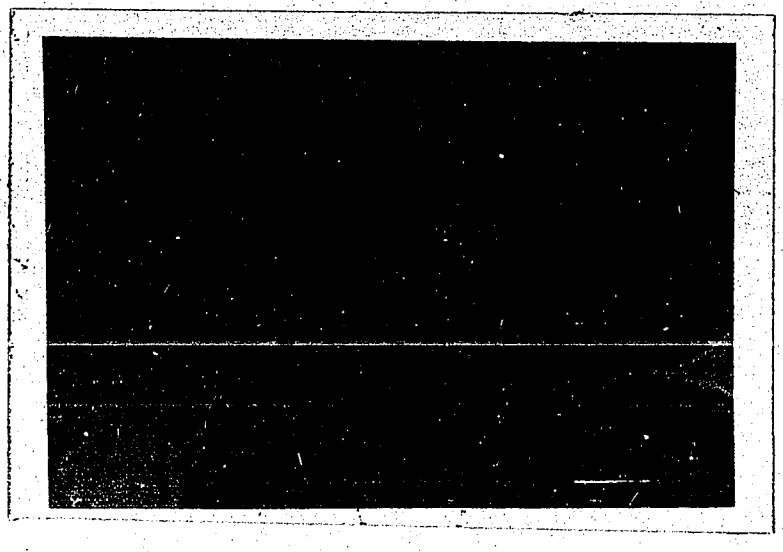

Figure 51. Cells showing anaphase and telophase.
x 7119

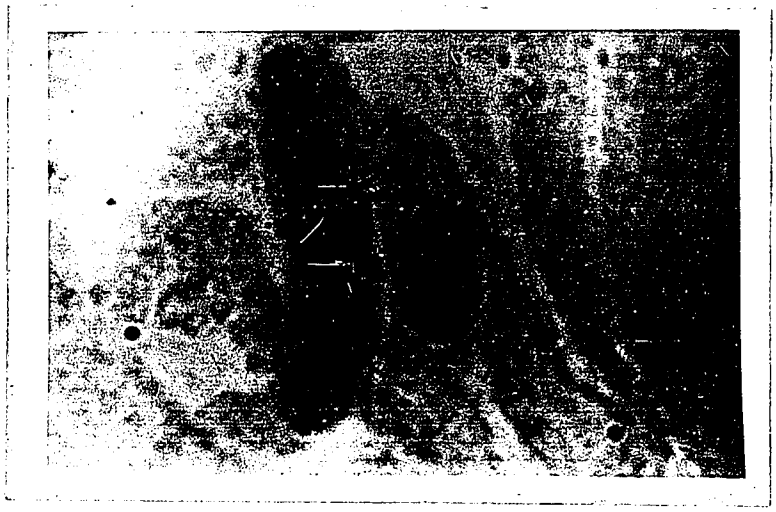

Figure 50. Cells showing late prophase.
x 4284

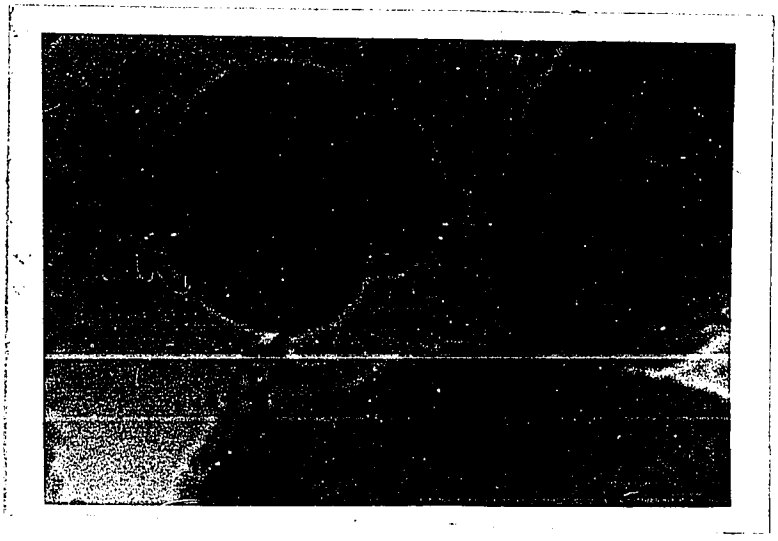

Figure 51. Cells showing anaphase and telophase.
x 7119

DISCUSSION

In the programme of investigations reported herein consideration has been given to the cush-cush plant (*Dioscorea trifida* L.f.) and some of its potentialities as a tropical tuber crop. The results of two classes of investigation are presented. First, there is a description of the plant and its parts and some aspects of growth based on direct observations and measurements; and second, the results of laboratory and field experiments carried out to determine seed germinability, sex expression and yielding ability in cush-cush are reported.

The Cush-cush Plant.

The plant description recorded in the foregoing section adds appreciably to the meagre accounts reported by previous workers. Observations and measurements in respect of the gross morphology of seeds and roots are presented for the first time, and additional information is provided on the characteristics of stem, leaf, inflorescence, flower, fruit, and tuber.

As would be expected in a predominantly dioecious plant which is freely pollinated by crawling and flying insects, present lines of cush-cush are undoubtedly highly heterozygous. How much this heterozygosity contributes to the tremendous variability found in the phenotype must be the subject for future investigations. It is sufficient to note here that the variability in some plant characters appears to be stable and relates to variability in other plant characters. Thus,

thick stems seem to be associated with long internodes (Figure ‼) and long leaf petioles with long leaf blades (Figure 28). Adopting methods devised by Anderson (1949) for analysis of association of characters, it is possible to separate cush-cush clones into distinct groups (Figure 32) thereby establishing a basis for classification within the species. A comprehensive programme of classification will inevitably involve other plant characters than those used in Figure 32. For this reason, and in order to complete the general description of the plant, other characters have been measured and described. An interesting result of the preliminary character association analysis reported herein (Figure 32) is the occurrence of accession 44/63 which originated in Jamaica as a distinct sub-group. After limited observation of Dioscorea trifida in Jamaica, and several discussions about the crop with Jamaican planters, the author has been led to suspect that the range of variability of cush-cush in Jamaica is not great and probably results from very limited original introductions of the plant into that country. Certainly all the plants in accession 44/63 (about 40) were very similar in form and habit and were all male. On the other hand, the wide range of variability of cush-cush in Trinidad has long been recognized and the occurrence of plants in many sub-groups is not unexpected.

The chromosome numbers determined in this study are all multiples of 9. These counts therefore support the view that 9 is the basic chromosome number of the genus Dioscorea throughout the Western Hemisphere (Martin and Ortiz, 1963, 1966). This is the first time that chromosome numbers have been reported in Dioscorea trifida. It is also the first report of forms of New World Dioscorea species having 2n = 81 chromosomes.

The specimens examined cytologically came from segregating material of which only the female parent was known. Further investigations are required to determine the range of polyploidy in the series and the chromosome number, or numbers, more commonly associated with desirable cultivars or clones. Further work is also needed before any attempt can be made to comment on the mechanism of sex in D. trifida.

Germination and the Seedling.

Particular attention was given to germination and seedling growth during the course of these studies. It was recognized that the ability to establish seedling plants successfully will be an important consideration in undertaking any crop improvement programme by means of hypridization. Because cush-cush is normally vegetatively propagated, its seeds have been virtually ignored by man. But, given the right conditions, these seeds will germinate and produce new plants. It is evident from germination tests reported in the previous section that high germination percentages can be obtained from cush-cush seeds. It is equally evident that this germination is unsatisfactory in terms of rate and uniformity. Under normal germinating conditions, the seeds of many plant species germinate 100% almost immediately. The situation is different with cush-cush seeds. They require 14 to 21 days for the first seed to germinate and another 15 days before the process is completed in the majority of the remaining seeds.

Burkill (1937) suggested that a period of after-ripening was involved in slow and irregular germination of the seeds of Tamus communis. The results of germination tests carried out with cush-cush seeds (Table 24)

suggest the occurrence of some form of dormancy in newly harvested seed. Seed sown in March when about 6 weeks old required 67 days to complete 96% germination. The process was faster (58 days) in seeds 11 weeks old and sown in April, but the germination percentage was lower (84%). Progressively older seed, planted in May, June, July and October began germination earlier but the germination percentage decreased rapidly suggesting rapidly diminishing seed viability. The results of the tests suggest that even if cush-cush seeds undergo a period of after-ripening or other form of dormancy, best germination results are obtained with new seed, germination percentage is higher and the actual period of germination (i.e. from time of emergence of the first seed to the time of emergence of the last germinating seed) compares favourably with that of older seed.

The treatments used in Seed Treatment Experiments I and II did not improve germination rate or percentage to any appreciable extent (Tables 25 and 26). Nor was germination under conditions of continuous darkness much different from that under normal laboratory conditions. In the second experiment (Table 26) the lowest germination percentages were obtained from seeds without seed coats. Under natural conditions the seed coat remains firmly attached to the seedling until development is well past the first shoot stage. It would seem that its protective function is critical throughout the germination process. Certainly, it was observed that seeds without seed coats were quickly invaded by micro-organisms and rotted in a few days.

The May seeding in the second seed treatment experiment generally gave lower germination percentages than the March seeding in the

first experiment (Tables 26 and 25). This result is in agreement with the observation made above that the germinability of new seed is relatively high but decreases fairly rapidly when seeds are stored. (Attention is directed to the difference in germination rates obtained in the seeding date experiment (Table 24) and the two seed treatment experiments. Much of this difference was due to the fact that the germinating mediums were different (soil versus filter paper) and evidence of germination was more quickly noted among seeds on filter paper than among those in soil.)

The results of the Open-pollinated Seed Test (Table 27) indicate differences in germinability of seeds from different clonal types. More testing is of course necessary and one expects that this aspect of study will be associated with work on the classification of cush-cush lines since the germinability of material will affect its value in a breeding programme.

The seedlings of the majority of crop plants are normally capable of developing into adult plants by means of continuous growth. In Dioscorea trifida and some other species of the Dioscoreaceae, the situation is different and one to several shoots are produced which never develop into true adult plants. These shoots are normally produced in succession and each successive shoot is more adult-like. The process of plant development is slow and by the end of one season of growth (6-8 months in Trinidad) the seedling plant is small, poorly developed, and has produced little tuber growth. There are also some indications that limited flowering at this stage is partially the result of the poor vegetative development. Plants grown from tubers, on the other hand,

complete vigorous growth during the same season and produce satisfactory yields of tuber. It is evident that seedling plants are inefficient tuber producers and will not in the foreseeable future replace clones in field production. However, since no plant breeding programme may proceed without seeds and seedlings, it is essential to understand their nature and potentialities if cush-cush improvement is contemplated.

Sex Expression and Flowering.

Flowering percentages ranged from 15.4 to 62.3 in the several populations grown at Central Experiment Station for the purpose of studying sex ratios in Dioscorea trifida. Thus, the sex ratios obtained involved only portions of the respective populations and may not be valid for the whole populations. It was demonstrated that different ratios may result depending on the overall number of flowering individuals in a given population by growing the same random populations twice in succession, - once as seedling plants, and then as clonal derivatives of the seedling plants. Only a few individuals flowered (15.4% - 34.0%) in the seedling populations and males outnumbered females 5 to 1 (Tables 29 and 30). In the subsequent clonal population the flowering percentage was 62.3 and the male to female ratio was 1:1. Hermaphrodite plants occurred in each population and comprised 16% of the flowering plants when the total flowering percentage was low (15.4%) and 4% when the total flowering percentage was high (62.3%). These results indicate that in any population of Dioscorea trifida male plants tend to flower more readily than female plants. Thus, when conditions are unfavourable for flowering only a few plants flower and these are mostly male. As

conditions improve more plants flower including an increasing majority of females resulting finally in a more uniform distribution of the sexes, one which approaches a 1:1 ratio. It is possible, of course, that with 100% flowering, a sex ratio other than 1:1 may result. Hermaphrodite plants are also usually present in small numbers but may constitute a relatively high proportion of the flowering plants when these are few. Occasionally male plants are observed bearing a few bisexual flowers indicating a slight tendency toward sub-androecy.

The method in which the seedling populations were established for sex expression studies provided an excellent opportunity for observing the effect of shade on flowering in cush-cush. The flowering percentage was higher among unshaded plants than among shaded plants. Sex ratios did not appear to be seriously affected by shade (Tables 29 and 30).

Seventy percent of the plants established by means of commercial tubers in 1963-1964 flowered (Table 28). According to the hypothesis enunciated above, a natural population with this relatively high flowering percentage would have approximately equal numbers of male and female plants. In this case, however, over 93% of the flowering plants were male and only 6% female. It could be inferred that this "commercial" population results from selections by growers to exploit some advantage which male plants have over female plants. In order to determine whether such a selective advantage involved differential yielding ability of males and females, tuber weights of individual plants in all of the populations were recorded (Tables 33 and 34). Males did not out-yield females. There may of course be other characters in which male plants

are superior to female plants but these are not known at the present time. Further investigations are needed.

Agronomy.

The results of the clone evaluation experiment carried out in 1964-1965 did not show any significant differences between the yields of the 8 clones tested (Tables 35 and 36). The average yield per plant in the experiment was 4.4 lb. of tuber. This is a good yield and at the customary rate of 11,400 plants per acre (i.e., 1 ft. x 3 ft. spacing and allowing for surface drains) would exceed 22 tons per acre. The yields of the same clones in the following year (Clonal Experiment, 1965-1966) were much lower and it is believed that this was due to lower fertility conditions in Piarco Fine Sands (Appendix III). In this second experiment, however, highly significant differences were obtained between the yields of the clones under test and it can be inferred that C/92/63, the highest yielding clone, is better adapted to conditions of low fertility than most of the other clones (Tables 37, 38 and 39). Since soils similar to Piarco Fine Sands are common in food garden areas in much of Trinidad, adaptability to severe soil conditions becomes an important selection criterion in any food crop improvement programme in the region. Thus, the results of this experiment are useful. It should be noted that although lower than the 1964-1965 results, the yields of C/92/63 and C/109/63 averaged over 2 lb. per plant - a performance which could hardly be regarded as poor. On the other hand, some of the clones are poor yielders and significant improvements in the local cush-cush production could be made by identifying and removing

these from available so-called varieties.

