

Genetic-Evolutionary Studies on Cultivated Cannas

VI. Origin and Evolution of Ornamental Taxa

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Summary. Hybridization has played a dominant and decisive role in the origin of ornamental cannas. This has been made possible by the ecospecific differentiation of the parental species, which implies lack of barriers and a good deal of recombination associated with reasonably high fertility.

Colour differences between species are controlled by a number of genes and their intensifiers, inhibitors, lethals, etc. From recombination in interspecific hybrids of such a wide range of genes, segregating simultaneously and involving complex segregation, arises a wide array of heterozygous genotypes with new colours and colour combinations, releasing much genetic diversity.

Hybridization has also been responsible for transgressive segregation, particularly in length and breadth of stamodia and luxuriance, affecting not only plant height but also flower size. Perhaps the most important single factor responsible for the evolution of ornamental cannas has been the repeated cycles of hybridization which have led to the breakage of size and other barriers; this seems to have been exploited continuously until very large flower size was built up and combined with other useful vegetative and floral characters such as colour and number of flowers per inflorescence, extended blooming period, cold resistance, etc. The efficient vegetative propagation made fixing of the useful genotypes no problem, although they may contain a high degree of heterozygosity and sexual sterility.

Along these lines, Année (hybrids between *C. indica* and *C. glauca*) and Ehemann (hybrids between *C. iridiflora* and *C. warszewiczii*) cannas came into being in 1848 and 1863 respectively. Although both were a distinct improvement over the original species, they were still relatively small-flowered and major improvements came roundabout 1868, when Crozy, Gladiolus or French Dwarf cannas (*C. × generalis* Bailey) were released. This group arose from hybrids and back crosses of the first two groups and contains diploids, interchange heterozygotes and autotriploids. When further intercrossing, inbreeding and selection yielded no significant improvement, „new blood“ in the form of *C. flaccida* was introduced. The result was the release of Italian, Iris, Orchid or Giant flowered cannas (*C. × orchiodes* Bailey) in 1872. These are asynaptic seedless diploids and allo- or segmental allotriploids. By and large, Crozy cannas are the result of exploiting new genetic diversity and transgression, while Italian cannas owe their excellence to the luxuriance accompanying the introduction of *C. flaccida*.

Next to hybridization, triploidy (14%) has been an important mechanism in the origin of cultivars with thicker, more durable and larger flower parts. The two types of triploids, autotriploids and segmental allotriploids, are distinguishable by their morphological and cytogenetical properties.

It is evident that during the 44 years 1848–1892 the speed of evolution was rapid and its direction governed by the following principles of selection: increase in hardiness, reduction in height, spikes well above foliage, free flowering, erect flowers, increase in flower size, colour diversity, circular form of flowers, increase in thickness of flower parts and durability of flower, self shedding flowers, etc. The result has been the transformation of cannas from simple foliage plants to attractive ornamental flowers.

It is noteworthy that selection for the two principal uses of canna not only involved different organs, but also took place in very different environments. While selection in ornamental canna was for floral parts under a temperate European climate new to *Canna*, that for starch involved the rhizome in its native habitat. It is interesting that the two different purposes of selection under different habitats have both ended in triploidy: in the ornamentals this has considerably enlarged the flowers, while in the starch-yielding *C. edulis* it has enlarged the fleshy rhizome but had a very limited effect on the flower.

Introduction

The other papers in this series deal with the variation in phenotype and breeding and meiotic systems, parallelism between spontaneous and induced mutations, taxonomic treatment, horticultural classification and intraspecific polyploidy within starch-yielding *C. edulis* (Khoshoo and Mukherjee, 1970; Mukherjee and Khoshoo, 1970 a–e). The present paper discusses the data given in the foregoing papers, together with other cognate findings, to bring out, for the first time, an integrated and coherent account of the mode of origin and evolution of the ornamental cannas, the principles involved in their

selection, the future aims of breeding and the underlying cytogenetic mechanisms.

Origin of Ornamental Cannas

Man's interest in ornamentals, as opposed to crop plants, is very recent. In contrast with crops, the origin, evolution and improvement of ornamentals has been accomplished in historical time and in many cases the intervening stages between the wild and cultivated conditions are still preserved. In the sweet pea, chinese primrose, hyacinth, narcissus, bearded iris, garden rose, chrysanthemum, dahlia, etc., the series of morphological, cytological and ge-

netical events accompanying such an evolutionary transformation is reasonably well documented (Darlington, 1963). Furthermore, cytogenetic study clarifies not only their genetic-evolutionary history but also unravels the reasons for such a history. The canna cultivars now in use are a tremendous improvement over the original botanical species (Mukherjee and Khoshoo, 1970a). At the beginning of this century cannas were very popular and were in great demand as bedding plants in public parks and for landscaping work. However, soon after the first World War, they went out of vogue and some important varieties, often representing intermediate steps in the evolutionary geneology, may have been lost. This may be a handicap to the proper interpretation. However, the present data on garden cannas and the species involved in their origin is sufficient, together with other published information, to produce a coherent picture of the evolution of this ornamental.

Ancestors

The genus including the five elemental species, *C. indica* Linn. (*C. nepalensis*), *C. glauca* Linn., *C. iridiflora* Ruiz & Pav., *C. warszewiczii* A. Dietr. and *C. flaccida* Salisb., is chiefly native to the tropical Americas and West Indies (Fig. 1). From their original habitats the species were introduced into Europe, beginning with *C. indica* in 1596 by Gerard. This was followed by *C. glauca*, whose exact year of introduction is not known but which was illustrated by Piso in 1648 (Baker, 1893b). Next came *C. flaccida* from the south Atlantic States of the U.S.A. in 1788, *C. iridiflora* was brought from the Andes of Peru by A. B. Lambert in 1816 and finally *C. warszewiczii* was brought from Costa Rica by Von Warszewicz in 1849 (Anonymous, 1893a; Baker, 1893a).

Most of these species were cultivated to impart a tropical effect to European gardens. They were often tall, leafy, long-jointed with comparatively small flowers.

Année Cannas

From 1840 to 1865, M. Année of France was the principal cultivator and was the first to raise *Canna* hybrids (*C. indica* × *C. glauca*), in 1848, which were named *C. × annaei* (Fig. 2). These had slender rhizomes, and were about 360–390 cm in height, with long internodes, oblong-acute leaves up to 60 cm in length, erect peduncles with many racemes, and flowers salmon-yellow or orange-yellow or tinged with rose-red and not longer than in *C. indica*. From this stock arose a large number of forms grown primarily for their foliage which was green to red-purple. According to M. André these hybrids became very po-

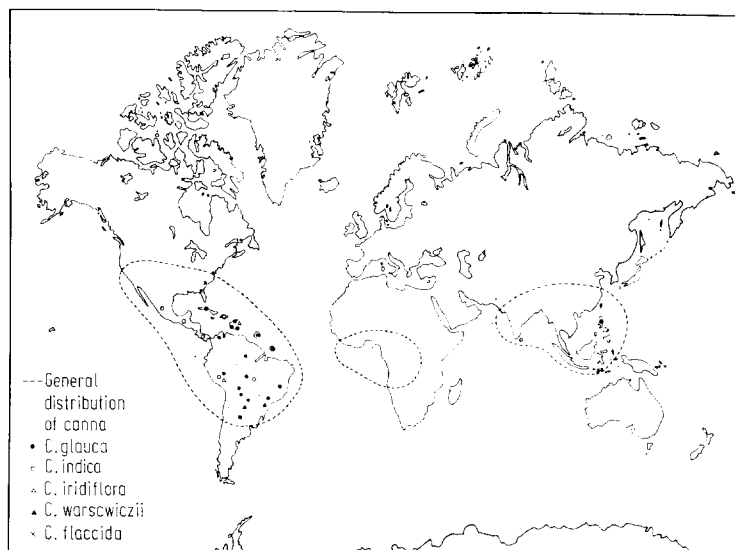


Fig. 1. Map showing the distribution of the five elemental species together with the over-all distribution of the genus *Canna*

pular for decorative purposes in France and in 1861 more than 20,000 tufts of Année cannas were used in parks and squares in Paris alone (Baker, 1893b).

