3 Classical Genetics, Cytogenetics, and Traditional Breeding in Castor Bean

C. Lavanya, A. Vishnuvardhan Reddy, Bhramar Dutta and Rajib Bandopadhyay

Abstract

Castor being a perennial, cross-pollinated, sexually polymorphic crop with high environmental sensitivity, initial plant breeding efforts were restricted to plant height and duration. Domestication of a wild, perennial crop to an annual crop of medium plant height and duration is the first success. Further, development of a two-line breeding system and standard seed production technology led to successful commercial exploitation of heterosis. Being a monotypic genus, diversification of parental base is restricted to intra-generic, intraspecific, or inter-varietal hybridization. Phenotypic expression is highly plastic and varies with locations and seasons. Majority of the morphological characters are monogenic, independently assorted with very limited linkages among the traits. However, information on genetics of major morphological characters is scattered in several old publications. Conventional breeding methods were successful in developing about 40 high-yielding hybrids and varieties with inbuilt resistance to major pests and diseases. An effort is made in the present chapter to consolidate the information on genetics and breeding methods followed in India and elsewhere.

3.1 Introduction

The castor plant, a member of Euphorbiaceae or spurge family, is a commercially valuable, non-edible oilseed crop due to its high yield potential even under optimum management conditions. It is an ideal commercial crop due to its high oil content (45–55%) of seed with high levels of a unique fatty acid, ricinoleic acid (80–90%). Ricinoleic acid (12-hydroxyl-*cis*-9-octadecenoic acid) has more than 250 industrial uses in addition to biofuels. Castor is cultivated in more than 29 countries over an area of 14.48 lakh ha with a production of 19.48 lakh tons and productivity of 1346 kg/ha (2015–16). India has the largest area of 8.3 lakh ha with a production of 14.2 lakh tons and 1713 kg/ha productivity. Though indigenous to Eastern Africa and Ethiopia, it is reported as polyphyletic in origin with four major centers of diversity, viz. Iran–Afghanistan–(former) USSR region, Palestine–South West Asia, India–China, and the Arabian Peninsula.

Castor, a drought-tolerant crop, usually grows well in relatively dry and warm regions having a well-distributed rainfall of 500–750 mm. In

C. Lavanya (✉) · A. Vishnuvardhan Reddy
ICAR-Indian Institute of Oilseeds Research, Hyderabad 500030, Telangana, India
e-mail: c.lavanya@icar.gov.in

B. Dutta · R. Bandopadhyay
Department of Botany, UGC-CAS, The University of Burdwan, Golapbag, Burdwan 713104, West Bengal, India

C. Kole and P. Rabinowicz (eds.), *The Castor Bean Genome*, Compendium of Plant Genomes,
https://doi.org/10.1007/978-3-319-97280-0_3

heavy rainfall areas, the crop puts an excessive vegetative growth and assumes a perennial habit. Castor requires a moderate temperature (20–26 °C) with low humidity throughout the growing season to produce maximum yields. A *kharif* crop is also being cultivated as a *rabi* crop in southern states like Telangana, Andhra Pradesh, Tamil Nadu, and Odisha with assured irrigation. The crop can withstand long dry spells but cannot establish under waterlogging conditions.

3.2 Monotypic Genus

Ricinus is a monotypic genus, and the species *communis* is subdivided to six subspecies, viz. *persicus, chinensis, zanzibarinus, sanguineus, Africans,* and *Mexicans* based on eco-geographical grouping (Kulkarni and Ramanamurthy 1977; Moshkin 1986; Weiss 2000). The species *R. communis* was also considered as a composite species (sp. *collectiva*) with three elementary species, while many considered this species as a monotype. There is no difference in the chromosome number ($2n = 20$) among the subspecies, and they all can cross easily with each other (Kulkarni and Ramanamurthy 1977; Atsmon 1989). Genetic variability though restricted to intraspecific variability, variable phenotypic expression due to its cross-pollinated nature and independent assortment of several phenotypic characters provided a wide genetic base for the breeders.