The customary method of planting cush-cush in Trinidad is to use the planting distances and seed sizes traditionally determined by trial and error on the part of farmers to be satisfactory for other yam species, mainly Dioscorea alata and D. cayenensis. The tubers of individual plants of both these species are large and usually deep rooting and spreading. It is evident that greater soil space is required for these tubers than for the smaller, more compact, shallow rooted cush-cush tubers, and that the soil space utilization is different. The results of the spacing and seed weight trial clearly indicate that closer (9" and 12") within-row spacing gives significantly higher yields (at the 1% point) (Tables 40, 41 and 42). These better yields appear to be dependent in some way upon the weights of the "seed" pieces as evidenced by the highly significant interaction between seed weight and within-row spacing. The shapes of the graphs in Figure 40 suggest that the interaction effect is greatest at the 4 oz. "seed" weight and there is a positive effect for the 9" and 12" spacings and a negative effect for the 18" and 24" spacings. It would seem that optimum production is achieved by "seed" pieces weighing 4 oz. and planted 9" or 12" apart in the row and that production falls off when heavier "seed" pieces are planted at these within-row spacings. Field observations indicate that very large "seed" pieces tend to produce a large number of shoots and a correspondingly large number of tubers. Within-plant competition becomes severe and although many tubers are ultimately produced, most of these are small and unmarketable and the final yield, measured in terms of marketable tubers, is low. The downward slopes of the graphs for the 18" and 24" spacings at the

4 oz. "seed" weight are difficult to explain. They are less acute than the corresponding peaks of the other two graphs and may have less significance.

In the yam variety trial, the tuber yield of Lisbon (Dioscorea alata) was significantly higher (at the 5% point) than that of cush-cush. The difference between the yields of cush-cush and the other D. alata variety (Oriental) was not significant (Tables 43, 44 and 45). Much more testing is required before firm conclusions may be drawn. The range in yielding ability among cush-cush clones must be determined and the spacing experiment discussed above indicates that there is much to be learned about the management of the cush-cush plant in the field.

In general, the seedling cush-cush plant, when compared with many other crops, is a somewhat awkward and difficult plant to manipulate. It is a slow-growing, low producer and, on the basis of present knowledge, special facilities in the form of shade are needed for adequate development especially in the early stages of growth. A crop improvement programme is therefore likely to be expensive if it involves breeding procedures. However, the vegetatively propagated plant possesses potentialities for large scale field production which if developed may justify the cost of a breeding programme. Already the plant bears its well-formed delicious tubers in shallow-rooted clusters - easy to harvest. It is believed that potentialities for quick vigorous growth and high yielding capacity exist in the germplasm studied.

Future Investigations.

As a result of the preliminary examination of the cush-cush plant reported herein, it is possible to indicate what lines of study are likely to contribute to agronomic improvement within the species both in the short term and in the long term. It is believed that the urgent need for greater food production in Trinidad and other West Indian territories demands that immediate measures be taken to supply local growers with improved cultivars as quickly as possible. It is equally true that some fundamental studies are needed so that any improvements achieved in the short term may be sustained and advanced.

Purely agronomic studies are likely to give the speediest results and it is recommended that these be adopted and that they include the following phases:

(a) Individual Clone Selection. The results of the present study indicate that, in addition to variations in gross morphology, there is a considerable range of variability in important characteristics such as yielding ability and cluster habit of tubers. It is believed also that these features are at least moderately heritable. The original selection should be based on these and other similarly desirable agronomic characteristics but other selection criteria should be flexible enough to include as wide a variety of types as research resources will permit. Morphological characters, especially those of stem, leaf and tuber, should be noted as a basis for clone identification and classification.

(b) Bulking of Clones for Agronomic Trials. This will require several clonal generations in order to provide enough planting material to establish critical and comprehensive experiments with adequate plot sizes. Selection procedures should be continued throughout this period and should result in some reduction in the number of original selections thereby achieving more workable complement of clones.

(c) Field Evaluation Programme. This would include the following major studies:

(i) Evaluation of yielding ability of clones.

(ii) Management studies including fertilizer trials and population density experiments.

It is expected that the programme outlined above should produce useful cultivars superior in yielding ability to those being grown at the present time in a relatively short period (10-12 years).

Somewhat more fundamental studies should be initiated concurrently with the field investigations. These should include the following:

(a) Studies on Seedling Growth. These should include an examination of the role of shade in the growth of the cush-cush seedling plant. Since growth rate investigations would undoubtedly be involved, some method of achieving uniform stands of seedlings would have to be devised. Hence the importance of the uniform germination of seeds.

(b) Studies on Cross- and Self-compatibility. The information to be derived from such a programme is of course essential if a

breeding programme is to be conducted. The fertility status of hermaphrodites would be of particular interest. These studies could profitably involve cytological and cytogenetical investigations.

(c) Sex Expression Studies. It is felt that these studies should be continued to determine conclusively whether there is any agronomic advantage of one sex over the other.

SUMMARY AND CONCLUSIONS

A study of the Cush-cush plant (Dioscorea trifida L.f.), its gross morphology and some aspects of its growth and development is presented. A simple application of published methods for analysis of association of characters is demonstrated and its possible value in a cush-cush classification scheme is discussed. A technique for counting the chromosomes in root tip squashes was developed and the chromosome numbers of male, female and hermaphrodite clones are reported.

Sex expression in Dioscorea trifida was investigated and consideration was given to possible relationships between yield and maleness and femaleness. Field experiments to determine yielding ability in cush-cush as well as response to varying management practices were conducted and the results are reported.

The findings presented are the result of a preliminary study of a crop plant about which recorded information is meagre. Most of the studies were carried out in Trinidad and the results are based on the conditions existing there (at Central Experiment Station) during the period when the work was done.

The results may be summarized as follows:

1. Cush-cush (Dioscorea trifida L.f.) is a tropical, twining, tuber-bearing plant with potentialities as an important food crop in Trinidad and other West Indian territories.

2. The seeds of Dioscorea trifida are flat, roughly triangular and winged. Considerable variation in size, shape and weight was found in the samples examined.

3. Germination is slow and irregular, but the germination percentage may be high in fresh seed. Pretreatment of seed by the removal of wings or by exposure to high and low temperatures did not affect normal germination rate and percentage. Germination rate and percentage was adversely affected by removal of seed coat. Differential germinability was observed among open-pollinated seed from different female clones.

4. Phase change is a characteristic feature of development in the seedlings of Dioscorea trifida. Erect stems with entire heart-shaped leaves are typical of the juvenile phase, and twining stems with deeply lobed leaves characterize the adult phase.

5. The transition from juvenile to adult phase is normally gradual and involves the successive production of several shoots (usually 5-6), which commencing with the first functional shoot (i.e. the smallest, most juvenile form) progressively increase in size and in the acquisition of adult characteristics until, finally, typically, twining adult shoots with deeply lobed leaves are produced.

6. Cush-cush seedlings are shade-loving plants. Growth is slow and mortality is high when they are exposed to full normal light intensity.

7. The primary root of the cush-cush seedling is short-lived. It is replaced by an adventitious root system early in the life of the seedling. In the adult plant the roots are normally found near to the surface of the soil.

8. Tubers originate by means of plagiotropic lobing in the hypocotyl of the seedling plant.

9. Adult cush-cush stems twine to the left (clockwise) and are winged throughout their lengths. Stems may have 2-6 wings, but 2-winged and

4-winged stems are most commonly found. The most common stem colour is green flecked with purple. Long stem internodes are usually associated with thick stems. Stems branch sparingly.

10. The adult leaf is borne alternately on the stem. It is prominently lobed. Three- and five-lobed leaves predominate and both may be found on a single plant. Distinct leaf shapes can be recognized based largely on the number of lobes, the depth of the sinus at the base of the leaf, and the relative lengths of the central lobes and adjacent lateral lobes. A relationship appears to exist between lamina length and petiole length.

11. Dioscorea trifida is predominantly dioecious. Male inflorescences are irregularly branched and staminate flowers are close together on stiff axes projecting obliquely outwards from the plant. Female inflorescences are less branched and usually consist of a few long pendant axes bearing relatively widely spaced pistillate flowers.

12. The female flower is longer than the male largely because of its long prominent, inferior ovary. The perianth is similar in both types of flowers. Rudimentary organs of the opposite sex are found in male and female flowers. Pollination appears to be effected by a wide range of crawling and flying insects.

13. The fruit is a trilocular capsule with 1-2 seeds per locule. Dehiscence is septicidal.

14. The tubers are borne in clusters and may have long necks or short necks. Tubers with long necks form loose, open clusters; those with short necks form compact clusters. Tubers vary in shape from fusiform to broadly club-shaped and variously lobed. Most tubers are shallow-rooted and are easy to harvest. Cush-cush plants are normally propagated by means of tubers.

15. The chromosomes are small and numerous. The chromosome numbers counted are all multiples of 9. A chromosome complement of 2n = 72 was observed in male and female clones. A single hermaphrodite had 2n = 81 chromosomes and the number was 2n = 54 in an open-pollinated seedling plant. An unusually large chromosome was observed in the chromosome complement of the male plants examined.

16. Male plants outnumbered females in natural populations with low flowering percentages. When flowering percentage increased to over 60%, the ratio of male to female was 1:1. A few hermaphrodite plants were observed in all of the populations studied.

17. No relationship between the sex of cush-cush plants and yield was found.

18. Differential yielding ability was observed among clonal material studied.

19. Experimental results indicate that spacing distances smaller than those used in the cultivation of other yams may increase the overall yield per acre of cush-cush. There is also the suggestion that increased yields by means of closer spacing may depend on the weight of "seed" tuber planted.

20. Further experimental work is required before firm conclusions regarding the relative yield potentialities of cush-cush and other yams can be made.

CLAIM OF CONTRIBUTION TO KNOWLEDGE.

The plant description presented is a distinct contribution to the knowledge of Dioscorea trifida L. f. Most of the information is reported for the first time and adds greatly to the meagre reports of previous workers.

The application of methods of analysis of plant character associations suggested may prove to be of importance in classification of the species.

The manner of germination and seedling growth in the species is described for the first time. Differences and similarities in respect of other species of the Dioscoreaceae are noted and it is evident that several characteristic features of growth distinguish Dioscorea trifida.

A technique was developed by modifying established cytological procedures for examining chromosomes in root tip squashes. This technique may prove to be important in future cytological work in Dioscorea trifida. Chromosome numbers in the species are reported for the first time.

The sex expression studies contribute to the knowledge of flowering and sex ratios in the Dioscoreaceae in general, as well as in Dioscorea trifida in particular.

The agronomic investigations mark the beginning of critical evaluation of the crop and methods of producing it.

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A P P E N D I X

Appendix Table 1. - Meteorological Data* - Trinidad, West Indies.

Monthly Averages (1958-1965)

Months	Rainfall inches	Sunshine hours	Maximum temp. °F**	Minimum temp. °F	Relative humidity. %
January	2.60	248	86.4	68.7	82
February	1.76	248	87.4	68.4	78
March	0.61	275	88.9	70.3	76
April	2.16	254	89.9	72.0	76
May	5.17	244	89.3	73.6	79
June	11.23	194	87.1	73.8	85
July	9.81	219	87.4	72.9	85
August	8.17	222	88.1	73.2	85
September	6.01	208	88.7	72.9	85
October	5.71	217	88.5	72.8	85
November	8.06	202	87.3	71.6	86
December	4.48	210	85.9	70.3	85

* Extract from report by Wilson (1966). Readings at Piarco Airport adjoining Cush-cush experimental sites at Central Experiment Station.

** Temperature in the shade.

Appendix 11. - Las Lomas Sands. *
Las Lomas fine sandy loam to loam .

"Drainage free

The topsoil consists of about 24 inches of bright yellowish brown loam or fine sandy loam which merges into a broad horizon of faintly orange mottled heavier loam. At about 5 feet reddish orange mottling appears in the heavier loams or if the soil is more sandy it will be uniform reddish orange colour or even brick red. Yellowish orange colours return at about 8 feet. Colour changes are just as variable laterally as they are vertically and cannot be used as a feature in mapping of these soils, except in a general way, for all the above variants are likely to occur. Concretions are not a constant feature but may be present as black pisoliths, e.g., to the East of Arima or as ironstone boulders in spots where the sandy soil is in contact with a shaly clay formation, e.g. Las Lomas district.

The whole profile is extremely acid in reaction and very low in plant nutrient content."

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* Extract from "The Soils of Central Trinidad" by E. M. Chenery (1949), Rothamsted Experimental Station, Harpenden, England.

Appendix 111. - Piarco Fine Sand.
Piarco fine sand to fine sandy loam [x].

"Drainage imperfect

They are derived from the variable deposits of the Quaternary Northern Range detrital terrace. The land surface has a well defined "hogwallow" micro-relief, the depressions of which are 12 to 18 inches deep with sharp sides, and several square yards in area. The topsoil consists of 6 to 12 inches of loose fine sand or fine sandy loam which is dark greyish brown wet and very pale brownish grey when dry. Below this occurs a more or less bleached horizon. Exposed surfaces are covered with a film of white fine sand wash. At about 30 inches a mottled horizon of silty clay is found which is at first light grey speckled with orange or stained with rust root traces, then broadly mottled with orange. All shades of red mottling from scarlet to purplish red then appear in a conspicuous horizon at least 3 feet thick and may even persist to 11 feet below the surface according to depth of the groundwater-table. When this is reached the red mottling is displaced by yellow and the typical blue of a wet gley horizon is seen. This blueness which often disappears on drying is sometimes a very bright pale blue colour without a sign of greyness. The red mottled horizon may contain both hard and soft crimson iron concretions but they are not invariably present nor are they very abundant. The red stained part of this horizon may harden on exposure like Buchannan's laterite. . . .

The Piarco soils are waterlogged for most of the wet season and completely desiccated in the dry season. Although they are waterlogged in the wet season the red mottled deep subsoils are usually quite dry and extremely hard to auger, even when the hogwallows are full of water. The profile is extremely acid in reaction (pH 3.8-4.5) and the plant nutrient status resembles that of Valencia fine sand."

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[x] Extract from "The Soils of Central Trinidad" by E. M. Chenery (1949), Rothamsted Experimental Station, Harpenden, England.

Appendix IV. - Cunupia Clay Loam. ⁑
Cunupia clay loam to silty clay .