Subsequently M. Année raised another hybrid involving *C. discolor*. The new hybrid was much reduced

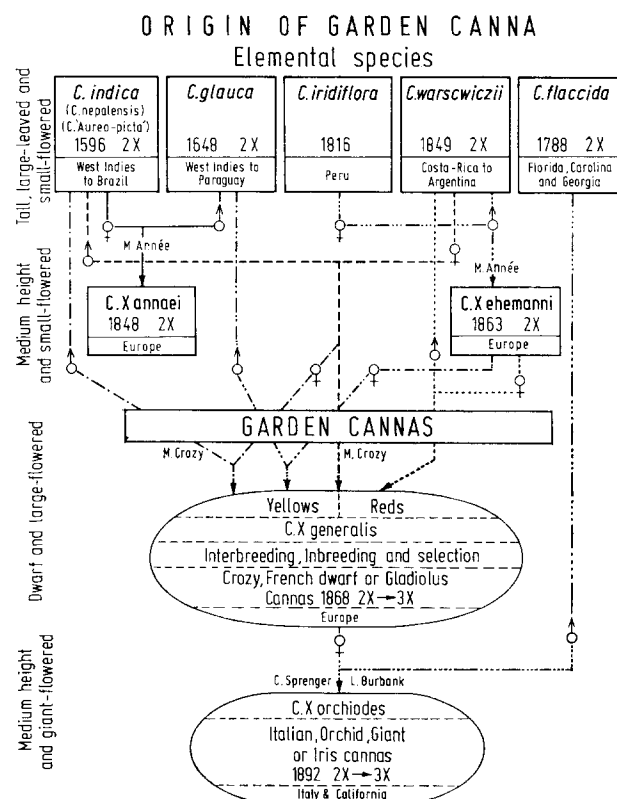


Fig. 2. Diagram depicting the origin of the two chief groups of garden cannas along with their characters like plant height and size of flower

in height (120–150 cm) with brilliant scarlet flowers of the size of *C. warszewiczii* and rather orbicular green or bronze leaves (Baker, 1893 b). It is clear that because of the inordinate height of the first group of hybrids, M. Année felt the need for a dwarfer type with more colourful flowers.

Ehemann Canna

This originated from the cross *C. iridiflora* × *C. warszewiczii*, raised originally in Paris by M. Année, but was distributed by M. Kolb, Inspector of the Botanical Garden at Munich, who first named it *C. iridiflora hybrida*, but later *C. × ehemanni* after Herr Ehemann (Fig. 2). This hybrid was very fine and closely resembled the female parent, *C. iridiflora*, in having rather pendulous large flowers and crimson coloured staminodia. However, the tube of the flower was considerably shortened like that of *C. warszewiczii*. It was of medium height (180 cm) with green foliage. This canna was fairly distinct in size, form and colour from the typical species (Anonymous, 1883 a and b; Baker, 1893 b).

Crozy or French Dwarf Cannas

By now, considerable interest had developed in canna breeding and a number of cannas, dwarf in habit and with large closely set flowers, were developed. All these are grouped here and appear to have been „polyphyletic“ in origin, involving at least four botanical species, *C. indica*, *C. glauca*, *C. warszewiczii* and *C. iridiflora* (Fig. 2).

M. Crozy of France was the first, and also the chief, architect of this group of cannas. He began hybridizing *C. nepalensis* (now known as *C. indica*) and *C. warszewiczii* (Anonymous, 1897). According to Kränzlin (1912), the form of *C. nepalensis* used by Crozy had „large yellow flowers and very long creeping tubers“ which he thought were the characters of *C. flaccida*. However, because of strong genetic differentiation of the genome of *C. flaccida*, not only is there asynapsis in the ensuing hybrids but also total seed sterility, and it is reasonable to assume that *C. flaccida* was not involved in the origin of this group. Furthermore, in view of the high degree of recombination and fertility of the hybrids which gave rise to Crozy cannas, Kränzlin's interpretation may not be correct. M. Crozy had actually used a form of *C. nepalensis* which he called *grandiflora* (Paul, 1893).

The first two hybrids raised by Crozy were 'Bonete' and 'Planteri'. The former resembled *C. warszewiczii* in having dark brown foliage and fairly large flowers; it was free flowering. The latter had green leaves and orange flowers. By crossing with *Canna* 'Aureo-picta' (a horticultural form of *C. indica*), Crozy was able to obtain yellow-spotted cannas which were selected over several generations for early blooming, more floriferous habit and larger and rounder flowers. Crozy raised 180 to 200 hybrids in a short time and gradually increased the flower diameter to 11–15 cm

in several glowing colours on large trusses (Anonymous, 1897).

From information by Vilmorin (Anonymous, 1898), also summarized by Baker (1893 b), it emerges that *C. × ehemanni* (*C. iridiflora* × *C. warszewiczii*) was closely connected with the origin of this group of cannas. This hybrid combined useful characters like short tube and large staminodia. Back crossing *C. × ehemanni* to *C. warszewiczii* resulted in red-flowered types, while yellow-flowered types emerged from crosses between *C. × ehemanni* and most probably *C. glauca* (Fig. 2). The red and yellow types intercrossed readily and the resultant hybrids were the source of a large number of new types. Further intercrossing, inbreeding and judicious selection resulted in still newer hybrids.

Crozy cannas were selected for hardiness and were therefore easy to grow in the open in Europe. They were dwarf in habit, the foliage was green or bronze and the spikes were floriferous loaded with very showy large flowers with broad staminodia of varied and brilliant colours. This group was a tremendous improvement over the Année cannas; it offered novelty and *Canna* now became a very effective bedding ornamental. Garden cultivars replaced all the *Canna* species such as *C. discolor*, *C. edulis*, *C. glauca*, *C. indica*, *C. flaccida* and *C. warszewiczii* commonly cultivated in gardens, and the emphasis shifted from the tall Année and medium Ehemann cannas to the dwarf Crozy cannas.

In addition to the French breeders like Crozy and Vilmorin, others, like Lemoine and Sisley from France, Messrs. Paul and Son in England, Messrs. W. Pfitzer and G. Ernst of Germany and A. Wintzer from the U.S.A., all contributed materially to the development of Crozy or French Dwarf cannas (Stuttgart, 1898). However, the principal architect was Crozy, who was the first to bring out such cultivars in France, and the group as a whole continues to be called Crozy or French Dwarf cannas. Crozy's contribution was so great that he was known in Lyons (France) as „Papa Canna“ (Anonymous, 1897).

One of the best cultivars, known all over the world, is 'Madame Crozy', a seeded diploid (Belling, 1921), which is orange-scarlet with narrow goldenyellow edge. The trusses are very stiff and the foliage is light green. Earlier varieties of this group were exclusively diploid, but soon, with the increased emphasis on greater durability of flowers and thicker flower parts, autotriploids appear to have been preferred (Fig. 2).

Italian Cannas

These cannas were developed primarily by C. Sprenger (Damman and Co., Italy), and secondarily by Luther Burbank (California), following continued intercrossing, inbreeding and selection of French cannas in which by now all possibilities of further improvement had been exhausted. Both the bree-

ders attempted to revitalise the garden cannas by introducing such „new blood“ as had not been used earlier. Both worked independently and pollinated Crozy cannas with *C. flaccida*, a species from the South Atlantic states of the U.S.A. The cross succeeded in only one direction and the resulting hybrid was remarkable and evoked widespread interest.