3.3 Cytogenetical Studies

The somatic diploid chromosome number of *R. communis* is $2n = 20$. The karyotype analysis indicated that chromosomes differ in size (4.6–19.2 µM) and distribution of heterochromatin. Castor is considered to be a secondary balanced autopolyploid with $N = 10$ (Richharia 1937). Based on the maximum number of secondary associations (5) observed at I and II metaphases, the haploid constitution was postulated as AAA, BB, CC, DD, E. Polyploidy has been induced using colchicine (0.3%) on apical meristems (Narain 1953). Increase in stomatal size and decrease in stomatal density were observed in colchicine-induced tetraploids of three castor genotypes, viz. 48-1, DCS-107, and AP-41 (ICAR-IIOR 2017). Pollen fertility varied from 0 to 35% in 48-1 and AP-41 mutants, while quadrivalent associations were more frequent in the tetraploid mutants.

3.3.1 Idiogram

The idiogram is constructed in different species of *Ricinus* to correlate the chromosome morphology variation with respect to changes in sex expression. Jakob (1956) has shown that each ten chromosome pairs of the compliment is easily morphologically distinguishable in pachytene stage of meiosis cell division, by the regions which stained deeply with acetic orcein. “Chromatic” region for deeply stained zones was coined by Brown in 1949 in *Lycopersicum esculentum.* Macro-chromosome-bearing region of pachytene chromosome of *Ricinus* sp. apparently supports the view. The micro-chromomere of the chromatic zone is not clearly distinguishable, whereas the achromatic zone, flanking both sides of the chromatic zone, shows the presence of lightly stained micro-chromomere. The ten pairs of chromosomes were numbered by Paris et al. (1978) in numeric fashion, whereas Alexandrov and Karlov (2016) marked the chromosomes pairs in alphabetic order. Paris et al. in (1978) described the details of chromosome morphology. It is clear from Fig. 3.1 that Chromosome 1 is the longest and least heterochromatic chromosome of the complement. Chromosome 2 is the main nucleolar organizer (NOR). Chromosome 3 contains proximal heterochromatic region. Chromosome 4 is second longest chromosome after Chromosome 1. Chromosome 5 is metacentric as it has two arms almost equal in length. In Chromosome 6, centromere is flanked by one large chromomere in long arm and proximal chromomere is in the one-third way of centromere. A NOR region is present in Chromosome 7 as of Chromosome 2.

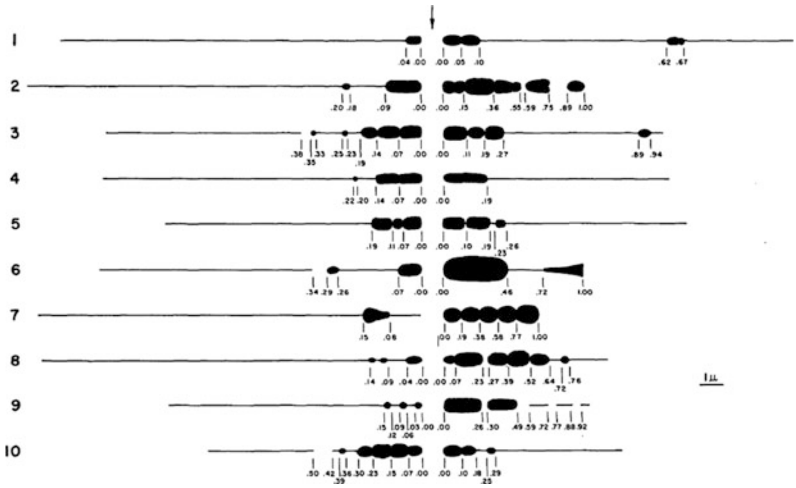

Fig. 3.1 Idiogram of ten pachytene bivalents of *Ricinus communis*; where centromere represented by arrows, long arms are in the left side and short arms are in the right side, euchromatic regions are the thin line and thickened lines represent heterochromatic regions. The space between the lines represents secondary constriction. Adapted from: Paris et al. (1978)

However, the NOR in chromosome 9, previously reported by Jelenkovic and Harrington in 1973, was not confirmed. Chromosome 8 is more or less similar with Chromosome 4. Chromosomes 9 and 10 are the shortest.