" Drainage imperfect

The topsoil is a yellowish brown silty clay, silty clay loam or clay loam which becomes thickly mottled with orange and darker yellowish brown at about 12 inches. Black manganese dioxide stains and semi-hard concretions may appear here and at any of the deeper horizons. Grey clay is found at about 24 inches and this is mottled with yellowish brown loamy material; these mottlings being the cross-sections of fissures or enlarged root traces filled in with lighter topsoil. The clay exhibits a definite blue cast at about 4 feet but is still mottled with yellowish brown loam and stained with manganese dioxide. This blue material is the gley horizon indicating water-saturation for most of the year - it persists down to about 15 feet with occasional loamy bands. Wet season water-tables are about 5 feet from the surface but the permanent groundwater-table is deeper than 15 feet. . . .

The whole profile is acid in reaction (pH 4.5-6.5) which decreases with depth and 30 to 60 per cent. saturated with calcium. Available potash is low to medium (60-110 p.p.m.)."

⁑ Extract from "The Soils of Central Trinidad" by E.M. Chenery (1949), Rothamsted Experimental Station, Harpenden, England.

Appendix Table V. - Preliminary description of tubers as received at Central Experiment Station - 1963.

Accession No.	Flesh colour	Colour of outer cortex	Skin texture.	Tuber shape	Tuber size.
1/63	cream	pink	thin,rough	round	small
2/63	white	pink	thin,rough	ovoid	large
3/63	white	pink	rough	round	small
4/63	cream	pink	thin,rough	round	small
5/63	pink	purple	thick,rough	ovoid	medium
6/63	white	purple	rough	round or club-shaped	medium
7/63	cream	pinkish	thin,rough	cylindrical	medium
9/63	white	cream	thin,rough	round	very small
10/63	white	greenish	thin,rough	fan-shaped	large
11/63	purple	purple	thin,rough	cylindrical	large
12/63	white	purple	thick	cylindrical	large
13/63	purple	purple	thin,smooth	cylindrical	medium
14/63	white	purple	thick	cylindrical	medium
15/63	purple	purple	thick,rough	club-shaped	medium
16/63	purple	purple	thick,rough	club-shaped	large
17/63	cream	purple	thin,rough	fan-shaped	medium
18/63	cream	purple	thick	ovoid	large
19/63	white	cream	thin,rough	ovoid	medium
20/63	purple	purple	thick,rough	cylindrical	medium
21/63	cream	greenish	thin,rough	ovoid	medium
22/63	white	cream	thin,rough	ovoid	medium
23/63	white	greenish	thin,rough	cylindrical	medium
24/63	purple	purple	thick,rough	ovoid	large
25/63	cream	white	thin,rough	fan-shaped	small
26/63	white	pink	very thin	round	small
27/63	purple	purple	thin,rough	round	medium
28/63	cream	pinkish	thin,rough	cylindrical	small
29/63	purple	purple	thin,rough	round	medium
30/63	white	pinkish	thin,rough	club-shaped	medium
31/63	white	pink	thin,rough	ovoid	medium
32/63	cream	pinkish	thin,rough	ovoid	large
33/63	cream	pink	thick,	club-shaped	small

Appendix Table V. - (continued)

Accession No.	Flesh colour	Colour of outer cortex	Skin texture	Tuber shape	Tuber size
34/63	cream	pink	thin,rough	club-shaped	medium
35/63	cream	greenish	thin,rough	round	large
36/63	cream	cream	thin,rough	club-shaped	small
37/63	white	purple	thin,rough	(club-shaped (lobed	small
38/63	cream	cream	thin,rough	ovoid	medium
39/63	white	cream	thin,rough	fan-shaped	small
40/63	white	white	thin	club-shaped	small
41/63	cream	pink	thin,rough	club-shaped	small
42/63	white	white	thin,rough	club-shaped	small
44/63	cream	pink	rough	(cylindrical (club-shaped	medium

* Based on limited quantities of tuber material.

Appendix Table V1. - Types of Tuber Clusters and Tubers.

Type 1

Habit: Compact Typical Accession: 17/3

Small irregular tubers with very short necks. Tubers vary in shape from globular to flat, fan-shaped and lobed. Immature undeveloped tubers globular and rounded.

Type 2

Habit: Compact Typical Accession: C/131/63

Tubers uniform in size and regular in shape. Generally large. Largest tubers with distinct tendency to flatten and lobe at distal end. Immature and undeveloped tubers cylindrical and thickish.

Type 3

Habit: Compact Typical Accession: 22/63

Tubers irregularly shaped with short necks. Tuberous portions large, thick and sometimes lobed. Lobed ends may be flattened or rounded. Immature and undeveloped tubers roughly club-shaped.

Type 4

Habit: Compact Typical Accession: 19/63

Tubers more or less uniformly shaped, thick and rounded with short necks; generally medium in size. Immature tubers rounded.

Appendix Table VI. (continued)

Type 5

Habit: Compact. Typical Accession 44/63

Tubers small and uniformly fan-shaped with short necks. Some slightly lobed at distal ends. Immature and undeveloped tubers fan-shaped.

Type 6

Habit: Open. Typical Accession 23/63

Tubers peculiarly lobed; some primary tubers radiate outwards diageotropically from the central corm. Smaller, secondary lobes grow out from these primary ones like perpendicular branches. Secondary tubers cylindrical in shape and small to medium in size. Immature, undeveloped tubers spindle-shaped.

Type 7

Habit: Open. Typical Accession C/69/63

Tubers variable in shape. Some roughly ovoid, others fusiform, and yet others, club-shaped. Club-shaped tubers may be deeply lobed. Tubers with long necks. Immature, undeveloped tubers slender, cylindrical and variously curved.

Type 8

Habit: Compact to open. Typical Accession C/67/63

Some tubers with long necks, others with short necks. Tubers large, roughly ovoid in shape. Immature and undeveloped tubers slender, cylindrical and variously curved.

Appendix Table VI. (continued)

Type 9

Habit: Open. Typical Accession: 2/63

Medium-sized, uniform tubers with longish necks, ovoid to cylindrical in shape. Some with small branch-like secondary tubers, usually on the necks. Immature, undeveloped tubers spindle-shaped or fusiform.

Type 10

Habit: Open. Typical Accession: 6/63

Tubers large, uniform in size, roughly club-shaped with long necks. Broadened ends occasionally lobed. Numerous long, slender, cylindrical, undeveloped tubers at the top of cluster.

Type 11

Habit: Open. Typical Accession: 15/63

Tubers uniformly fusiform with long necks. Tubers small. Undeveloped, immature tubers numerous and spindle-shaped.

Type 12

Habit: Open Typical Accession: 27/63

Small, uniform tubers, roughly ovoid with long, slender necks. Immature, undeveloped tubers long and spindle-shaped.

Appendix Table VII. - Dimensions of stems. Mean stem thickness and internode length* (as represented by dimensions of 5th internode).

Clone No.	Stem Diameter. mm.	Internode length. cm.
1/63/4	5.25	19.63
1/63/5	5.25	16.50
1/63/6	5.00	19.40
2/63/7	4.25	12.93
2/63/8	4.00	14.40
2/63/10	5.00	10.00
5/63/6	4.75	12.15
6/63/7	5.50	19.98
10/63/7	8.00	27.85
12/63/6	5.00	24.70
12/63/8	5.00	25.50
12/63/9	5.00	29.80
15/63/6	4.00	8.53
15/63/9	3.50	6.50
16/63/7	6.00	17.23
16/63/8	6.25	16.00
23/63/5	5.50	22.08
27/63/7	3.75	16.08
29/63/4	5.00	25.70
35/63/4	4.75	10.60
37/63/7	6.50	18.18
39/63/5	7.50	16.80
40/63/6	7.00	20.10
42/63/6	4.00	14.28
42/63/7	4.25	13.70
44/63/13	3.00	14.20
44/63/31	3.50	14.80
44/63/41	3.50	14.50

*Each mean based on 4 determinations.

Appendix Table VIII. - Dimensions of leaves.
Clone No. 1/63/4.

Leaf No.	Petiole length cm.	LAMINA				
		Length of lobes (cm.)				
		1	2	3	4	5
1	12.8	13.3	19.2	19.5	17.0	13.7
2	11.4	15.7	18.7	20.6	19.6	15.5
3	10.0	9.5	13.8	17.6	16.4	9.5
4	11.8	12.5	19.6	18.0	17.3	12.5
5	12.8	10.7	16.2	20.0	18.0	8.2
6	14.8	13.2	20.9	18.0	20.0	11.2
7	14.6	11.0	14.5	15.8	14.4	8.8
8	11.8	12.2	16.1	16.2	17.0	13.2
9	14.4	13.3	19.7	20.5	19.6	12.9
10	11.5	15.7	20.8	21.0	9.5	15.7
11	13.6	14.2	19.5	19.8	18.6	13.8
12	10.7	7.2	11.2	11.3	10.7	6.8
13	12.3	11.9	15.3	16.7	17.0	11.7
14	13.0	12.7	18.7	21.6	16.3	12.2
15	13.2	13.4	17.7	19.6	17.8	14.3
Totals	189.7	186.5	261.9	276.2	249.2	180.0

Appendix Table VIII. - Dimensions of leaves.
Clone No. 1/63/5.

Leaf No.	Petiole length cm.	LAMINA				
		Length of lobes (cm.)				
		1	2	3	4	5
1	12.8	12.7	13.9	13.3	11.6	8.0
2	15.7	9.4	14.0	16.1	12.9	7.5
3	13.0		17.2	18.3	17.0	
4	14.2	12.8	19.3	23.7	16.9	10.9
5	15.6		13.6	15.7	12.9	
6	12.6	11.3	16.6	20.2	16.2	11.1
7	12.8	16.7	21.1	22.2	20.2	16.6
8	15.0	15.7	19.4	16.7	18.5	14.4
9	13.9	11.4	16.8	17.9	16.7	12.3
10	11.7	14.2	16.9	19.6	20.6	15.2
11	17.5	14.4	17.8	18.4	19.7	12.6
12	11.3	10.7	15.5	17.2	15.8	12.2
13	10.5	11.7	15.5	16.1	15.3	12.2
14	18.0	10.5	13.0	13.7	12.8	10.3
15	11.3	10.0	15.4	19.0	14.4	11.0
Totals	205.9	162.5	246.0	268.1	241.5	154.3

Appendix Table VIII. - Dimensions of leaves.
Clone No. 1/63/6

Leaf No.	Petiole length cm.	LAMINA				
		Length of lobes (cm.)				
		1	2	3	4	5
1	10.3		14.3	14.9	14.2	
2	11.2	10.3	15.8	18.3	14.5	9,8
3	12.7	8.5	15.2	15.7	14.6	9.6
4	12.5	8.3	13.5	17.5	12.4	8.6
5	10.1	8.4	12.8	15.2	12.1	7.8
6	15.8	12.3	18.7	18.4	16.4	11.2
7	17.6	9.5	19.8	26.4	18.6	8.2
8	11.8	7.7	14.9	16.0	14.3	7.7
9	13.4	11.2	15.8	17.6	16.4	10.0
10	15.0	8.0	12.9	20.3	15.3	9.0
11	15.0		13.8	13.9	12.3	
12	11.9		10.5	14.0	14.2	
13	15.0		7.8	12.7	14.6	13.3
14	10.8	8.8	16.1	17.6	16.4	11.3
15	9.5	8.6	16.1	16.9	15.5	6.2
Totals	197.6	101.6	218.0	255.4	221.8	112.5

Appendix Table VIII. - Dimensions of leaves.
Clone No. 2/63/7.

Leaf No.	Petiole length cm.	LAMINA				
		Length of lobes (cm.)				
		1	2	3	4	5
1	12.8	8.4	13.5	13.2	9.3	9.3
2	13.3	9.2	15.1	20.4	15.0	10.1
3	12.6		15.9	16.1	14.3	
4	10.5	7.3	12.2	13.7	10.9	8.0
5		10.0	8.4	12.5	11.0	9.6
6	12.9	9.5	14.3	14.8	14.1	8.9
7	10.3	9.8	11.7	13.3	12.2	8.3
8	13.5	14.0	18.8	19.6	17.2	12.1
9	7.5	8.2	10.9	11.7	10.6	7.7
10	8.4	6.3	10.5	14.5	10.1	7.0
11	9.0		11.0	14.5	11.2	6.5
12	8.0	9.0	13.5	13.5	12.5	9.0
13	13.0	9.5	15.0	15.0	16.0	10.0
14	14.0	12.0	14.5	16.0	14.0	10.2
15	13.0	12.2	15.5	15.5	15.0	11.5
Totals	160.8	126.4	200.8	224.1	193.4	128.2

Appendix Table V111. - Dimensions of leaves.
Clone No. 2/63/8

Leaf No.	Petiole length cm.	LAMINA				
		Length of lobes (cm.)				
		1	2	3	4	5
1	11.0	9.0	15.5	17.0	16.0	9.5
2	7.5	10.0	13.5	11.2	11.0	8.5
3	7.2	8.0	11.2	11.5	10.0	7.5
4	10.0	9.5	12.5	15.5	12.8	8.7
5	8.0	9.2	12.7	14.0	12.8	8.0
6	7.5		10.7	10.5	10.8	
7	9.0		11.0	13.2	10.5	
8	14.7	11.5	16.0	17.7	16.5	10.2
9	8.0	8.5	12.5	14.0	14.4	9.5
10	9.0		11.0	12.5	10.4	
11	11.0		12.5	14.5	12.4	
12	10.0	9.0	13.7	16.0	13.5	
13	12.0	12.0	6.0	18.5	15.5	9.0
14	12.0	7.0	13.2	16.0	13.8	8.0
15	9.0	8.7	13.5	14.0	12.0	9.7
Totals	145.9	102.4	185.5	216.1	192.4	88.6

Appendix Table VIII. - Dimensions of leaves.
Clone No. 2/63/10

Leaf No.	Petiole length cm.	LAMINA				
		Length of lobes (cm.)				
		1	2	3	4	5
1	12.0	9.0	12.8	13.7	12.1	5.9
2	11.5	9.1	15.4	17.2	14.0	10.2
3	10.3	7.0	14.1	16.7	14.0	7.1
4	9.6	9.8	13.3	13.7	13.4	9.4
5	9.7	10.0	14.9	17.0	14.5	10.2
6	10.0	9.0	14.5	14.2	12.8	6.5
7	11.6	8.3	12.7	12.2	13.2	9.3
8	12.0	11.5	16.0	17.9	16.4	12.0
9	10.7	9.4	12.6	11.9	13.2	8.5
10	9.5		10.0	11.5	10.0	
11	11.0	9.4	12.3	12.0	13.0	9.1
12	9.0	10.2	15.0	18.5	14.2	10.0
13	11.0	9.6	14.3	14.8	14.5	9.0
14	10.0		14.2	18.6	15.2	9.4
15	11.9	9.0	16.2	16.0	13.5	
Totals	159.8	121.3	210.3	225.9	204.0	116.6

Appendix Table VIII. - Dimensions of leaves.
Clone No. 5/63/6

Leaf No.	Petiole length cm.	LAMINA				
		Length of lobes (cm.)				
		1	2	3	4	5
1	6.5	6.5	10.7	10.0	10.5	8.1
2	14.0	9.6	13.6	14.5	13.0	8.5
3	14.5	9.5	13.0	13.0	12.7	11.7
4	6.0		10.9	9.9	9.5	
5	15.5	8.3	15.0	16.0	16.0	6.0
6	10.0		15.2	17.6	15.3	9.8
7	6.5	6.3	10.5	10.4	10.2	7.9
8	10.4		10.8	11.7	11.2	
9	12.0	9.5	13.3	14.1	12.8	9.8
10	7.0	6.5	10.9	10.0	11.0	6.5
11	12.5	9.4	13.5	14.1	12.8	10.0
12	14.5	14.4	20.0	20.5	21.0	11.6
13	14.0	10.5	13.0	14.8	12.3	8.4
14	14.5	12.4	16.3	16.0	16.5	12.2
15	12.0	10.2	13.0	14.3	13.5	10.2
Totals	169.9	117.1	203.7	210.9	198.3	120.7

Appendix Table VIII. - Dimensions of leaves.
Clone No. 6/63/6.