Italian cannas were robust, 120–200 cm high, very vigorous and floriferous. The flowers ranged from 12.5 to 17.5 cm in diameter, with strongly reflexed corolla lobes and very broad staminodia. The flowers were broadly open with a hitherto unknown flattened face like the orchid *Cattleya* or a Japanese iris, which gave them the name Orchid, Iris or Giant flowered cannas. Among the first two varieties raised by Sprenger in 1893 (Anonymous, 1898; Clayton, 1895) were 'Italia' and 'Austria'. These were selected out of 1000 seedlings. The former was unusual in the size of flower which was a beautiful golden vermilion colour, while in the latter the colour was yellow shaded with purple. 'Burbank', raised by L. Burbank, was yellow with heavy red spotting on the inner staminodium.

In spite of the overall improvement and magnificent appearance, the flowers in Italian cannas are soft, evanescent and fragile, characters which came from the night-flowering *C. flaccida*. Cytological investigations show that they are asynaptic non-seeded diploids (Khoshoo and Mukherjee, 1970; see also Belling, 1927). 'Bharat', an Indian cultivar of similar origin, belongs to this class (Percy Lancaster, 1967; Khoshoo and Mukherjee, 1970).

Some of the characters of the flowers were disadvantageous, but Sprenger (1901) used pollen of Italian cannas to raise new hybrids which had „still larger, more beautiful, much more resistant flowers and flowering was more abundant than in the earlier orchidaceous cannas“. The first such variety was 'King Humbert', which according to Sprenger was destined to „surprise the horticultural world“. The present investigation shows that this variety is allo- or segmental allotriploid (Khoshoo and Mukherjee, 1970). In contrast with 'Italia' and 'Austria', which are asynaptic diploids and night-flowering, the flowers in 'King Humbert' open in the very early hours of morning as do Crozy cannas.

In all the Italian cannas, whether diploid or triploid, one common characteristic is the strong influence of *C. flaccida* (Fig. 5). They are all totally seed-sterile although partially pollen-fertile (Mukherjee and Khoshoo, 1970a, b), and are better suited to Southern Europe, Italy and subtropical and tropical countries; they do not perform well under northern climates.

Other Hybrids

The foregoing account deals with the chief events leading to the principal hybrid combinations of garden cannas, summarized in Fig. 2. Apart from these,

several other combinations were developed between 1848–1892 (Baker, 1893b). These are briefly described below.

A number of crosses involving *C. discolor* were raised by Année and reported in 1862. These were 120 to 150 cm high with brilliant scarlet flowers and orbicular green or claret-brown leaves.

Maron reported in 1892 a hybrid between the white-flowered species *C. liliiflora* and some Crozy cannas allied to *C. warszewiczii*. The hybrid resembled *C. × ehemanni* in having a short tube but spreading, bright red staminodia about 5 cm long and 2.5 cm broad.

Sprenger crossed *C. flaccida* and *C. iridiflora* and the hybrid had large light green leaves and flowers about 7.5 cm long with a short tube but long obovate staminodia about 2.5 cm broad. He also raised several hybrids between *C. flaccida* and other cannas, and between *C. × ehemanni* and *C. glauca* and *C. discolor*.

Arcangeli obtained three hybrids between *C. iridiflora* × *C. glauca*. These were distinct from both parents and were named *C. 'Raphaelis'*, *C. 'Thomasae'* and *C. 'Clementis'* (Kränzlin 1912).

Most of these combinations, although of not much consequence, may have contributed to the evolution of garden cannas as a whole.

Principles of Selection

It is clear from the foregoing account that the major developments in garden canna took place within about 44 years (1848–1892 A. D.) and the different principles underlying selection among hybrid segregates may now be made clear. Various cultivars were scored for some of the most important characters, such as plant height, diameter and length of flower and breadth of staminodia, that have guided the selective processes (Mukherjee and Khoshoo, 1970a). In the light of other information (Anonymous, 1883–1898; Baker, 1893a–b; Clayton, 1895; Paul, 1893; Sprenger, 1901; Stuttgart, 1898), these data, plotted in Figs. 3–5, are discussed below in chronological order but not necessarily in their order of importance.

Increase in hardiness: *Canna* is essentially a genus of subtropics and tropics. From such a stock there has been selection for hardy characters imparting

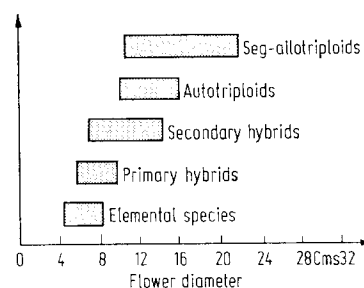


Fig. 3. Histogram showing progressive increase in flower diameter from elemental species to segmental allotriploids

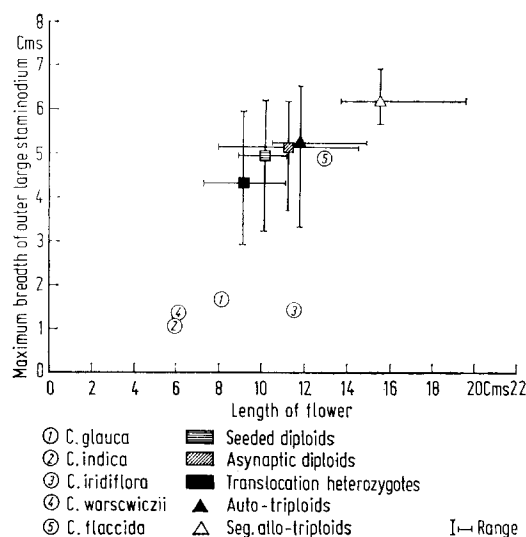


Fig. 4. Scatter diagram showing progressive increase in flower length and breadth of stamens from elemental species to segmental allotriploids

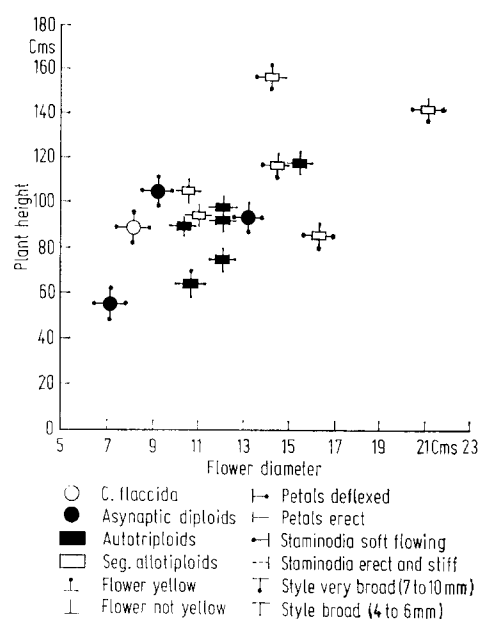


Fig. 5. Scatter diagram showing the involvement and influence of *C. flaccida* in the origin of asynaptic diploids and segmental allotriploids

greater cold resistance. The Crozy cannas are particularly adaptable and are easy to grow in the open in relatively severe European climates.

Reduction in height: Before 1848, botanical species were cultivated for their tall and leafy habit. This was also true of the Année cannas, which were 360–390 cm tall, but soon a trend for dwarf habit set in, and the result was the evolution of French Dwarf or Crozy cannas with a robust and graceful habit. This also resulted in replacement of the original lax habit by compact growth with smaller leaves.

With the introduction of *C. flaccida* in canna breeding, luxuriance in growth habit gave plants of medium height.

Form and colour of leaves: Although the emphasis shifted from leaves to flowers early in the history of canna breeding, form and colour of the leaves was also taken into account along with colour of the flowers because both together made an effective display.

Spikes well above foliage: Selection for this character became imperative in order to make the flowers more conspicuous.