3.3.2 Molecular Cytogenetics of Castor Bean

The study of molecular cytogenetics spread some light on genome sequencing of castor plant. The organization of the major DNA repeat sequences can be studied by fluorescence in situ hybridization (FISH) mapping. Earlier, several authors (Paris et al. 1978; Zhong et al. 1996) characterized pachytene chromosome by high-resolution FISH technique. But FISH-based mapping done for the first time showed that 45S rDNA and 5S rDNA signals on the pachytene chromosome are on the short arm; contrarily, Vasconcelos et al. (2010) showed that they were localized on the long arm. Alexandrov et al. in 2016 experimented the FISH-mediated karyotype which constitutes ten pairs of chromosomes shown in Fig. 3.2. Six chromosomes among them, viz. B, C, D, F, H and J, emit heterochromatin bands and rcsat39 probe labeled with digoxigenin-11-dUTP signals that are depicted in Fig. 3.3. A chromosome pair which is non-heterochromatic carries rcsat390 probe signals. The telomeric probe rcsat47 emits faint yellow signal, if it is placed at the chromosome terminals.

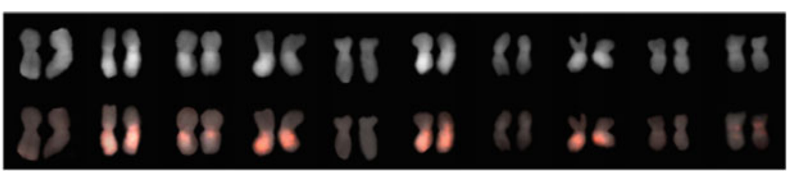

Fig. 3.2 Castor bean Karyotype based on FISH signals. Adapted from: Alexandrov and Karlov (2016)

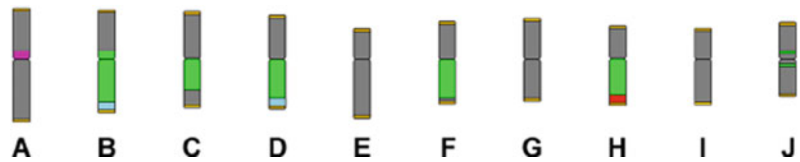

Fig. 3.3 FISH signal-based ideogram of castor bean where 45S rDNA represent in cyan color, 5S rDNA in red, rcsat39 probe emits green, magenta emitted by rcsat390 probe, telomere produces very little yellow signals. *Source* Alexandrov and Karlov (2016)

3.4 Pollination Mechanism

Due to monoecious nature, castor is highly cross-pollinated, and wind is the main agent for pollination indicating cross-pollination to the extent of 5–36% (Sesadhadri and Muhammad 1951). Pollen can travel up to even 1 km on a clear day with normal wind velocity, but no pollen movement happens on a rainy day. Weather factors like continuous cloudy weather during flowering, low temperature due to continuous rains cause infertility as low temperature, and/or high humidity produce abnormal pollen grains and also restrict the free movement of viable and healthy pollen.

Castor is a cross-pollinating plant but unlike other cross-pollinating crops, it is inclined toward self-pollination with low inbreeding depression (Moshkin 1986). Flowers of central spike are inclined toward self-pollination (30–70%), and flowers of lateral spikes pollinate by cross-pollination. In large areas of the crop, pollen flies up to 2.5–3 km. Maximum quantity of pollen was on the level of castor plants (60 cm), and it was ten times less at a height of 3 m. Isolation distance varied from as low as 300 m for certified seed production to 1500 m for nucleus seed production of female lines (Zaveri et al. 2010; Varaprasad and Lavanya 2015). Due to its low inbreeding depression, breeding techniques are not restricted to that of a cross-pollinated crop.

3.5 Genetics of Major Morphological Characters

Three morphological characters including stem color, bloom, and spines on the capsules are essential for characterization or description of a genotype. Several other characters like plant type, leaf shape, nature of the spike, echinate nature of stem, and petiole are also useful as morphological descriptors.

3.5.1 Stem Color

Stem color is a stable, distinct morphological trait of monogenic inheritance. A wide variation ranging from bright green to dark red through green with reddish–bluish tinge on sunny side, carmine or rose red, mahogany red, sulfur white, etc., is observed in the germplasm. Earlier botanists classified stem color into five categories while classification as three categories, viz. red, green, and mahogany, or two categories as among the cultivated varieties, green and faint red is most common.