Leaf No.	Petiole length cm.	LAMINA Length of lobes (cm.) 1	2	3	4	5
1	10.8		9.9	11.6	9.6	
2	10.8		9.2	12.9	9.6	
3	10.5		7.1	11.6	6.4	5.0
4	10.6		11.5	13.1	10.9	
5	10.2	8.0	12.1	14.0	12.1	
6	13.4	11.1	17.2	17.9	17.2	9.6
7	10.2		12.8	15.3	12.8	
8	10.2		12.4	15.0	12.1	
9	10.5	6.4	10.2	13.4	10.8	
10	10.8	8.9	13.7	15.3	12.8	9.6
11	8.9		9.6	12.8	9.6	
12	10.2	9.9	14.0	15.6	13.4	8.7
13	10.2		9.9	10.2	8.3	
14	12.8		8.7	12.4	9.0	
15	14.7	8.9	16.5	19.1	15.6	10.8
Totals	164.8	53.2	174.8	210.2	170.2	43.7

Appendix Table V111. - Dimensions of leaves.
Clone No. 10/63/7

Leaf No.	Petiole length cm.	LAMINA				
		Length of lobes (cm.)				
		1	2	3	4	5
1	11.9	8.5	11.3	12.8	11.6	8.0
2	14.5	11.5	18.4	22.0	19.2	10.5
3	14.8	8.4	13.0	14.2	11.0	
4	12.0	6.3	8.4	11.7	9.0	6.0
5	14.0		9.3	12.6	9.5	
6	13.5	11.3	15.0	20.1	19.5	12.0
7	12.5	9.3	14.6	15.5	14.8	8.0
8	11.0	11.8	14.8	15.0	13.5	9.4
9	13.5	8.0	10.5	11.3	12.3	8.0
10	15.1	7.0	12.5	14.0	12.2	8.4
11	10.9	9.6	11.8	11.8	11.5	8.6
12	16.0	6.0	15.2	17.5	14.4	9.6
13	12.5	10.9	14.4	16.6	14.3	10.0
14	13.3	8.5	12.4	11.0	12.5	9.3
15	13.9	9.3	16.6	16.8	16.8	11.3
Totals	199.4	126.4	198.2	222.9	202.1	119.1

Appendix Table V111. - Dimensions of leaves.
Clone No. 12/63/6

Leaf No.	Petiole length cm.	LAMINA				
		Length of lobes (cm.)				
		1	2	3	4	5
1	8.0		8.5	14.5	11.3	
2	8.3		10.0	11.6	7.9	
3	10.3		9.3	13.5	7.6	
4	12.0		10.3	16.6	11.8	
5	11.8		10.0	17.0	10.0	
6	11.2		9.1	13.5	10.3	
7	8.9	11.8	13.5	17.3	13.8	10.6
8	9.0	9.5	13.6	14.6	13.2	8.3
9	8.4	7.8	13.0	13.3	12.9	8.1
10	7.0	7.5	11.3	11.4	10.7	8.0
11	13.8	10.4	13.0	16.5	13.6	10.4
12	13.0		12.4	15.0	11.8	
13	12.3	9.4	13.7	15.4	12.5	11.6
14	11.0	9.5	15.4	16.1	14.1	10.0
15	11.7		13.7	13.3	13.9	
Totals	156.7	65.9	176.8	219.6	175.4	67.0

Appendix Table V111. - Dimensions of leaves.
Clone No. 12/63/8.

Leaf No.	Petiole length cm.	LAMINA				
		Length of lobes (cm.)				
		1	2	3	4	5
1	9.0	11.7	16.2	18.8	14.9	10.0
2	9.5	10.0	14.2	17.3	13.5	11.6
3	9.9	9.0	13.6	17.0	14.8	10.0
4	11.5	9.6	15.5	17.0	14.1	9.0
5	8.6	9.4	14.0	17.5	14.1	8.0
6	12.5	9.0	14.8	16.6	14.1	9.0
7	13.3	13.6	19.1	20.5	17.7	11.0
8	10.6	10.8	17.1	19.4	17.3	12.0
9	14.3	13.1	19.4	21.0	17.5	12.0
10	13.0	12.7	18.0	22.3	17.3	13.0
11	11.0	9.9	16.1	20.0	16.0	11.0
12	12.1	11.0	17.7	20.1	17.9	12.0
13	11.6	14.0	19.0	22.1	17.6	13.0
14	14.3	11.0	16.7	18.4	16.4	11.3
15	12.6	14.9	18.0	22.5	19.1	13.2
Totals	173.8	169.7	249.4	292.5	242.3	166.1

Appendix Table VIII. - Dimensions of leaves.
Clone No. 12/63/9.

Leaf No.	Petiole length cm.	LAMINA				
		Length of lobes (cm.)				
		1	2	3	4	5
1	12.5	11.5	18.0	22.5	18.5	12.0
2	16.5	12.0	17.0	18.5	17.5	11.0
3	12.0	11.5	12.0	16.0	13.5	12.5
4	16.0		16.0	20.0	18.0	
5						
6	12.0	11.3	18.5	21.5	19.2	12.2
7	15.0	11.5	18.0	19.4	17.2	12.5
8	12.8	9.0	14.0	18.3	15.0	9.5
9	11.0	11.0	15.8	22.5	16.4	12.4
10	13.0	13.5	19.0	20.5	18.0	12.4
11	12.5	12.4	17.6	21.7	18.4	12.4
12	14.4	10.0	17.2	20.7	17.4	10.3
13	12.6	8.5	14.0	15.7	14.5	8.3
14	9.6	10.6	15.3	18.0	17.2	11.2
15	10.6	14.2	18.4	22.4	19.0	14.1
Totals	180.5	148.5	230.8	278.7	239.8	150.8

Appendix Table VIII. - Dimensions of leaves.
Clone No. 15/63/6.

Leaf No.	Petiole length cm.	LAMINA				
		Length of lobes (cm.)				
		1	2	3	4	5
1	10.5	11.7	16.6	20.6	17.0	9.6
2	10.8	13.5	17.7	21.6	19.1	13.0
3	13.4	10.4	17.8	19.4	18.4	10.7
4	11.0	12.5	18.0	21.6	15.8	10.7
5	12.5	12.8	18.5	21.0	18.7	11.9
6	12.8	10.0	17.5	19.1	18.0	11.0
7	13.5	8.5	11.0	15.0	22.8	19.4
8	12.4	12.8	19.5	20.6	19.3	10.3
9	14.9	12.0	17.7	17.5	17.0	12.7
10	13.5	12.5	21.1	23.5	20.7	14.2
11	15.0	12.0	15.9	19.0	18.0	12.7
12	17.0	10.9	14.0	14.0	14.0	9.8
13	13.0	17.5	23.4	22.5	20.0	13.2
14	13.9	17.0	22.0	27.4	21.7	18.0
15	15.0	11.0	16.7	17.1	16.7	11.0
Totals	199.2	185.1	267.4	299.9	278.2	188.2

Appendix Table V111. - Dimensions of leaves.
Clone No. 15/63/9.

Leaf No.	Petiole length cm.	LAMINA				
		Length of lobes (cm.)				
		1	2	3	4	5
1	6.8	6.4	9.8	14.9	9.5	5.4
2	11.0		15.0	19.5	15.0	
3	16.2	6.5	11.5	17.0	11.2	7.0
4	10.5	9.8	16.5	20.0	16.0	10.8
5	8.5	12.0	16.5	20.2	17.4	11.9
6	12.4	9.5	16.4	18.8	16.4	9.0
7	14.8	8.0	12.5	20.0	14.9	6.6
8	11.0	9.6	12.6	17.3	14.9	12.5
9	10.5	12.5	19.0	21.0	18.9	11.4
10	12.9	16.5	20.4	22.0	19.8	13.5
11	14.0	11.5	18.0	19.0	17.3	10.5
12	11.8	13.4	20.0	22.5	21.5	15.0
13	11.0	8.2	14.0	16.5	12.9	7.5
14	12.0	13.5	21.4	24.4	21.0	13.6
15	11.5	8.2	14.0	16.8	12.8	7.0
Totals	174.9	145.6	237.6	289.9	239.5	141.7

Appendix Table VIII. - Dimensions of leaves.
Clone No. 16/63/7

Leaf No.	Petiole length cm.	LAMINA				
		Length of lobes (cm.)				
		1	2	3	4	5
1	14.0	11.7	20.2	23.0	19.3	13.8
2	7.0		8.0	11.4	8.8	
3	9.5	11.0	15.0	17.8	13.3	11.7
4	9.2		15.0	17.9	14.6	
5	10.8	9.5	20.4	21.1	19.4	11.4
6	12.5	15.0	16.1	20.7	11.6	12.6
7	11.8	11.5	17.6	23.2	20.6	15.0
8	10.6	14.0	24.3	23.6	22.0	14.3
9	12.0	10.5	18.6	20.4	18.3	11.5
10	13.6	11.4	19.0	21.8	18.4	10.1
11	12.2	9.9	18.8	21.4	17.4	13.1
12	13.3	13.1	24.0	24.0	23.8	15.0
13	14.6	16.0	22.6	24.0	21.8	15.1
14	16.0	16.5	25.1	27.2	24.6	18.4
15	14.4	15.4	23.8	26.4	24.5	17.7
Totals	181.5	165.5	289.5	323.9	278.4	179.7

Appendix Table VIII. - Dimensions of leaves.
Clone No. 16/63/8

Leaf No.	Petiole length cm.	LAMINA				
		Length of lobes (cm.)				
		1	2	3	4	5
1	11.2		9.8	11.3	7.5	
2	17.1		13.7	21.0	13.8	
3	17.3		14.1	19.4	15.3	
4	15.3		11.2	17.1	11.2	
5	10.0	11.6	17.0	21.5	16.4	9.1
6	9.4	9.8	17.2	23.0	16.4	9.6
7	14.3	14.4	19.2	25.4	21.1	9.5
8	15.3	14.5	22.6	22.6	23.9	16.4
9	13.0	11.0	15.0	18.2	15.2	10.4
10	12.1	13.6	21.2	23.5	20.1	10.2
11	13.6	7.0	16.0	13.4	10.2	7.0
12	15.1	15.6	23.4	25.8	24.2	15.1
13	13.3	10.4	19.6	24.2	19.0	11.5
14	17.2	9.6	15.8	20.1	23.2	13.6
15	12.0	10.0	19.1	20.7	18.4	10.5
Totals	206.2	129.5	254.9	307.2	255.9	122.9

Appendix Table V111. - Dimensions of leaves.
Clone No. 23/63/5

Leaf No.	Petiole length cm.	LAMINA				
		Length of lobes (cm.)				
		1	2	3	4	5
1	8.2		10.9	13.4	9.8	
2	11.4	14.2	20.8	18.0	15.8	14.0
3	8.0	10.2	15.2	16.7	14.6	11.1
4	9.9	7.8	11.9	12.5	10.9	7.8
5	12.0	11.2	17.4	18.4	17.6	11.5
6	19.8	12.5	18.1	18.4	18.7	13.7
7	9.2	8.0	12.1	13.4	12.5	8.8
8	12.0	11.5	17.5	18.0	16.9	12.9
9	9.5	9.5	15.4	16.8	12.6	8.0
10	6.5	7.0	11.0	12.2	10.6	7.3
11	8.0		11.5	11.8	11.7	
12	9.8	12.6	16.8	18.4	17.0	11.5
13	7.9	9.5	12.5	14.5	12.3	9.4
14	9.5	6.5	11.4	15.2	13.3	7.4
15	9.8	4.5	8.5	10.4	7.5	4.5
Totals	151.5	125.0	211.0	228.1	201.8	127.9

Appendix Table VIII. - Dimensions of leaves.
Clone No. 27/63/7

Leaf No.	Petiole length cm.	LAMINA				
		Length of lobes (cm.)				
		1	2	3	4	5
1	11.5	8.9	13.0	17.1	13.5	9.0
2	11.0	11.0	17.1	19.0	16.4	11.0
3	12.5		10.5	19.0	11.0	
4	11.0	11.7	14.5	18.0	15.6	12.0
5	11.6	12.0	17.4	18.6	17.0	11.0
6	11.1	10.1	17.5	18.8	16.5	11.0
7	12.2	12.0	17.1	17.2	16.1	11.0
8	12.0	12.2	18.7	19.5	18.6	11.2
9	13.4		16.1	21.2	17.0	
10	11.7	10.3	16.0	18.4	16.0	11.0
11	12.8	11.7	17.7	18.7	18.2	11.4
12	13.0	11.5	17.5	20.3	17.5	12.0
13	13.0	9.7	15.4	14.0	6.3	8.1
14	12.0	10.5	15.5	19.1	16.4	11.0
15	12.0	11.5	16.4	17.6	16.5	11.7
Totals	180.8	145.1	240.4	276.5	232.6	141.4

Appendix Table VIII. - Dimensions of leaves.
Clone No. 29/63/4

Leaf No.	Petiole length cm.	LAMINA				
		Length of lobes (cm.)				
		1	2	3	4	5
1	8.9	8.5	13.0	13.7	14.0	10.0
2	8.0		8.5	11.5	6.3	
3	8.5		9.0	12.4	9.4	
4	12.0		10.5	12.5	10.0	6.3
5	9.4		8.5	11.3	7.5	
6	9.5	7.5	10.5	12.3	11.3	7.5
7	10.0	9.6	15.0	16.0	15.5	9.0
8	8.0	6.4	8.0	10.5	9.0	6.6
9	11.0	9.6	16.0	16.0	16.3	10.2
10	9.7	9.5	13.0	14.5	13.6	10.1
11	8.5		11.5	14.0	11.0	
12	9.5	8.0	12.5	14.4	13.0	8.5
13	10.0	7.4	12.4	13.4	11.5	7.0
14	10.0	10.5	16.5	16.0	15.5	9.4
15	10.1	7.0	11.4	14.1	12.2	7.0
Totals	143.1	84.0	176.3	202.6	176.1	91.6

Appendix Table VIII. - Dimensions of leaves.
Clone No. 35/63/4.