Free flowering: The lower freedom of flowering and restriction of flowering to short seasons in the ancestral species were replaced by free flowering and an extended flowering season in the hybrid cultivars. These characters were associated with seed sterility, resulting from the selection of mechanically self-sterile diploids (e.g. with differences in the height of stigma and stamen), the accumulation of sterility factors in diploids or the selection of triploid types (Mukherjee and Khoshoo, 1970b). All such mechanisms restrict seed setting and therefore enable continued flowering.

Erect flowers: Types were selected with erect instead of pendulous flowers together with inflorescences opening on all sides rather than on only one side.

Increase in flower size: As soon as the emphasis shifted from cannas as foliage plants to cannas for flowers, the success with Ehemann cannas was followed up assiduously until large flowers were produced in Crozy cannas. A limit on size was reached and breeders sought to „revitalize“ by introducing new genes from *C. flaccida*. This was tremendously successful in increasing the flower size further. By 1892 flower length had increased from 6–13 cm in the ancestral species to 7–19.5 cm in the cultivars, diameter from 4–8 cm to 11–21 cm and breadth of stamens from 1–5 cm to 4.3–7 cm.

Colour diversity: From the recombination of genes controlling not only the two basal colours, red and yellow, but also between genes responsible for their intensification and extensification, tremendous colour diversity emerged and was thoroughly exploited. There was a preference for pure, intense colours for bedding types, so as to make them resistant to sun-burn, and light and delicate shades in plants for pot culture.

Circular form of flower: There was an increasing preference for circular flowers to give an appearance to flowers other than that of *Canna*. Hence the names Gladiolus, Orchid or Iris flowered cannas were increasingly given to describe the new diversity in flower form.

Increase in thickness of flower parts and durability of flower: These characters not only made the texture

of the flower parts better and colours more intense, but the flowers also became longer lasting. These, together with the increase in breadth of the staminodia, were the direct result of selection and preference for triploids among otherwise largely diploid cultivars in both Crozy and Italian cannas. All these characters also made the flowers resistant to rain and heat when cannas were grown in the open.

Self-shedding of flowers: Types in which faded flowers were soon abscised naturally and did not remain attached to the flowering stem were preferred.

Future Aims of Breeding

A conservative estimate of the number of canna cultivars developed by European and American breeders would be more than 1000. However, only about 600 are recognized, out of which only about 60 are available today under their original names. The demand for cannas declined considerably after World War I, but there appears to have been a revival of interest in cannas as decorative plants since 1950, when there was a considerable migration of city dwellers to suburbs (Donahue, 1965; Buckley, 1968). Thus there is still hope that the canna can catch up, particularly if more novelties are forthcoming.

Apart from continuing selection along the lines previously discussed, emphasis needs to be placed on developing characters in the following ways.

There is already a large number of colours in pure and mixed form, but blue and a true white are conspicuous by their absence. While blue cannas may not become a reality, from time to time cannas approaching white have been evolved. 'Eureka' is a near-white canna developed in the U.S.A. in 1918 (Donahue, 1965). It may be of some interest that *C. liliiflora* Wars., a rare species from Veraguas on the Isthmus of Panama, is a white-flowered tall canna. This is difficult to cultivate and died soon after its introduction into Europe in the nineteenth century. With this species, or even *C. brittonii* Rusby as the base, one could hope to evolve pure white cannas.

C. liliiflora also has the distinction of being the sole odoriferous canna and this may be useful in evolving scented cannas. In this connection the attempts of Howard in 1896 to cross *Hedychium coronarium* (a scented Scitamineaceae) with species of *Canna* failed totally (Kränzlin, 1912).

The canna flower is in one sense already double because the stamens are in the form of petaloid staminodia. Double flowers were often obtained in radiation-induced mutants by the present writers (Mukherjee and Khoshoo, 1970c) but these were caused by fusion of flower primordia rather than genuine multiplicity of parts, a possibility that remains to be explored in the genus.

Selection of types with considerably branched inflorescences held well above the foliage, and with

flowers that open on all sides and are more lasting and self-shedding, needs to be intensified.

Cytogenetic Mechanisms Underlying Evolution

The origin of garden canna from the 5 ancestral species took about 44 years (1848 to 1892). The changes in the genetic system accompanying the rapid transformation from wild to the cultivated condition may now be examined. Such a study would reveal the nature of the evolutionary steps and clarify the changes that the breeding system and chromosomes underwent. The genetic and cytogenetic reasons for the diversity in garden canna would also be unravelled.

Breeding system

The genus *Canna* is essentially a herbaceous rhizomatous perennial with reasonably showy nectariferous flowers, and such plants are usually predominantly, if not exclusively, cross-pollinated, often accompanied by self incompatibility (STEBBINS, 1950). However, the elemental species under study have small, erect, rather narrowly funnel-shaped, compact flowers which are self-pollinated and self-fertile. The stigma and the half anther lie at the same level before opening of the flower (Mukherjee and Khoshoo, 1970b). Pollen is deposited on or very near the stigma. The present material came from European and American gardens and it is not known if the same situation is found in the wild populations of these species in their native tropical-subtropical habitats. It is also not clear whether this condition is derived from the original cross-pollinated condition, in response to the enforced inbreeding that must have taken place under the temperate conditions of Europe due to the small size of the breeding group and absence of the original pollinators in the new habitats. European gardeners imported the seed of these cannas but not the climate which these plants were used to. In Europe, both natural as well as artificial selection must have acted in selecting for self pollination. This point remains conjectural until a study is made in the native habitat.

At any rate, even now the species have both inbreeding, due to anther and stigma being at the same level, and outbreeding, due to the visits of insects and also sunbirds. However, the diploid cultivars are predominantly cross-pollinated primarily because the anther is about 0.5 to 1.9 cm shorter than the level of the stigma (Mukherjee and Khoshoo, 1970b) and, accordingly, no seed is set if the flowers are bagged, although they set seed after self pollination by hand. These are essentially cross-pollinated under natural conditions. Thus we see that firstly, in the original species self-incompatibility is lacking and there is perfect physiological adjustment between pollen and style. Such a situation may be regarded as a genetic adjustment for avoiding any inbreeding depression which is otherwise an important property

of cross-pollinated species. Secondly, there is a mechanical adjustment between stigma and anther, favouring self-pollination in the species, which is broken down in the diploid cultivars and cross-pollination results. Therefore in the majority of garden cannas outbreeding replaces inbreeding. The partial restoration of such mechanical relationships favouring self-pollination in some triploids, particularly the segmental-allotriploids, is of no consequence because of their total sterility. Thirdly, the sexual and vegetative modes of reproduction could enable the selection, fixation and perpetuation, both under natural and garden conditions, of almost any genotype, irrespective of the extent of its fertility, provided it has some adaptive value in nature or under garden conditions. In the absence of sexual fertility, a serious disadvantage of vegetative reproduction is that it imposes a limitation on the extent of improvement. Some of these features have attendant genetic implications which have been discussed in this section (Khoshoo, 1968).

Mutations

The good chromosomal pairing and reasonably high fertility and recombination among some of the ancestral species, particularly *C. glauca*, *C. indica*, *C. warszewiczii*, *C. discolor*, *C. humilis* and *C. aureo-vittata* (Honing, 1928; Offerijns, 1935; Oomen, 1948; Khoshoo and Mukherjee, 1970), show that in most of them differentiation is essentially at the genic level. Gene mutations are of primary importance for morphological, physiological and genic differentiation of the species. In fact this property has permitted wide recombination between some of the species and enabled the release of new variability. It is possible that during this process some of the recessive mutants, ordinarily covered or masked in the species in their native habitat, may have been released, as has happened in the case of recessive mutation for extended blooming period and pelargonidin in roses (Wylie, 1955; Darlington, 1963). The release of these two recessive genes has revolutionized rose breeding (Pal, 1966). This may have taken place among the large number of canna cultivars but it is also possible that some may represent spontaneous gene mutations for colour, etc., that have been selected and propagated as new cultivars. The most obvious spontaneous mutations in this case are somatic in nature.

The detection of somatic mutations has been greatly helped by the constancy imparted by clonal propagation in canna. Several spontaneous somatic mutations have been recorded which involve leaf variegation, colour changes, change of floral parts (Mukherjee and Khoshoo, 1970c), etc. There is also a close parallelism between spontaneous and induced somatic mutations, greatly aided by the heterozygous nature of cultivars which are likely to show more somatic variation than homozygous cultivars. Some of these variations are rather more frequent in poly-

ploids than in diploids (see also Crane and Lawrence, 1952).

Most of the somatic mutants in canna have the appearance of sectorial chimeras but are actually mericlinal in nature. They may occur at any stage of development with results ranging from small colour changes in the form of spots or stripes, to changes in a complete staminodium, whole flower and also whole inflorescence in 'Queen of Italy'. The detailed investigation of 'Queen of Italy' *vis-a-vis* 'King Humbert' has shown that the latter may be regarded as 'Queen of Italy' with an over-play of red colour in the staminodia. 'Queen of Italy' has actually arisen from 'King Humbert' and the former reverts to its ancestral or near ancestral condition (Mukherjee and Khoshoo, 1970c).

The tendency of 'Queen of Italy' to revert may indicate either its chimeric nature and reassortment of tissues, or a mutation in the unstable nuclear gene (or genes) responsible for red colour. If the latter, it could be a real back-mutation involving the original mutational site or may involve the gene (or genes) responsible for suppressing red colour in 'Queen of Italy'.

The present investigations support the theory that the 'Queen of Italy' has arisen as a periclinal chimera from 'King Humbert', and thus the role of somatic mutations in the origin of new garden cultivars in *Canna* is clarified. However, because of total sterility the exact cytogenetic nature of this somatic mutation is not known. This example, together with the similarity in leaf variegations and flower abnormalities between natural and induced mutations investigated by the writers and Nakornthap (1965), shows the role somatic mutations have played and can play in the origin of new cultivars.

As pointed out earlier, the heterozygous nature of the cultivars, resulting from excessive hybridization, may be conducive to an increased mutation rate so that bud sports or somatic mutations are a very important source of new cultivars in vegetatively propagated ornamentals like canna. One of the best examples is the rose (Wylie, 1955; Darlington, 1963; Pal, 1966).

Yet another way in which mutations have been responsible for the evolution of new cultivars in canna may have been the inadvertent selection of mutations responsible for increased cell size. This may have helped in the origin of shorter and sturdier growth habit and larger flowers even though chromosome number continued to remain at the diploid level. Such a trend occurs widely and has accompanied the origin of many cultivated plants (Schwanitz, 1951, 1959; Khoshoo and Singh, 1966).

Chromosomal repatterning and differentiation

The present data (Khoshoo and Mukherjee, 1970) indicate that out of about 54 species belonging to the genus, the 14 worked out so far are all diploid based

on $x=9$. The karyotypes resolve into 9 homomorphic pairs. Meiosis is normal both in the species and in the seeded cultivars of *C. generalis*. However, chiasma frequency in the former is higher (from 17.08 to 17.48 per cell) than in the cultivars (15.65–17.50). Pollen and seed fertility are lower in the cultivars. In the non-seeded cultivars of *C. orchoides*, meiosis is either apparently normal or shows varying degrees of asynapsis and low chiasma frequency, 5.76 to 9.00 per cell. They also show some karyotypic heteromorphism. As is clear from the analysis of characters and the history of canna breeding, the partially asynaptic group of non-seeded cultivars shows the direct influence of *C. flaccida* (Fig. 5). From these data it appears that while the elemental species involved in the origin of *C. generalis* are sufficiently close genetically, they are also reasonably differentiated and there appear to be definite genic and/or cryptic chromosomal differences between them which affect chiasma frequency, pairing and fertility. This is corroborated by the generally normal meiosis with low frequency of univalents found in two interspecific hybrids, *C. glauca* \times *C. indica* (Honing, 1928 = *C. glauca* \times *C. discolor* of Offerijns, 1935; see also Honing, 1939) and *C. aureo-vittata* \times *C. humilis* (Khoshoo and Mukherjee, 1970) but both have somewhat reduced fertility. This may be due to disharmonious combinations resulting from not completely homologous chromosomes. In view of the lack of gross segregational errors, sterility in hybrids and cultivars appears to be the result of segregation of minute cryptic structural differences. The species *C. discolor*, *C. humilis* and *C. aureo-vittata* form another complex. According to Honing (1939) these are all varieties of the same species in which differentiation depends upon a relatively small number of Mendelian factors.

The only discernable chromosomal rearrangement is the occurrence of interchange heterozygosity in about 3% cultivars in *C. generalis* (Khoshoo and Mukherjee, 1966, 1970) and in *C. glauca* \times *C. indica* (Honing, 1928) and *C. glauca* \times *C. discolor* (Offerijns, 1935). In the three cultivars, 'Electra', cv. 153 and cv. 196 of *C. generalis*, two heteromorphic pairs of chromosomes have been noticed in the karyotype which can be correlated with an interchange complex of 4 chromosomes during meiosis. The complex is generally in the form of a non-disjunctional ring. Out of the three, cv. 196 is totally sterile and the others are reasonably so. Interchange heterozygosity seems to be operative in the differentiation of the species and also in the origin of garden cultivars. The possible value of the three cultivars for selection lies in the colourful flowers in 'Electra' and cv. 153, and the pygmy habit and very small (the smallest in *C. generalis*) but colourful flowers in cv. 196. Because all these cultivars are vegetatively reproduced, the predominant occurrence of non-disjunctional arrangement in them is in total contrast to the position in

sexual species where, for proper incorporation of the interchange into the genetic system, disjunctional arrangements are selected. Again, fertility is of no consequence here because of the vegetative reproduction (Khoshoo, 1968).

Hybridization

In recent years there has been a better appreciation of the role of hybridization (unaccompanied by polyploidy) as a genetic mechanism in the origin of taxa with totally new characters, than was the case when Lotsy (1916) published his classical work. Stebbins (1956, 1959) believes that this could happen in three ways: transgressive segregation; latent mutations with an adaptive value in the new genetic background; and increased mutation rate in the hybrid condition perhaps as a result of elimination (through recombination) of mutation suppressors. Before any of these mechanisms could operate, the main prerequisite would be compatibility between the two hybridizing species (Khoshoo, 1968).

The occurrence of good chromosomal pairing, accompanied by few meiotic irregularities, and fertility between some of the species, *C. glauca*, *C. indica*, *C. warszewiczii*, *C. discolor*, *C. humilis* and *C. aureo-vittata* (Honing, 1928, 1939; Offerijns 1935; Oomen, 1948; Khoshoo and Mukherjee, 1970), shows that differentiation is essentially at the genic level. In view of the low restriction on homology, high recombination and vigorous progeny, the differentiation between the parents may be at an ecospecific level. Probably the only barriers are ecogeographic, preventing these species from hybridization under natural conditions. While most of the elemental species show predominantly morphological differentiation unaccompanied by barriers to interbreeding, *C. flaccida* shows a high degree of genetic differentiation because all the hybrids between Crozy cannas and *C. flaccida* have a highly reduced degree of pairing (Belling, 1927; Khoshoo and Mukherjee, 1970) and lack of fertility. This was the last species to be introduced into canna breeding.

It is now well established that wild species usually contain new „gene pools“ whose action is generally suppressed by inhibitors (Clausen, 1951). This is very clear from the work of Honing (1923–1942), who used *C. indica*, *C. glauca*, *C. humilis* and *C. aureo-vittata*, mostly the first two, to study the genic basis of stem height, colour, length, breadth and wax coating of flowers, flower colour (red, yellow, yellow flaked with red), number of staminodia, length and breadth of staminodia, dehiscence of fruit, and seed size and shape. He paid particular attention to flower colour which may be deep scarlet (due to bluish-red anthocyanin in the cell sap and deep yellow plastids) as in *C. indica*, or pale yellow (due to plastids) as in *C. glauca*. The former is a monogenic dominant over non-red i. e. yellow. Although there are not

enough data for some and others need verification, he established 18 genes firstly and added 7 more subsequently.