Leaf No.	Petiole length cm.	LAMINA				
		Length of lobes (cm.)				
		1	2	3	4	5
1	11.1	10.0	15.6	17.3	15.1	9.1
2	9.5	6.8	12.3	13.0	11.9	8.6
3	8.3	6.5	13.5	18.2	13.6	6.1
4	10.7	5.4	13.5	15.6	15.0	6.8
5	9.6	6.5	13.6	17.1	13.1	7.8
6	13.5	9.1	12.5	13.4	12.2	6.7
7	11.6	8.8	14.5	14.0	14.5	10.4
8	10.8	8.5	11.5	13.0	12.4	7.0
9	9.7	8.0	12.2	14.2	12.5	8.6
10	9.0	7.5	13.0	13.4	13.0	
11	12.5	6.9	12.6	14.0	13.8	8.3
12	10.1	8.2	11.4	11.4	11.5	8.9
13	15.6		11.1	12.4	10.0	
14	10.0		11.0	12.3	10.8	
15	10.0		11.0	12.2	10.7	
Totals	162.0	92.2	189.3	211.5	190.3	89.3

Appendix Table VIII. - Dimensions of leaves.
Clone No. 37/63/7.

Leaf No.	Petiole length cm.	LAMINA Length of lobes (cm.) 1	2	3	4	5
1	10.0		14.4	16.3	16.4	
2	17.3		8.1	11.6	8.9	
3	10.0		16.4	18.9	18.5	
4	12.0		20.5	24.5	19.8	
5	11.8	8.5	18.4	21.0	20.4	8.8
6	12.5	8.2	17.1	19.3	18.0	8.1
7	10.3		12.6	16.0	11.1	
8	12.9	10.8	19.0	19.3	17.5	
9	13.4	11.5	17.0	20.0	17.1	9.0
10	13.5	7.9	15.6	17.5	15.2	7.6
11	12.0	9.8	20,0	22.0	21.0	9.0
12	9.6	8.8	18.2	20.0	18.6	8.7
13	11.9	8.0	16.1	18.8	16.4	6.4
14	12.0	9.5	19.5	22.6	20.7	14.5
15	14.9	13.3	21.6	23.0	17.5	10.4
Totals	184.1	96.3	169.7	193.9	171.4	91.7

Appendix Table V111. - Dimensions of leaves.
Clone No. 39/63/5

Leaf No.	Petiole length cm.	LAMINA				
		Length of lobes (cm.)				
		1	2	3	4	5
1	9.0	7.8	13.5	14.8	13.0	8.1
2	9.0		12.0	13.1	11.1	
3	9.0	5.0	11.2	13.3	11.0	7.0
4						
5	9.5	7.5	12.4	14.3	13.5	8.0
6	7.5	9.9	12.9	14.0	12.3	8.7
7	8.0	8.8	12.0	14.7	12.7	8.0
8	11.3	8.8	10.8	13.7	12.4	8.1
9	12.3	7.5	10.6	11.5	11.6	8.2
10	8.5	9.5	13.3	15.0	13.5	7.8
11	11.4	9.8	13.0	15.5	13.9	8.4
12	8.0	9.5	13.4	13.9	14.0	9.0
13	7.6	9.1	14.9	16.0	13.0	10.0
14	8.5	9.0	14.2	15.1	14.5	8.5
15						
Totals	119.6	102.2	164.2	184.9	166.5	99.8

Appendix Table VIII. - Dimensions of leaves.
Clone No. 40/63/6

Leaf No.	Petiole length cm.	LAMINA Length of lobes (cm.) 1	2	3	4	5
1	8.2	8.3	13.4	13.4	12.4	8.0
2	14.0		9.2	10.2	9.2	
3	11.4	11.0	19.0	18.9	18.6	
4	10.2	6.4	13.5	18.0	12.8	
5	8.9	10.0	14.1	16.4	14.2	9.4
6	12.0	11.6	19.4	19.7	20.2	13.5
7	10.8	9.1	16.8	17.2	15.0	10.9
8	11.0	9.3	16.7	18.0	17.1	10.7
9	12.9	9.0	13.0	13.2	12.5	6.7
10	15.0	14.8	21.0	20.1	20.5	15.4
11	11.4	12.9	13.5	17.9	17.5	12.0
12	13.0	12.7	16.5	16.0	14.4	11.5
13	14.9	15.0	22.3	20.9	21.7	14.4
14	9.4	10.9	13.0	15.1	13.8	11.4
15	12.5	10.0	13.8	16.3	15.5	9.3
Totals	175.6	151.0	235.2	251.3	235.4	133.2

Appendix Table V111. - Dimensions of leaves.
Clone No. 42/63/6.

Leaf No.	Petiole length cm.	LAMINA				
		Length of lobes (cm.)				
		1	2	3	4	5
1	13.1	7.0	13.8	15.8	13.0	7.8
2	9.9	7.9	11.9	15.0	11.4	7.5
3	10.5	7.0	12.2	13.3	14.4	8.2
4	10.5	7.9	12.9	15.4	12.2	7.6
5	10.9	7.4	11.8	14.1	12.0	7.6
6	10.6	8.2	12.5	15.4	12.4	8.0
7	9.5	7.6	11.7	14.1	15.1	9.0
8	12.5	10.4	16.1	18.0	17.0	10.0
9	11.4		13.0	16.1	14.1	5.4
10	10.8	4.5	6.8	10.0	11.0	6.8
11	12.5	8.7	12.0	13.8	11.0	6.8
12	12.5	8.0	16.3	16.3	14.8	8.5
13	11.2	8.8	12.1	14.5	12.5	6.8
14	11.0	6.0	11.5	12.7	11.7	4.8
15	13.3	11.0	16.5	17.7	16.0	11.0
Totals	170.2	110.4	191.1	222.2	198.6	115.8

Appendix Table V111. - Dimensions of leaves.
Clone No. 42/63/7

Leaf No.	Petiole length cm.	LAMINA				
		Length of lobes (cm.)				
		1	2	3	4	5
1	10.9	5.2	9.4	8.5	10.7	5.2
2	10.0	6.2	11.5	10.4	11.9	6.0
3	14.0	8.9	10.2	15.1	9.9	7.4
4	10.9	6.0	13.5	13.4	10.8	8.4
5	12.7	8.5	12.5	15.0	12.1	8.0
6	11.0	8.1	14.1	18.5	13.8	8.2
7	13.9	8.5	12.7	14.5	15.5	7.6
8	13.0	7.4	15.5	20.1	15.0	7.3
9	10.0	7.6	12.4	14.5	9.1	9.0
10	14.4	7.0	14.0	16.7	11.6	7.8
11	9.0	6.0	9.4	9.6	11.7	6.2
12	11.0	7.5	11.1	11.7	13.0	7.6
13	17.0	7.5	13.6	16.8	13.0	8.4
14	10.5	7.8	12.0	12.4	12.0	8.4
15	10.4		13.0	15.5	13.0	
Totals	178.7	102.2	186.7	212.7	183.1	105.5

Appendix Table V111. - Dimensions of leaves.
Clone No. 44/63/13

Leaf No.	Petiole length cm.	LAMINA Length of lobes (cm.) 1	2	3	4	5
1	7.9		12.6	15.1	11.4	
2	7.0		13.0	17.0	12.6	
3	9.1		11.9	13.4	9.6	
4	8.9	8.3	11.1	15.7	14.6	8.0
5	9.1	7.0	12.4	14.4	12.0	7.5
6	8.0		12.0	13.5	11.6	
7	9.0		11.3	13.2	10.7	
8	7.8	7.9	12.5	14.8	12.6	
9	8.0		13.8	16.0	14.0	
10	10.0		11.0	12.6	12.0	
11	9.4		11.6	14.0	10.6	
12	9.4		12.2	14.0	11.5	
13	8.4	6.5	12.3	12.4	11.2	
14	10.7		12.4	15.2	11.9	
15	8.5		12.7	15.4	12.7	
Totals	131.2	29.7	181.8	216.7	179.0	15.5

Appendix Table V111. - Dimensions of leaves.
Clone No. 44/63/31

Leaf No.	Petiole length cm.	LAMINA				
		Length of lobes (cm.)				
		1	2	3	4	5
1	11.0		13.0	18.0	12.3	
2	8.9		10.0	13.4	10.3	
3	8.4		9.2	12.6	10.1	
4	7.0		11.7	13.8	11.0	
5	7.0		9.8	12.4	9.4	
6	7.4		9.6	12.5	9.7	
7	9.8		14.0	14.5	13.7	
8	7.3	6.8	11.7	14.5	12.0	
9	9.0		12.5	14.4	12.8	
10	8.5		8.4	13.0	10.6	
11	11.0		15.0	14.0	14.7	
12	7.5		8.5	12.3	8.6	
13	7.5		9.0	10.9	8.8	
14	8.8		10.0	13.0	10.0	
15	8.8		8.7	11.8	9.0	
Totals	127.9	6.8	161.1	201.1	163.0	

Appendix Table VIII. - Dimensions of leaves.
Clone No. 44/63/41

Leaf No.	Petiole length cm.	LAMINA Length of lobes (cm.) 1	2	3	4	5
1	12.3		11.9	13.4	11.3	
2	6.5		10.5	11.6	9.8	6.0
3	12.6	6.8	10.6	13.6	9.8	6.8
4	5.6	7.5	12.3	13.0	12.2	7.6
5	8.0		11.0	13.7	12.0	
6	12.3		14.5	19.0	13.5	
7	9.1	5.7	9.0	12.1	8.6	
8	9.4		13.0	16.0	14.0	
9	10.5	8.6	14.5	15.0	14.2	
10	10.5		12.5	16.5	12.0	
11	10.0		13.0	16.1	12.4	
12	10.0		9.6	15.3	11.8	
13	9.7		12.0	16.0	10.8	
14	8.9		11.0	15.0	11.1	
15	8.9		10.0	12.8	10.3	
Totals	144.3	28.6	175.4	218.7	173.4	20.4

Appendix Table IX. - Data on Male and Female Inflorescences Accession 12/63 (Male).

Inflorescence No.	Number of branches.	Flowering branch No.	Number of flowers per branch.	Number of flowers per site.	Length of flowering branch mm.
1	3	1	19	1	63.75
		2	5	1	19.14
		3	8	1	38.25
2	2	1	15	1	63.75
		2	13	1	51.00
3	3	1	25	1	89.25
		2	29	1	114.75
		3	24	1	102.00
4	4	1	23	1	102.00
		2	10	1	44.64
		3	22	1	95.64
		4	29	1	127.50
5	4	1	28	1	114.75
		2	11	1	38.25
		3	21	1	108.38
		4	28	1	140.25
6	3	1	20	1	102.00
		2	14	1	57.38
		3	27	1	127.50
7	3	1	21	1	102.00
		2	16	1	82.88
		3	21	1	89.25
8	5	1	31	1	133.88
		2	14	1	76.50
		3	19	1	89.25
		4	37	1	153.00
		5	17	1	146.64
9	3	1	36	1	146.64
		2	25	1	108.38
		3	21	1	89.25
10	3	1	31	1	114.75
		2	26	1	108.38
		3	20	1	70.14

Appendix Table IX. (continued)
Accession 12/63 (continued).

Inflorescence No.	Number of branches.	Flowering branch No.	Number of flowers per branch.	Number of flowers per site.	Length of flowering branch mm.
11	2	1	23	1	102.00
		2	26	1	95.64
12	2	1	20	1	89.25
		2	14	1	57.38
13	14	1	21	1	82.88
		2	17	1	76.50
		3	22	1	82.88
		4	23	1	102.00
		5	24	1	89.25
		6	11	1	51.00
		7	29	1	108.38
		8	24	1	95.64
		9	23	1	95.64
		10	12	1	51.00
		11	19	1	76.50
		12	18	1	63.75
		13	12	1	51.00
		14	3	1	12.75
14	2	1	12	1	57.38
		2	13	1	76.50
15	4	1	27	1	108.38
		2	14	1	51.00
		3	18	1	82.88
		4	32	1	121.14

Appendix Table IX. (continued)
Accession 13/63 (Male)

Inflorescence No.	Number of branches.	Flowering branch No.	Number of flowers per branch.	Number of flowers per site.	Length of flowering branch. mm.
1	5	1	22	1,2,3,	57.38
		2	43	1,2,3,	102.00
		3	24	1,2,3,	114.75
		4	36	1,2,3,	89.25
		5	9	1,2,3,	19.14
2	5	1	28	1,2,3,	82.88
		2	42	1,2,3,	95.64
		3	30	1,2,3,	70.14
		4	6	1,2,3,	12.75
		5	11	1,2,3,	19.14
3	22	1	17	1,2,3,	31.88
		2	12	1,2,3,	31.88
		3	27	1,2,3,	44.64
		4	9	1,2,3,	19,14
		5	16	1,2,3,	38.25
		6	17	1,2,3,	31.88
		7	22	1,2,3,	44.64
		8	10	1,2,3,	19.14
		9	18	1,2,3,	44.64
		10	22	1,2,3,	31,88
		11	6	1,2,3,	12.75
		12	17	1,2,3,	28.69
		13	21	1,2,3,	31.88
		14	13	1,2,3,	28.69
		15	7	1,2,3,	12.75
		16	21	1,2,3,	44.64
		17	15	1,2,3,	31.88
		18	12	1,2,3,	25.50
		19	19	1,2,3,	51.00
		20	14	1,2,3,	25.50
		21	6	1,2,3,	25.50
		22	12	1,2,3,	25.50

Appendix Table IX. (continued)
Assession 13/63 (continued)

Inflorescence No.	Number of branches	Flowering branch No.	Number of flowers per branch.	Number of flowers per site.	Length of flowering branch. mm.
4	5	1	20	1,2,3,	38.25
		2	10	1,2,3,	12.75
		3	33	1,2,3,	70.14
		4	37	1,2,3,	89.25
		5	21	1,2,3,	57.38
5	2	1	21	1,2,3,	51.00
		2	26	1,2,3,	63.75
6	3	1	28	1,2,3,	76.50
		2	10	1,2,3,	25.50
		3	16	1,2,3,	51.00
7	2	1	4	1,2,3,	12.75
		2	18	1,2,3,	38.25
8	10	1	36	1,2,3,	70.14
		2	17	1,2,3,	31.88
		3	44	1,2,3,	102.00
		4	18	1,2,3,	51.00
		5	30	1,2,3,	76.50
		6	13	1,2,3,	38.25
		7	7	1,2,3,	19.14
		8	23	1,2,3,	31.88
		9	16	1,2,3,	38.25
		10	6	1,2,3,	12.75
9	4	1	29	1,2,3,	57.38
		2	18	1,2,3,	44.64
		3	34	1,2,3,	76.50
		4	31	1,2,3,	70.14
10	4	1	33	1,2,3,	76.50
		2	35	1,2,3,	70.14
		3	35	1,2,3,	79.69
		4	47	1,2,3,	102.00

Appendix Table IX. (continued)
Assession 13/63 (continued).