The different genes together with the trait they control are briefly listed below:

A: Anthocyanin pigment for red flower colour.

B and *C*: Red leaf margin.

D, *E* and *F*: Intensification of the effect of *A* and *R*.

G: Extensification of anthocyanin in leaves.

H and *I*: Deep yellow plastids.

J: Deeper vein colouration, perhaps also central red colouring in a yellow margin.

K and *L*: Wax layer on leaves.

M, *N* and *O*: Third staminode.

P: Extensification of central red colouring in yellow border.

Q: Lethal.

R: Red patches in yellow flowers.

S: Red flaking on yellow background.

T to *T*₃: Balanced lethals linked with *S* and *s* in *C. glauca* 'Java' and 'Montevideo' and absent in 'Bolivia'.

U: Lethal in recessive condition (*u*) with *s*, but not with *S*.

V: Red leaf margin, perhaps complementary with *B* and *C*.

W: Inhibitor for purple, *ww* causes purple in *ss* plants.

On the basis of the analysis presented by Honing (1923–1942) the various species are represented below:

C. indica: *AA BB (CC) DD (EE) FF gg HH II jj kk ll (mm nn oo) pp qq rr SS VV*

C. glauca: *aa bb (cc) Dd ee ff G. hh ii Jj Kk L. (M. N. O.) Pp Qq Rr vv*

The five races of this species are differentiated as:

'Bolivia': *SS WW or SS ww*

'Java': *S T₁ t₂ t₃/S t₁ T₂ T₃ WW*

'Montevideo': *S T₁ t₂ t₃/s t₁ T₂ T₃ ww*

'Pure yellow': *ss WW*

'Old purple': *ss ww*

C. humilis: *AA bb HH II vv*

C. aureo-vittata: *aa bb hh ii vv*

The doubtful genic components are within brackets; for those marked by a point, it is not known whether a particular gene is present in homo- or heterozygous condition. Several data suggest linkages.

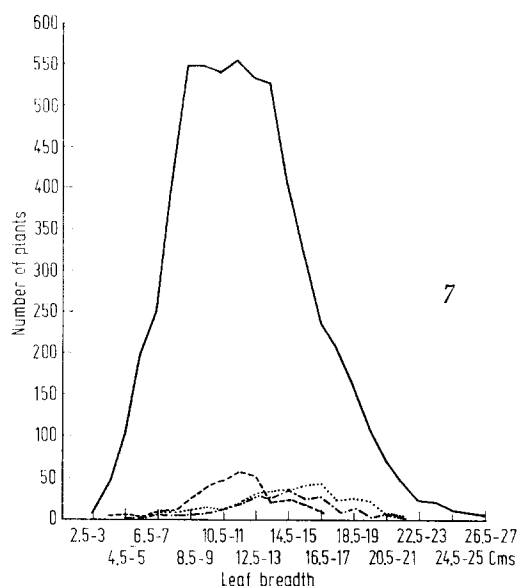
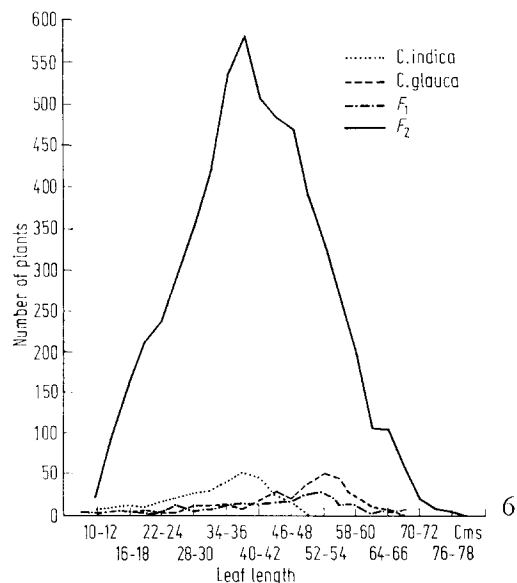
As stated earlier, one of the first interspecific crosses involved in the origin of garden canna is *C. indica* × *C. glauca*, and between these two species there is a large number of differences; in flower colour, both sap-soluble and plastid pigments are controlled by several genes involving colour genes proper and their intensifiers, inhibitors, lethals, etc. From the recombination of such a wide range of genes, se-

gregating simultaneously and involving complex segregation, a wide array of homo- and heterozygous genotypes with new colours and colour combinations is expected to arise. Furthermore, similar segregation is expected in plant height, blooming period, flower size, and texture and colour of staminodia. Under the circumstances, recovery of the parental types is difficult and new combinations of characters with new phenotypes are expected to arise (see also Clausen and Hiesey 1958; Stebbins 1959).

The recombination between red and yellow, which are the two basic colours in the genus, is of particular interest. The red colour is an anthocyanin and is sap-soluble. The yellow is a plastid pigment and is structurally different from anthocyanin. There is no direct interaction between sap-soluble anthocyanins and plastid pigments. In the absence of anthocyanins, plastid pigments are responsible for flower colour, but in its presence the effect of plastid pigments is purely that of a background colour. Although red flower colour is monogenic dominant, intensity of colour, flaking, etc., are controlled by several genes whose ratios are disturbed by linkage, lethal genes, etc. Inheritance of red leaf margin is also complex.

The *F*₁ of *C. glauca* (yellow) × *C. indica* (red) was fiery red and in the *F*₂ there were 11 shades of red colour under the influence of different shades of yellow. There were 4 different types of flaking of red and differences in size and intensity of red flakes (Honing, 1923). This background effect of different shades of yellow, together with mutation and or recombination in genes controlling and affecting red colour and changes in cell pH, may be responsible for the great variety of colours that emerged from the original yellow and red. This was possible only after the barrier between species possessing two colours broke down.

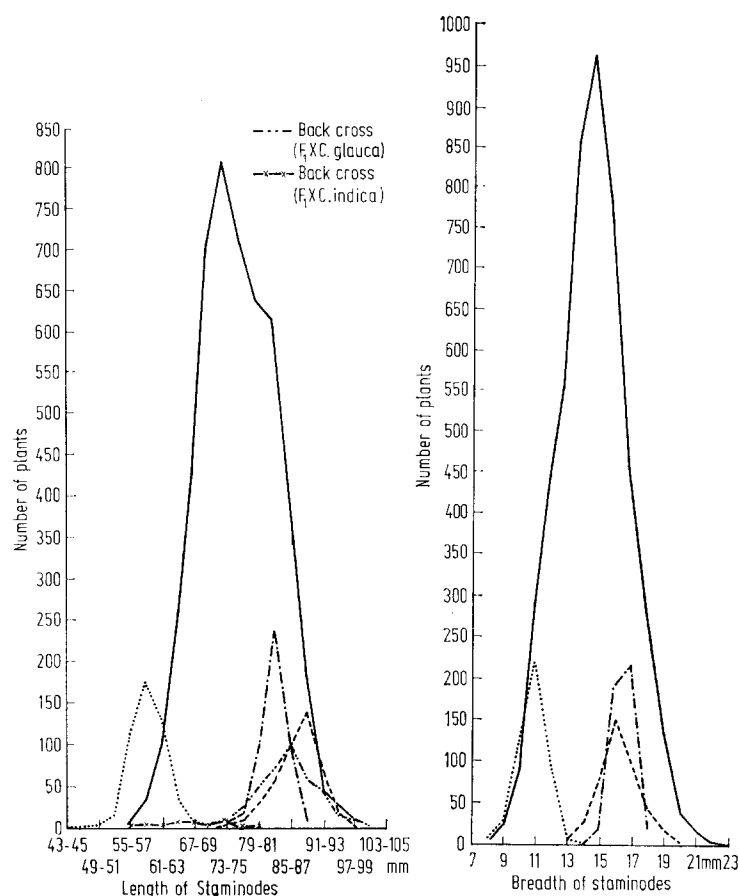
Analysis of the data of Honing (1923, Tables 1, 2, 17 and 18) gives strong indications of transgression in the length and breadth of leaves and, what is most pertinent to canna breeding, of staminodia. In order to bring out this point, Honing's data were plotted in Figs. 6–9. Plants with new types of leaves shorter than those of *C. indica* and narrower than *C. glauca*, also arose. What is more important, in backcrosses to *C. glauca*, the length of the staminodia was increased further and registered an increase in the mean. Coupled with such transgressive segregation significant cases of luxuriance (sensu Dobzhansky, 1950, 1952), affecting not only plant height but particularly length and breadth of staminodia and flower size, were observed in all hybrids between Crozy cannas and *C. flaccida*. In essence, one of the most important single factors responsible for the evolution of garden canna is hybridization in that it has been responsible for the origin of new recombinants, transgressive segregation and luxuriance. Transgression was exploited repeatedly to build up very large flower



Figs. 6—7. Graphs of leaf length and breadth in *C. indica*, *C. glauca*, F_1 and F_2

size which was combined with other useful vegetative and floral traits like colour and number of flowers per inflorescence, blooming period, etc.

One of the most significant examples of transgression in flower size has been recorded by Smith (1953) in the progeny of crimson-flowered ornamental *Nicotiana alata* \times *N. langsdorffii*. Individuals with flowers larger than those of either parent could be fixed by selection. According to Smith, flower size can be increased much beyond the present limits only by recombination. Transgression in number of flower parts beyond the normal of 5 was reported by Grant (1956) in *Gilia* hybrids. Coupled with the transgression a reasonable degree of isolation developed in *Nicotiana* (Stebbins, 1959).



Figs. 8—9. Graphs of length and breadth of staminodes in *C. glauca*, *C. indica*, F_1 , F_2 and back crosses

Much genetic diversity has been released from fertile or semifertile interspecific *Canna* hybrids, and, although many of the recombinants may have been inferior, some that showed favourable character combinations accompanied by transgression must have been of interest to canna breeders. Thus the possibilities and limits of selection were increased by hybridization (Khoshoo, 1968).

Generally, important characters are polygenic in inheritance and the genetic mechanism responsible for transgression and luxuriance probably involves the accumulation in intervarietal or interspecific hybrids of dominant favourable genes and/or coadapted heterozygous combinations which cover the recessives responsible for the restrictions in size in the parental cultivars or species (see also Dobzhansky, 1950; Crow, 1952). It is also possible that some genes of one parent interact rather more favourably with those of the other parent than when they are in their own genotype. Such recombinants are very useful.

Once such size barriers broke, the transgressive segregates and F_1 hybrids with luxuriance were immediately fixed in canna through vegetative reproduction. However, in sexual taxa this can also be achieved by inbreeding which permits accumulation of the

most favourable gene complexes or alleles in a homozygous condition, as in *Nicotiana rustica* (Smith, 1964).

The parental species, *C. indica*, *C. glauca*, *C. iridiflora* and *C. warszewiczii*, are reasonably interfertile. Many of the cultivars arising from this species complex at diploid level, are seeded while others at diploid and triploid levels are totally sterile. Even in the seeded types, seed germination is rather poor because of embryo degeneration. Cultivars with low pollen sterility are seeded, but those with higher pollen sterility are non-seeded, as also are autotriploids. With the introduction of *C. flaccida*, all hybrids, whether at diploid or at triploid level, are totally sterile. This may be the result of strong genic differentiation between Crozy cannas and this species. Although most of the above species, except *C. flaccida*, are genically related, some amount of sterility always ensues due to segregation and recombination. This is the result of the disharmonies arising from genetic inviability caused by rings, chains and cryptic rearrangements, all of which indicate some lack of structural homology. Although a very large number of recombinants is possible, some may be eliminated because of genetic inviability. However, vegetative reproduction has been very important in counteracting partial or complete sterility in garden cannas as in diploid and segmental allotriploid cultivars involving *C. flaccida*. Vegetative reproduction is also helpful in fixing the useful variability arising from interspecific hybridization and recombination in spite of the extreme heterozygosity of the recombinants (Khoshoo, 1968). An indication of the extent of heterozygosity of most of the seeded cultivars can be obtained from the fact that most, if not all, of them never breed true to type. However, vegetative reproduction also has its own limitations. Continued vegetative reproduction may help the accumulation of the lethals causing sterility, as has happened in *Pelargonium* (Daker, 1967). Without sexual reproduction such mutations do not have a chance to get eliminated.

Similar progress has been made by consistent hybridization over a period of 60 years in begonia, where the flower is now five times the size of the original, and there has been developed a tremendous range in flower colour and other useful characters like profusion and persistence of blooms, vigorous growth, fringed forms and the ability to grow as pot plants out-of-doors (Legro, 1964). As in canna, such progress has been possible because of the ecospecific differentiation of the parental species with a large number of genetic differences and rather high mutation rate.

Polyploidy

Next to segregation and recombination in the interspecific hybrids, polyploidy has been an important mechanism in the origin of new cultivars in garden canna (Khoshoo and Mukherjee, 1970). The effective

level of polyploidy has been triploidy, although tetraploids must have arisen in the course of innumerable crosses, as happened in *Narcissus*, *Hyacinthus*, etc. That they arise spontaneously under garden conditions in *Canna* species, both through somatic and gametic doubling, is clear from the experiments of Honing (1931) and Oomen (1948). However, as remarked by Oomen (1948), tetraploids cannot compete with diploids because of their slow growth and low fertility. This is also borne out by the present experiments on one parental species and two cultivars of garden canna (Khoshoo and Mukherjee, 1970). All attempts to induce tetraploidy in the latter failed probably because cell size has reached an optimum and further increase has deleterious consequences on normal physiology, metabolism and fertility. It is clear that triploid level is the optimum level both in garden canna and *C. edulis* (Mukherjee and Khoshoo, 1970d).

Two types of triploids have been found: autotriploids among the Crozy cannas and *C. edulis*; and allo- or segmental allotriploidy in hybrids resulting from the use of pollen of the first Italian cannas (Crozy cannas \times *C. flaccida*) on Crozy cannas. In both types of triploids there has been doubling only on one side (Khoshoo and Mukherjee, 1970; Mukherjee and Khoshoo, 1970d).

The autotriploids may well be the result of self or cross fertilization among Crozy cannas. They do not appear to result from any of the self incompatibility systems such as those in *Tulipa* and *Pyrus*, where unreduced gametes are selected in fertilization in preference to reduced ones (Lewis, 1943). Autotriploid cannas are the result of chance fertilization between reduced and unreduced gametes in diploid Crozy cannas. They have been selected because of their somewhat larger flowers, thicker vegetative and floral parts, rather more intense colours, longer duration of blooms, etc. (Khoshoo, 1968).

The crossing of Crozy cannas with *C. flaccida* has resulted initially in asynaptic diploids, but segmental allotriploids arose from subsequent crosses using pollen of the initial hybrids. In such triploids, there has been a very significant increase in size of flower; the largest (21 cm) known in any canna belongs to this class of triploids.

Unlike triploids in other ornamentals such as hyacinth, both auto- and allotriploids in canna are totally seed-sterile although they have 40 to 70% pollen stainability. The pollen is unable to grow and/or fertilize eggs in triploids, so that we do not have the whole series of forms, with chromosome numbers ranging from diploid to tetraploid, found in hyacinth where some of the aneuploid forms themselves became important cultivars (Darlington, Hair and Hurcombe, 1951). With this in mind, the present writers made many attempts to raise some aneuploids by making $3x \times 3x$, $2x \times 3x$ and $3x \times 2x$ pollinations but with no result (unpublished data).