Inflorescence No.	Number of branches.	Flowering branch No.	Number of flowers per branch.	Number of flowers per site.	Length of flowering branch. mm.
11	10	1	10	1,2,3,	19.14
		2	6	1,2,3,	12.75
		3	18	1,2,3,	38.25
		4	21	1,2,3,	44.64
		5	11	1,2,3,	38.25
		6	19	1,2,3,	44.64
		7	12	1,2,3,	31.88
		8	5	1,2,3,	12.75
		9	11	1,2,3,	19.14
		10	7	1,2,3,	12.75
12	5	1	31	1,2,3,	51.00
		2	22	1,2,3,	44.64
		3	9	1,2,3,	25.50
		4	14	1,2,3,	25.50
		5	4	1,2,3,	12.75
13	3	1	22	1,2,3,	31.88
		2	21	1,2,3,	51.00
		3	23	1,2,3,	51.00
14	4	1	11	1,2,3,	12.75
		2	44	1,2,3,	89.25
		3	28	1,2,3,	82.88
		4	62	1,2,3,	114.75
15	5	1	12	1,2,3,	19.14
		2	21	1,2,3,	44.64
		3	14	1,2,3,	31.88
		4	8	1,2,3,	22.31
		5	13	1,2,3,	25.50

Appendix Table 1X. (continued)
Accession 15/63 (Female)

Inflorescence No.	Number of branches.	Flowering branch No.	Number of flowers per branch.	Number of flowers per site.	Length of flowering branch. mm.
1	2	1	20	1	127.50
		2	10	1	76.50
2	1	1	14	1	102.00
3	2	1	25	1	153.00
		2	18	1	121.14
4	1	1	18	1	108.38
5	1	1	21	1	114.75
6	2	1	17	1	89.25
		2	25	1	114.75
7	1	1	28	1	191.25
8	3	1	18	1	127.50
		2	10	1	82.88
		3	8	1	51.00
9	2	1	10	1	82.88
		2	21	1	133.88
10	2	1	16	1	108.38
		2	10	1	82.88
11	3	1	33	1	165.75
		2	27	1	133.88
		3	14	1	89.25
12	2	1	17	1	95.64
		2	26	1	121.14
13	2	1	32	1	153.00
		2	26	1	153.00
14	2	1	14	1	89.25
		2	22	1	114.75
15	2	1	21	1	165.75
		2	24	1	184.88

Appendix Table 1X. (continued)
Accession 16/63 (Female)

Inflorescence No.	Number of branches.	Flowering branch No.	Number of flowers per branch.	Number of flowers per site.	Length of flowering branch. mm.
1	3	1	22	1	114.75
		2	13	1	57.38
		3	26	1	127.50
2	2	1	31	1	216.75
		2	28	1	191.25
3	2	1	22	1	178.50
		2	16	1	114.75
4	2	1	12	1	102.00
		2	18	1	114.75
5	2	1	18	1	127.50
		2	18	1	146.64
6	2	1	24	1	178.50
		2	18	1	127.50
7	3	1	19	1	153.00
		2	12	1	114.75
		3	14	1	140.25
8	2	1	17	1	140.25
		2	16	1	140.25
9	1	1	18	1	159.38
10	3	1	26	1	204.00
		2	16	1	121.14
		3	30	1	210.38
11	1	1	26	1	216.75
12	1	1	9	1	95.64
13	2	1	22	1	178.50
		2	14	1	114.75
14	2	1	28	1	165.75
		2	21	1	210.38
15	3	1	25	1	140.25
		2	11	1	82.88
		3	18	1	102.00

Appendix Table 1X. (continued)
Accession 39/63 (Female).

Inflorescence No.	Number of branches.	Flowering branch No.	Number of flowers per branch.	Number of flowers per site.	Length of flowering branch. mm.
1	2	1	20	1	127.50
		2	26	1	178.50
2	3	1	14	1	102.00
		2	24	1	140.25
		3	19	1	127.50
3	2	1	6	1	76.50
		2	18	1	108.38
4	2	1	9	1	76.50
		2	10	1	76.50
5	2	1	10	1	82.88
		2	16	1	114.75
6	3	1	23	1	140.25
		2	13	1	102.00
		3	15	1	102.00
7	3	1	12	1	95.64
		2	12	1	95.64
		3	4	1	51.00
8	3	1	18	1	127.50
		2	7	1	70.14
		3	11	1	89.25
9	3	1	11	1	89.25
		2	5	1	63.75
		3	19	1	114.75
10	2	1	17	1	114.75
		2	19	1	133.88
11	2	1	17	1	102.00
		2	11	1	76.50
12	4	1	31	1	159.38
		2	20	1	121.14
		3	22	1	127.50
		4	12	1	51.00

Appendix Table IX. (continued)
Accession 39/63 (continued).

Inflorescence No.	Number of branches.	Flowering branch No.	Number of flowers per branch.	Number of flowers per site.	Length of flowering branch. mm.
13	3	1	23	1	146.64
		2	13	1	102.00
		3	15	1	89.25
14	3	1	12	1	89.25
		2	11	1	89.25
		3	18	1	127.50
15	1	1	10	1	89.25

Appendix Table 1X. (continued)
Accession 44/63 (Male).

Inflores-cence No.	Number of branches.	Flower-ing branch No.	Number of flowers per branch.	Number of flowers per site.	Length of flowering branch. mm.
1	1	1	29	1	153.00
2	1	1	24	1	127.50
3	2	1	22	1	95.64
		2	19	1	82.88
4	3	1	33	1	165.75
		2	28	1	140.25
		3	34	1	165.75
5	2	1	32	1	178.50
		2	32	1	165.75
6	2	1	16	1	82.88
		2	8	1	38.25
7	3	1	22	1	127.50
		2	28	1	140.25
		3	25	1	121.14
8	3	1	21	1	114.75
		2	26	1	133.88
		3	5	1	38.25
9	3	1	23	1	114.75
		2	22	1	121.14
		3	33	1	153.00
10	2	1	21	1	114.75
		2	29	1	140.25
11	2	1	15	1	82.88
		2	20	1	95.64
12	1	1	28	1	140.25
13	2	1	17	1	63.75
		2	20	1	95.64
14	2	1	28	1	146.64
		2	22	1	102.00
15	1	1	21	1	95.64

Appendix Table X. - Dimensions of flowers.
Accession 12/63 (Male).

Flower No.	Length Attachment to extremity mm.	Width Span of perianth. mm.
1	6.38	6.38
2	6.38	7.95
3	6.38	6.38
4	6.38	7.95
5	6.38	7.95
6	6.38	7.95
7	6.38	7.95
8	6.38	6.38
9	6.38	6.38
10	4.77	6.38
11	4.77	4.77
12	4.77	4.77
13	4.77	6.38
14	4.77	6.38
15	4.77	6.38
16	4.77	4.77
17	4.77	6.38
18	6.38	7.95
19	4.77	6.38
20	6.38	7.95
Totals	113.11	133.76
Means	5.65	6.69

Appendix Table X. - Dimensions of flowers.
Accession 13/63 (Male).

Flower No.	Length Attachment to extremity. mm.	Width Span of perianth. mm.
1	4.77	6.38
2	4.77	6.38
3	3.19	6.38
4	6.38	7.95
5	4.77	6.38
6	3.19	4.77
7	4.77	7.95
8	3.19	4.77
9	4.77	7.95
10	4.77	7.95
11	4.77	6.38
12	4.77	6.38
13	6.38	6.38
14	4.77	7.95
15	4.77	6.38
16	4.77	6.38
17	3.19	4.77
18	3.19	6.38
19	4.77	6.38
20	4.77	6.38
Totals	90.72	130.62
Means	4.54	6.53

Appendix Table X. - Dimensions of flowers.
Accession 17/63 (Male).

Flower No.	Length Attachment to extremity mm.	Width Span of perianth. mm.
1	4.77	6.38
2	4.77	6.38
3	6.38	7.95
4	4.77	6.38
5	4.77	6.38
6	6.38	7.95
7	5.57	7.16
8	6.38	7.95
9	6.38	7.95
10	6.38	6.38
11	6.38	7.95
12	6.38	6.38
13	6.38	7.95
14	4.77	6.38
15	4.77	6.38
16	6.38	6.38
17	4.77	6.38
18	4.77	7.95
19	4.77	6.38
20	4.77	7.95
Totals	110.69	140.94
Means	5.53	7.05

Appendix Table X. - Dimensions of flowers.
Accession 41/63 (Male).

Flower No.	Length Attachment to extremity. mm.	Width Span of perianth. mm.
1	4.77	6.38
2	4.77	6.38
3	6.38	7.95
4	6.38	6.38
5	6.38	6.38
6	4.77	6.38
7	4.77	6.38
8	6.38	7.95
9	4.77	6.38
10	4.77	6.38
11	6.38	7.95
12	7.95	7.95
13	6.38	7.95
14	6.38	7.95
15	6.38	7.95
16	-	-
17	-	-
18	-	-
19	-	-
20	-	-
Totals	88.61	106.69
Means	5.91	7.11

Appendix Table X. - Dimensions of flowers.
Accession 44/63 (Male).

Flower No.	Length Attachment to extremity. mm.	Width Span of perianth. mm.
1	4.77	7.95
2	6.38	7.95
3	4.77	7.95
4	4.77	7.95
5	4.77	7.95
6	4.77	7.95
7	6.38	7.95
8	6.38	7.95
9	4.77	7.95
10	4.77	7.95
11	4.77	7.95
12	4.77	7.95
13	4.77	7.95
14	4.77	7.95
15	4.77	6.38
16	4.77	7.95
17	4.77	7.95
18	4.77	7.95
19	4.77	7.95
20	6.38	7.95
Totals	101.84	157.43
Means	5.09	7.87

Appendix Table X. - Dimensions of flowers.
Accession 1/63 (Female).

Flower No.	Length Attachment to extremity. mm.	Width Span of perianth. mm.
1	12.75	6.38
2	12.75	6.38
3	12.75	6.38
4	11.13	6.38
5	11.13	6.38
6	12.75	6.38
7	12.75	6.38
8	11.13	6.38
9	12.75	6.38
10	12.75	6.38
11	11.13	6.38
12	11.13	6.38
13	12.75	6.38
14	11.13	6.38
15	9.54	6.38
16	11.13	6.38
17	11.13	6.38
18	12.75	6.38
19	12.75	6.38
20	12.75	6.38
Totals	238.83	127.60
Means	11.94	6.38

Appendix Table X. - Dimensions of flowers.
Accession 16/63 (Female).

Flower No.	Length Attachment to extremity. mm.	Width Span of perianth. mm.
1	14.31	9.54
2	14.31	9.54
3	14.31	8.75
4	11.13	7.95
5	11.93	8.75
6	16.70	10.34
7	15.90	8.75
8	15.90	8.75
9	14.31	8.75
10	15.90	8.75
11	15.10	8.75
12	13.55	8.75
13	14.31	9.54
14	12.75	9.54
15	15.90	8.75
16	14.31	8.75
17	14.31	9.54
18	12.75	7.95
19	12.75	8.75
20	15.90	8.75
Totals	286.33	178.94
Means	14.32	8.95

Appendix Table X. - Dimensions of flowers.
Accession 23/63 (Female).

Flower No.	Length Attachment to extremity mm.	Width Span of perianth. mm.
1	11.13	7.16
2	9.54	4.77
3	12.75	6.38
4	11.13	3.98
5	11.13	4.77
6	11.13	5.77
7	11.13	6.38
8	9.54	5.57
9	11.13	5.57
10	11.13	5.57
11	11.13	4.77
12	11.13	5.57
13	11.13	5.92
14	12.75	4.77
15	11.13	5.57
16	11.13	6.38
17	11.13	6.38
18	11.13	6.38
19	11.13	6.38
20	11.13	6.38
Totals	222.66	114.42
Means	11.13	5.72

Appendix Table X. - Dimensions of flowers.
Accession 42/63 (Female).

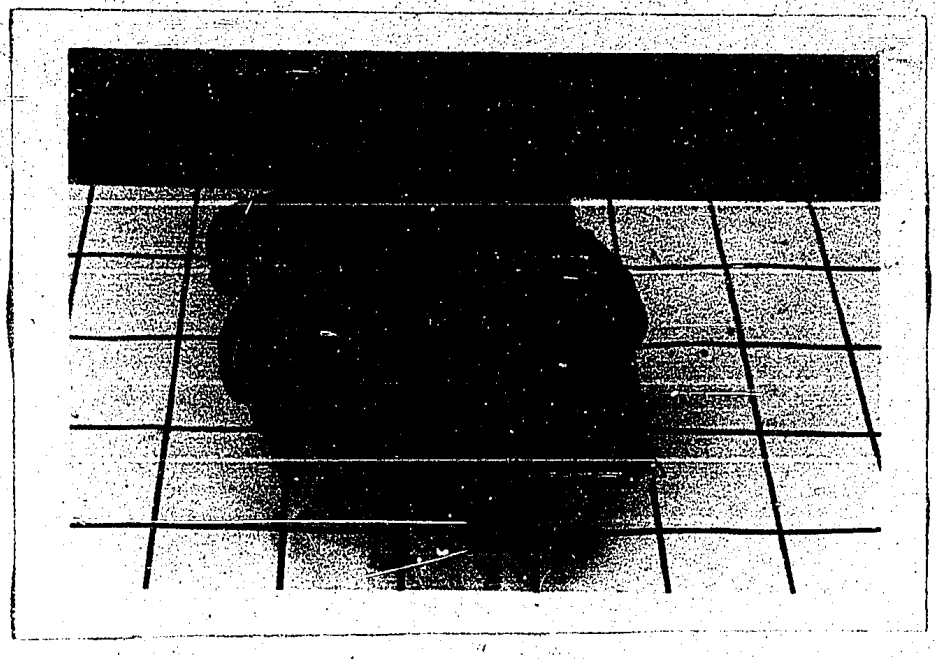
Flower No.	Length Attachment to extremity. mm.	Width Span of perianth. mm.
1	14.31	7.95
2	12.75	7.95
3	12.75	7.95
4	12.75	7.95
5	12.75	7.95
6	12.75	7.95
7	12.75	7.95
8	12.75	7.95
9	11.13	7.95
10	11.13	6.38
11	12.75	6.38
12	12.75	6.38
13	12.75	7.95
14	12.75	6.38
15	12.75	6.38
16	12.75	6.38
17	12.75	6.38
18	12.75	7.95
19	14.31	6.38
20	12.75	7.95
Totals	254.88	146.44
Means	12.74	7.32

Appendix Table X. - Dimensions of flowers.
Accession 41/63 (Hermaphrodite)

Flower No.	Length Attachment to extremity. mm.	Width Span of perianth. mm.
1	11.13	7.95
2	11.13	7.95
3	11.13	6.38
4	11.13	7.95
5	11.13	7.95
6	9.54	7.95
7	11.13	7.95
8	9.54	6.38
9	9.54	7.95
10	9.54	6.38
11	12.75	7.95
12	9.54	6.38
13	11.13	6.38
14	11.13	7.95
15	9.54	7.95
Totals	159.04	111.40
Means	10.60	7.43

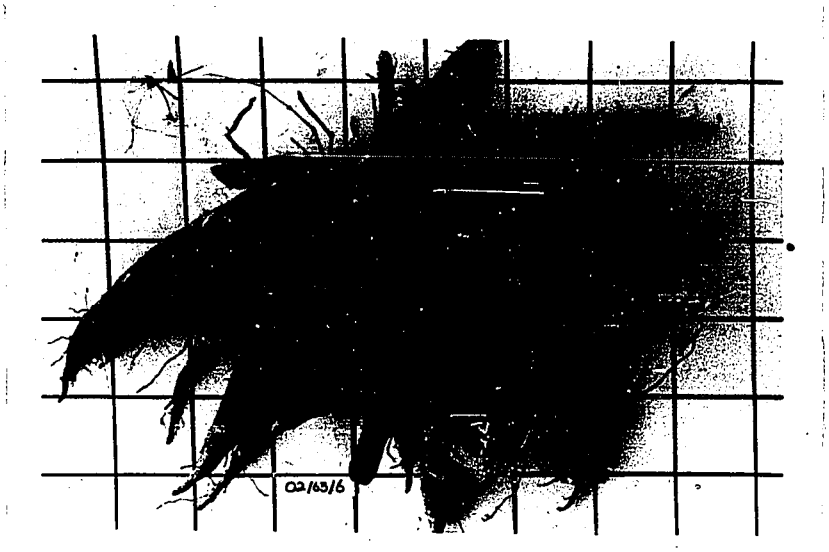
Appendix XI. - Tubers

Open cluster

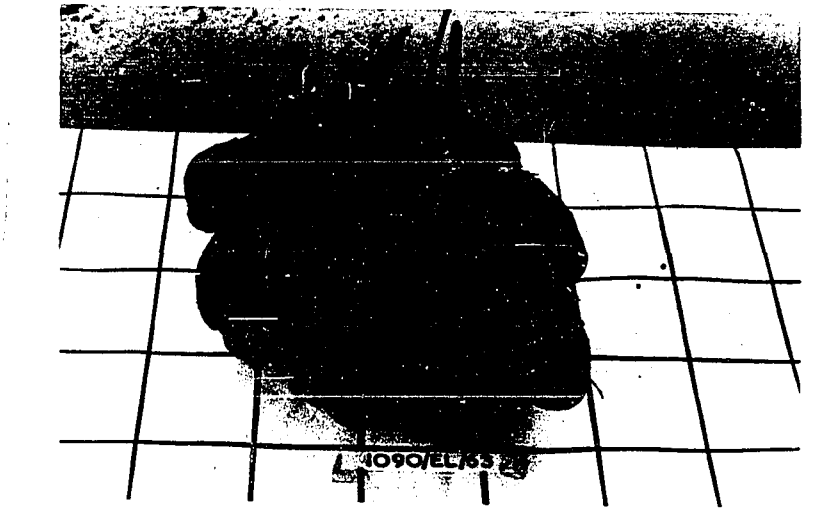


Compact cluster.

Appendix XI. - Tubers

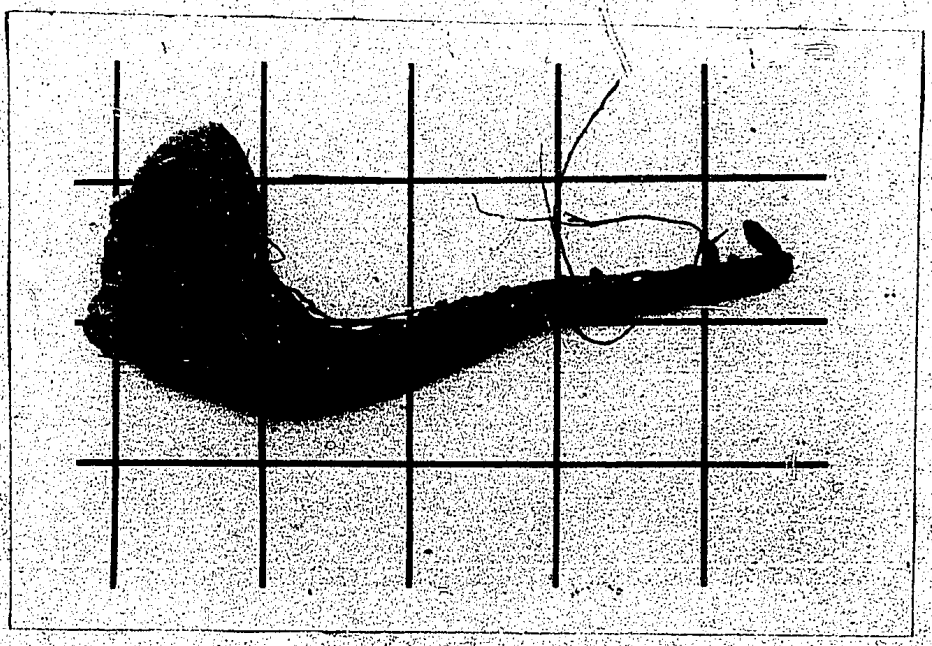


Open cluster



Compact cluster.

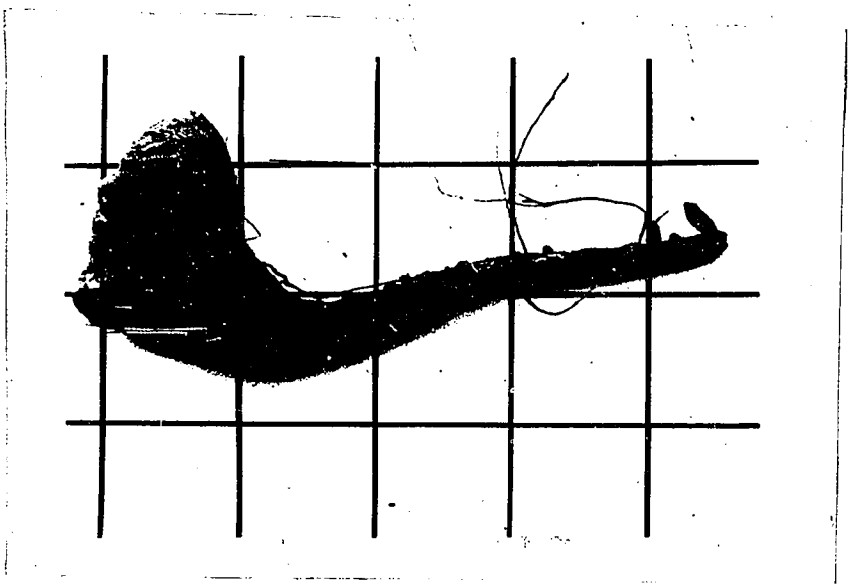
Appendix Xl. - Tubers



Club-shaped.

Ovoid.

Appendix XI. - Tubers

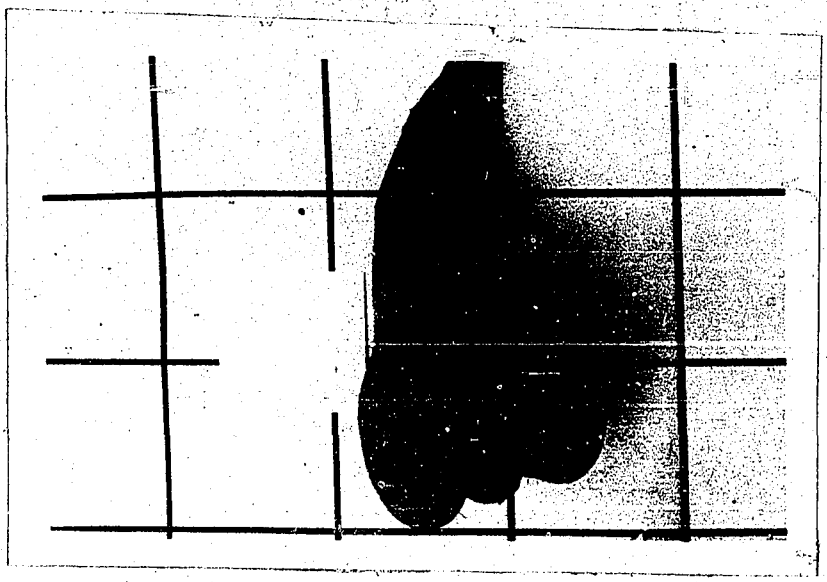


Club-shaped.

Ovoid.

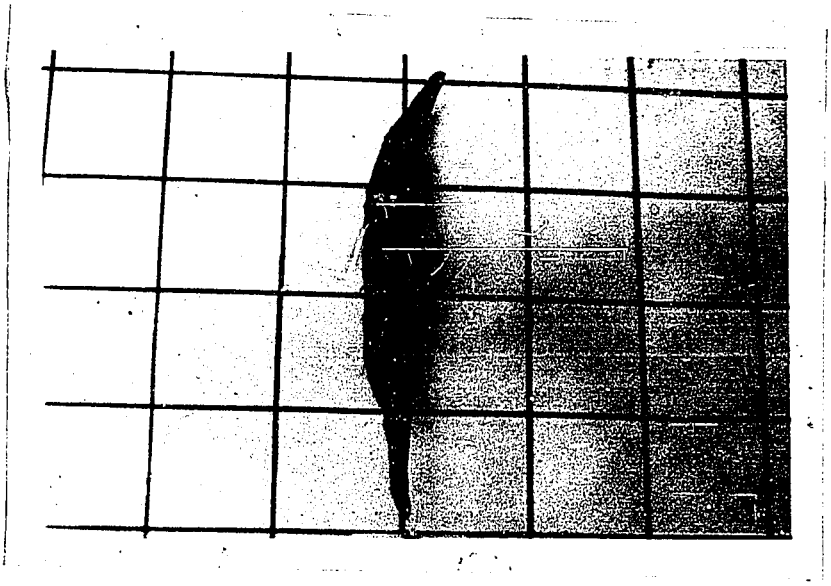
Appendix XI. - Tubers.

Spindle-shaped.

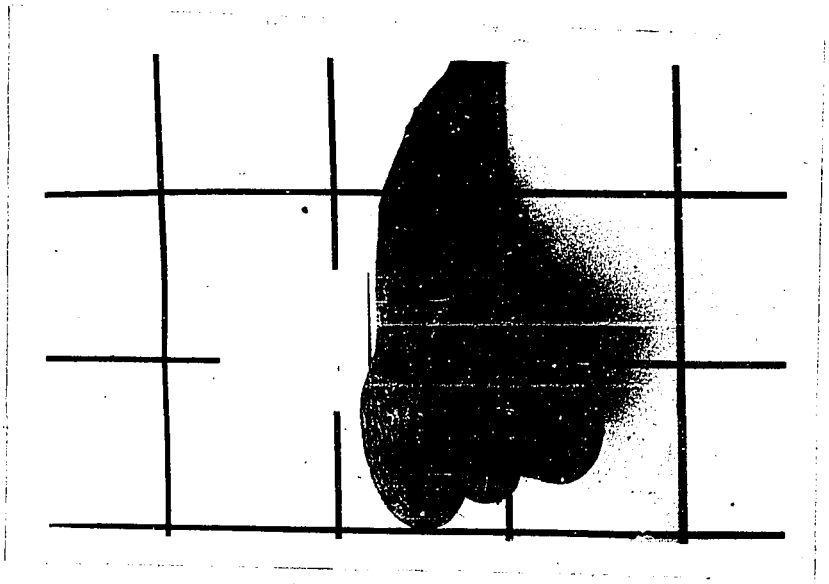


Large, lobed.

Appendix XI. - Tubers.