The sterility associated with polyploidy is a definite bottleneck to future possibilities in canna breeding. In roses, where triploids also proved to be problems, full fertility was restored through the production of rare tetraploids from triploids. Accordingly, although there are some well known triploid roses, a new era in rose breeding was ushered in by the production of tetraploids from triploids (Pal, 1966). All attempts to do this in canna have failed so far.

Of the two types of triploid cannas, the Giant, Italian or Orchid flowered have inherited the short-lived, large and somewhat delicate flowers (which are fewer per inflorescence) from *C. flaccida*. Also they are taller than the autotriploids within Crozy cannas.

Good examples of valuable triploids in vegetatively propagated ornamentals are reported in Japanese cherry, *Narcissus*, *Iris*, *Gladiolus*, etc. In most of these cases, the origin of the polyploids is the inadvertent selection for valuable properties associated with polyploid ornamentals *per se*.

Conclusions

In essence, plant breeding is plant evolution under the direction of man. Taking this view, garden cannas offer an example where the ancestral species are native to subtropical-tropical regions of the West Indies and Central and South America, but the evolution of cultivated types took place under the temperate environment of Europe, i. e. far away from the centre of origin of the genus (Fig. 1). Such change in habitat in itself may have induced considerable modifications in the genetic system of the ancestral species. This is particularly possible when extensive hybridization took place under the influence of man; this was begun in 1848 with Année, going on to 1892 under Sprenger and Burbank. Plants evolve very rapidly under domestication and latent or unexpressed genetic variability stored in the ancestral species is exploited to the fullest extent in ornamentals particularly with changes in the fashions, fads and fancies of man.

Primarily, the factors for selection have revolved round the shift of emphasis from cannas as foliage plants in the middle of the nineteenth century to cannas for colourful and large flowers and greater adaptability to cold climate. This affected the type of inflorescence, blooming period, durability, flower shape, etc.

Crozy or French Dwarf and Italian or Giant flowered are the two main classes of cannas. At least four species have gone into the production of the former group, and just when continued interbreeding, inbreeding and selection had ceased to be effective, Crozy cannas were outcrossed to *C. flaccida*, with remarkable results in vigour and increased flower size, to give rise to the Italian group.

During the 44 year period (1848–1892), particularly the last 24 years (1868–1892), opportunities for very rapid evolution were provided and much of the

transformation was effected. Among the different genetic-evolutionary processes involved, hybridization, to be exact selection among hybrid segregates, has been the most important single factor.

The parental species of canna contain numerous genes often of the multiple type which together form a stable system. When such gene systems, originally separate, were brought together by early breeders and the original ecogeographic barriers between them broke, a tremendous amount of variability was released, enabling the rapid evolution of the garden cultivars by man. This variability covered most of the vegetative and floral characters. Particular attention was paid to variation in flower colour and size which are controlled by different colour genes, intensifiers, inhibitors, lethals, etc. The colours are both sap-soluble and in the plastids. A wide spectrum of types was released, largely through recombination, and useful ones were fixed and further moulded by selection. Some of the segregants and backcrosses showed transgression particularly in flower size and colour and some other hybrids showed luxuriance. Man has tried to exploit both these properties in cultivated plants and even in domestic animals. All these characters were fixed by vegetative reproduction. Therefore, in cannas, crossing increased the possibilities and limits of selection and breeding by hybridization and recombination led to the evolution of types of much ornamental value. The new types may be the result of either new gene combinations, the release of rare recessive genes already present in the species or new mutations.

Repeated cycles of interspecific hybridization followed by selection have also played a very important role in several vegetatively reproduced ornamentals such as roses, irises, gladioli, tulips, rhododendrons, begonias, etc., where the demand is for novelty in flower size, shape and colour, quality of blooms, etc. So far such hybridization has been done empirically by gardeners, but with a better knowledge of the genetics of the parents such a programme could be carried out with definite aims.

Next to hybridization, polyploidy has been important in the evolution of garden canna. This has appeared in the two chief categories of cannas, Crozy and Italian. Both groups began as diploid but soon individuals with better texture and thicker flower parts, imparting greater durability and flower size, were preferred. Such individuals were triploid, particularly in Italian cannas where the flowers were originally rather soft and evanescent and wilted early. The triploids in Crozy cannas are autotriploid in character, while those of Italian cannas are segmental allotriploid. The autotriploids in Crozy cannas indicate less differentiation of the genomes of the four ancestral species which have recombined to form this class. In fact they appear to be at ecospecific level which in itself has aided large-scale recombination. The differentiation of the genome of *C. flaccida* is

apparent both from the asynaptic meiosis of the diploid, and from the allo- or segmental allopolyploid nature of the triploid Italian cannas.

Although tetraploids have appeared under garden conditions in *Canna* species (Honing, 1931; Oomen 1948), triploidy appears to be the highest effective level of polyploidy achieved. This is also true of cannas yielding starch (*C. edulis*). Perhaps cell size increases to an optimum at this level and higher levels, as well as aneuploid progeny, are not possible because of total seed sterility. Therefore, unlike hyacinth, also a vegetatively reproduced ornamental, unbalanced progeny is not possible.

Under all circumstances, mutations are the most important source of variation. The differentiation of several parental species seems to be at the genic level because of the near-normal recombination and fertility in the ensuing generations. The most obvious mutations are the somatic mutations of which several have been observed. These are variegations in foliage, and colour changes in flowers. They have been responsible for the production of new cultivars and often such changes are reversible. In plants like canna, detection of even small changes in phenotype is possible because of the constancy imparted through clonal propagation. If in pure form, these in turn can be preserved, although they may involve a good deal of sexual sterility.

The last change in order of importance is the chromosomal repatterning which involves cryptic structural hybridity and interchange heterozygosity. The latter, coupled with vegetative reproduction, may be regarded as a way of preserving structurally hybrid combinations. Some of the interchange heterozygotes are attractive cultivars which seems to have helped in their preservation.

The two groups of ornamental cannas, Crozy, French Dwarf or Gladiolus, and Italian, Orchid, Giant or Iris flowered cannas, belong to two different synthetic species of hybrid origin. These are, *C. × generalis* Bailey and *C. × orchoides* Bailey respectively. The former contains diploids, interchange heterozygotes and autotriploids, while the latter contains non-seeded asynaptic diploids and allo- or segmental-allotriploids (Mukherjee and Khoshoo 1970d).

Selection for the two principal uses of canna involves not only different organs but what is more important, has been undertaken in contrasting environments: in the ornamental canna selection for floral parts has been made in European environments, a habitat unknown to cannas; selection for starch content has involved the rhizome in its native habitat in the West Indies and South American tropics-subtropics. It is interesting to find that in both cases selection has ended in triploidy. Triploidy in ornamental types produces enlarged flowers with less effect on the rhizome, while in starch-yielding types it has enlarged

the fleshy rhizome but affected the flower to a very limited extent.

If the situation in the *Canna* species studied so far is representative of the genus in its wild condition, then they seem to have been differentiated essentially by gene mutation and repatterning of the chromosomes. However, under the influence of man, selection among the segregates from interspecific hybrids and polyploids is able to speed up evolution. This difference in evolutionary rates, with and without the influence of man, is caused by the tremendous changes to which the species have been subjected, creating a great effect within the short period of 24 years (1868–1892).

So far canna breeding has been somewhat empirical, being based on an intuitive approach by breeders. However, if it is pursued on genetic considerations, there may be better utilization of the untapped variation. Perhaps new ground can be broken in colour, form and size of flower which themselves are under complex genetic control.

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Received January 8, 1970

Communicated by H. Stubbe

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