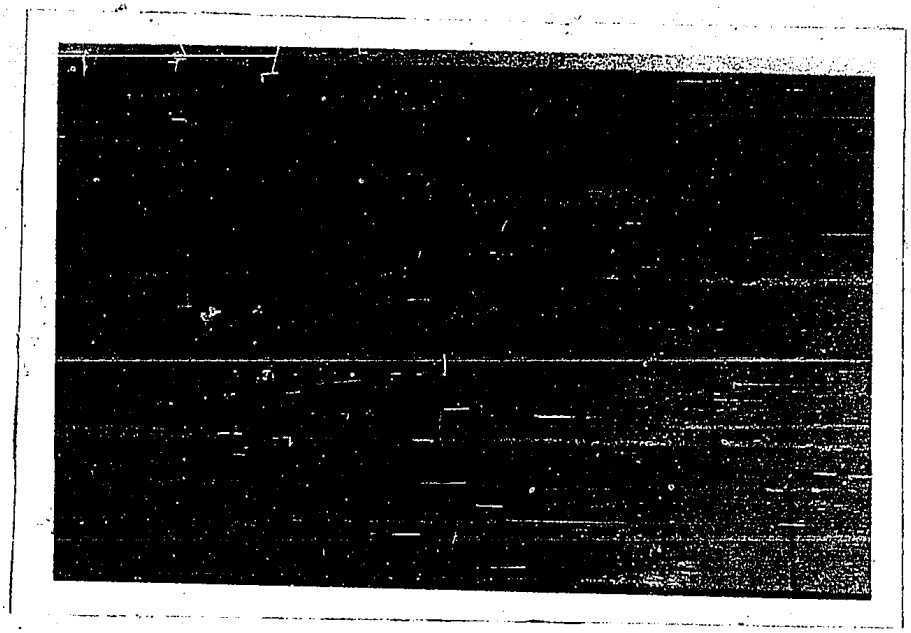
Spindle-shaped.



Large, lobed.

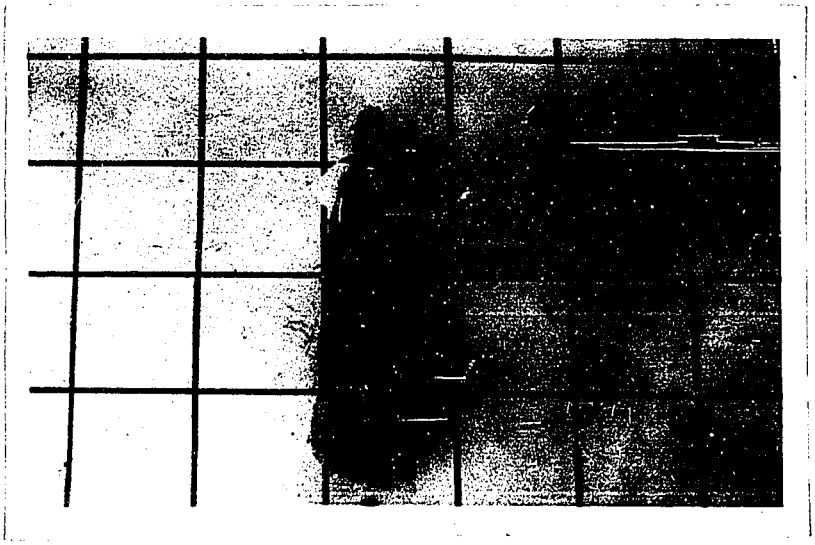
Appendix XI. - Tubers.

Cylindrical.

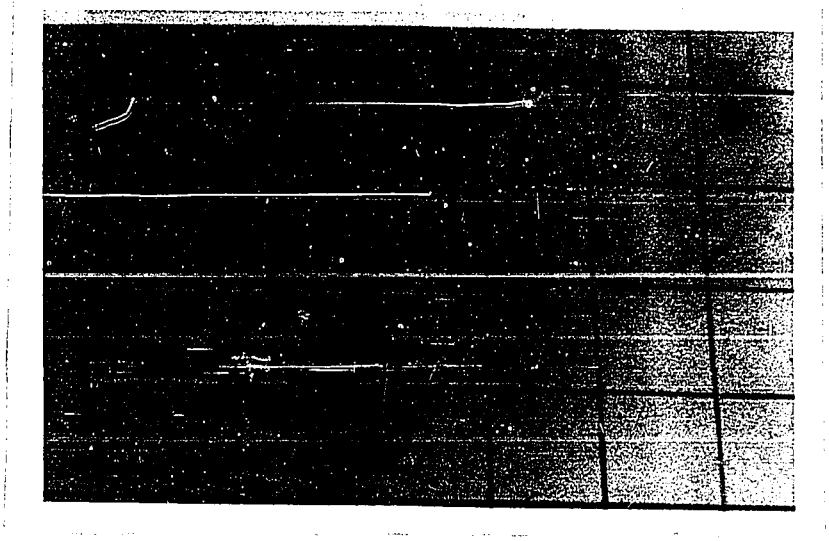


Fan-shaped.

Appendix XI. - Tubers.



Cylindrical.



Fan-shaped.

Appendix Table XII. - Yield of Female plants (shaded field) 1965 - 1966.

1/63/5 oz	2/63/6 oz	2/63/9 oz	12/63 oz	15/63 oz	16/63 oz	35/63 oz
13.5	31.0	64.0	76.0	137.0	57.0	10.0.
13.5	52.0	48.0	178.0	11.0	1.0	30.0
35.0	27.0	27.0	44.0	72.5	152.5	28.0
15.5	90.0	16.0	48.0	32.0	74.0	46.0
16.0	94.0	40.0	44.0	22.0	93.0	33.0
100.0	27.0	112.0	50.0	32.0	160.0	88.0
33.0	33.0	34.0	43.0	30.5	13.0	193.0
42.0	44.0	28.0	7.0	39.5	66.0	169.0
34.0	12.0	34.0	16.0	77.5	114.0	34.0
36.0	26.0	119.0	103.5	53.0	18.0	24.0
31.0	32.0	84.0	86.0	19.5	22.0	16.0
77.0	128.0	106.0	65.0	54.0	53.0	74.0
73.0	74.0	56.0	14.5	55.5	77.0	11.0
23.0	112.0	36.0	59.0	53.5	64.0	10.0
44.0	27.0	23.0	150.0	71.5	20.0	4.0
32.0	64.0	64.0	39.5	70.0	46.0	90.0
25.0	56.0	110.0	71.0	47.0	97.0	48.0
59.0	81.0	50.0	68.0	32.0	66.0	70.0
44.0	83.0	96.0	23.0	90.5	82.0	70.0
54.0	50.0	48.0	81.0	48.0	41.0	
32.0	67.0	119.0	66.0	120.5	70.0	
112.0	105.0	32.0	79.0	154.0	34.0	
42.0	36.5	88.0	106.0	73.5	144.0	
44.0	137.0	32.0	22.0	45.5		
116.0	16.0	45.0	48.0			
101.0	60.0	48.0	61.0			
41.0	24.0	55.0	25.0			
15.0	20.0	106.0	73.0			
71.0	46.0	24.0	17.0			
30.0	38.0	20.0	157.0			
20.0	80.0	57.0	178.0			
131.0	26.0	120.0	64.0			
	76.0	48.0	164.0			
	101.0	44.0	33.0			
	24.0	64.0	51.5			
	50.0		34.0			
	6.0		90.0			
	20.0		46.5			
	17.0		156.0			
	29.0		66.0			
	48.0		152.0			
	38.0		112.0			
			211.0			
			2.0			
			95.0			
			9.0			
Totals 1555.5	2207.5	1997.0	3384.5	1442.0	1564.5	1048.0

Appendix Table XII. - Yield of Male plants (shaded field) 1965 - 1966.

1/63/5 oz	2/63/6 oz	2/63/9 oz	12/63 oz	15/63 oz	16/63 oz	35/63 oz
17.0	24.0	48.0	50.0	17.0	38.0	6.0
17.0	93.0	50.0	72.0	49.5	101.0	32.0
10.5	30.0	32.0	79.0	8.5	81.0	107.0
1.0	12.0	51.0	80.0	55.5	83.0	32.0
42.0	29.0	64.0	23.5	64.0	31.0	14.0
10.0	66.0	32.0	19.0	19.5	38.0	50.0
138.0	45.0	28.0	42.0	48.0	80.0	49.0
80.0	37.0	94.0	130.0	33.0	17.0	64.0
30.0	2.0	32.0	167.0	98.0	60.0	21.0
20.0	19.0	64.0	45.0	63.0	106.0	18.0
48.0	48.0	96.0	92.0	86.0	33.0	51.5
48.0	90.5	16.0	45.0	96.0	76.0	8.5
60.0	32.0	16.0	60.0	131.0	58.0	7.0
51.0	11.0	7.0	17.0	64.0	24.0	37.0
24.5	36.0	25.0	25.0	93.0	56.0	98.0
32.0	100.0	10.0	93.0	33.0	35.0	13.0
45.0	16.0	3.0	162.0	75.0	93.0	38.0
80.0	48.0	55.0	193.0	101.5	22.0	82.0
39.0	2.0	54.0	86.0	48.0	11.0	81.0
115.0	37.0	48.0	11.0	32.0	50.0	65.0
42.0	112.0	61.5	16.0	93.0	24.0	13.0
59.0	44.0	32.0	24.5	64.0	49.0	20.0
90.0	14.0	104.0	67.0	48.0	17.0	45.0
23.0	4.0	64.0	18.0	188.0	24.0	54.0
28.0	16.0	12.0	66.0	64.0	23.0	118.0
52.0	6.0	67.0	74.0	96.0	73.0	75.0
10.0	26.0	48.0	37.0	49.0	37.0	
55.0	87.0	32.0	9.0	58.5	33.0	
30.0	75.0	64.0	127.0	64.0	148.0	
84.0	101.0	96.0	89.0	30.0	32.0	
24.0	57.0	102.0	113.0	24.0	66.0	
15.0	86.0	28.0	45.0	73.0	50.0	
77.0	92.0	12.0	45.0	50.0	90.0	
29.0	38.0	71.0	91.5	49.5	100.0	
30.0	25.0	32.0		33.0	160.0	
123.0	16.0	69.0		58.5	72.0	
73.0	39.0	44.0		16.0	35.0	
84.0	80.0	16.0		18.0	64.0	
50.0	55.0	64.0		20.0	50.0	
48.0	46.0	96.0			61.5	
18.0	48.0	128.0			58.0	
44.0	117.0				17.0	
					90.0	
					14.0	
					14.0	
Totals 1996.0	2258.5	2067.5	2333.5	2312.0	2494.5	1199.0

Appendix XII. - Yield of Male plants (unshaded field) 1965 - 1966.

1/63/5 oz	2/63/6 oz	2/63/9 oz	12/63 oz	15/63 oz	16/63 oz	35/63 oz
11.0	16.0	13.0	4.0	23.0	70.0	22.0
67.0	11.0	11.0	5.0	4.0	19.0	15.0
42.0	2.0	21.0	7.0	5.0	18.0	8.0
30.5	26.0	13.0	45.5	6.0	37.0	10.0
5.0	6.0	24.0	21.0	6.0	2.0	18.0
17.0	2.0	18.5	6.0	37.0	6.0	6.5
26.0	3.0	23.0	6.0	35.0	9.0	38.0
18.0	38.0	5.0	14.0	50.0	51.5	20.0
37.0	1.0	9.0	67.0	13.0	13.0	8.5
86.0	2.0	4.0	28.0	5.0	10.0	2.0
7.0	4.0	7.0	13.0	3.0	38.0	11.0
72.0	18.0	89.0	16.0	7.0	56.0	38.0
70.0	10.0	9.0	14.0	6.5	11.0	36.0
15.0	36.0	11.0	2.0	4.0	8.0	7.0
32.0	38.0	8.0	3.5	5.0	4.0	7.0
32.0	46.0	21.0	22.0	4.0	16.0	
3.0	7.0	86.0	19.0	2.0	16.0	
36.0	7.0	53.0	2.0		2.0	
20.0	42.0	39.0	16.0		3.0	
18.0	5.0	27.0	9.0		66.0	
17.0	9.0	5.0	11.0		36.0	
3.0	5.0	6.5	13.0		6.0	
6.0	7.0	5.0	3.0		50.0	
9.0	20.0	4.0	9.0		3.0	
4.0	9.0	9.0	6.0		5.0	
	9.0	11.0	3.0		8.0	
	59.0	7.0	22.5		1.5	
	28.0	27.0	38.0		8.0	
	1.5	4.0			19.0	
	6.5	32.0			53.0	
	7.0	64.0				
	12.0	19.0				
	22.0	13.0				
		7.0				
		21.0				
		3.5				
		13.5				
		53.0				
		26.0				
		11.0				
		11.0				
		5.0				
		20.0				
Totals 683.5	515.0	809.0	425.5	215.5	645.0	247.0

Appendix XII. - Yield of Female plants (unshaded field) 1965 - 1966.

1/63/5 oz	2/63/6 oz	2/63/9 oz	12/63 oz	15/63 oz	16/63 oz	35/63 oz
41.0	52.0	9.0	4.0	35.0	2.0	1.0
19.0	32.0	35.0	13.0	9.0	3.0	8.5
20.0	64.0	19.0	48.0	5.0	4.0	64.0
26.0	16.0	5.0	15.0	13.0	3.0	50.0
20.0	32.0	11.0	31.0	7.0	70.0	4.0
32.0	34.0	16.0	22.0	19.0	49.0	6.0
62.0	3.0	9.0	22.5	53.0	18.0	18.0
31.0	42.0	11.0	32.0	7.0	5.0	50.0
16.0	17.0	5.5	8.0	11.0	99.0	66.0
8.0	48.0	32.0	19.0	2.0	27.5	39.0
19.0	32.0	6.0	7.0	5.0	22.0	26.0
9.0	17.0	35.0	13.0	39.0	48.0	8.0
24.0	12.0	18.0	45.0		7.0	6.0
126.5	18.0	32.0	3.0		3.0	19.0
18.0	3.0	16.0	4.5		5.5	6.0
32.0	42.0	3.0	19.0		82.0	
78.0	18.0	18.0	6.0		38.0	
3.0	19.0	17.0	36.0		5.0	
20.0	20.0	82.0	8.0		22.0	
15.0	1.0	50.0	19.0			
19.0	16.0	6.0				
23.0	16.0	19.0				
108.0	2.0	19.0				
176.0	12.0	25.0				
2.0	97.0	22.0				
2.0	1.0	25.0				
16.0	27.0	6.0				
6.0	10.0	3.0				
4.0	13.0	13.0				
11.0	18.0	7.0				
56.0		3.0				
48.0		13.0				
		50.0				
		37.0				
		13.0				
Totals 1090.5	734.0	690.5	375.0	205.0	513.0	371.5