Stem color is due to the pigmentation of sap color in epidermal palisade cells and parenchymatous areas of the stem and used to classify the genotypes (Kulkarni and Ramanamurthy 1977). Recent studies conducted under Distinctiveness, Uniformity, and Stability (DUS) tests on anthocyanin pigmentation starting from seedling to flowering stage indicated that green is the basic, distinct color while the presence of anthocyanin pigmentation over the green color turns to red, while its magnitude and intensity result into either light red, mahogany, or dark red. The intensity of anthocyanin pigmentation varies with sunshine, presence and intensity of bloom, and age of the plant, etc. Stem color is more deep and intense when there is no bloom on any plant parts or zero bloom. In DUS testing, stem color is determined with the color charts of Royal Horticultural Society, after the removal of bloom as it distorts the original color (Chakrabarty et al. 2006, 2009).

Genetic studies conducted during 1920 s indicated monogenic inheritance for stem color and dominance of colored stem over green stem. In crosses between red-blush × green, Kulkarni (1959) reported monogenic inheritance where F_1 was all red-blush with 3 red-blush: 1 green in F_2 which was later confirmed by Solanki and Joshi (2001), Rao et al. (2005), Lavanya and Gopinath (2008), and Gourishankar et al. (2010). Epistatic ratios for stem color indicated two factors M and G for three colors, where factor G converts tinged green to green and mahogany to rose and M is the factor for mahogany (Seshadri and Mohammd 1951). A single-gene *Rst/rst* for stem color in three crosses of castor also indicated digenic epistatic ratio of 9 green: 6 red: 1 mahogany where green stem color is dominant to red stem color (Lavanya and Gopinath 2008). The presence of either of two genes *Rst* or *Gst* individually produces red stem color, while the presence of both the two genes *RstGst* polymerizes the effect to turn to green color. The presence of two recessive genes *rstgst* produces mahogany stem color in cross DPC 13 × M 574. Mahogany color has both green and red colors with predominance of red color.

A distinct dark purple color morphotype, collected from Assam and Manipur states, however showed maternal inheritance in a cross between purple and green color morphotypes (Anjani et al. 2007).

3.5.2 Bloom

Bloom or waxy coating on the stem and other parts like leaves, capsules, and spines in castor serves as a natural protection against extremes of weather and infestation of insect-pests (Seshadri and Seshu 1956; Chandrasekharan and Sundaraj 1946). Cold injury and leaf hopper incidence are higher in plants without bloom than in plants with bloom, while it is vice versa for white flies. The intensity of ashy white bloom increases with sunlight and decreases with the fog or humidity. Castor plants are classified mainly based on the absence or presence of bloom on all external plant parts as zero bloom or with bloom. However, further classification is based on the presence of bloom on combination of plant parts, as single bloom (stem + petiole + capsule stalks), double bloom (stem, petiole, capsule + lower side of the leaf), and triple bloom (all the above parts + upper side of the leaf) (Kulkarni 1959; Narian 1961; Kulkarni and Ramanamurthy 1977).

Bloom is monogenic dominant or partially dominant over zero bloom (Kulkarni 1959; Kulkarni and Ramanamurthy 1977; Lavanya and Gopinath 2008). Single bloom was monogenic and dominant over zero bloom while double bloom had a dominant digenic complementary action of 9 double:3 single:4 zero bloom in a cross between double bloom and zero bloom (Peat 1926). Double bloom was controlled by two complementary genes B and C, where B alone expresses single bloom while C can express double bloom only in the presence of B (Peat 1926). The variation in the intensity of bloom was also controlled by another dominant gene D. Triple bloom was always dominant to other bloom variations (Seshadri and Muhamed 1951; Narian 1961; Pathak and Asthana 1962). Dominant nature of a single gene for bloom (PtBl) was confirmed in F_2 ratios of 3 triple bloom: 1 single and double bloom (Lavanya and Gopinath 2008).

The intensity of bloom within the plants varies with the age of the leaves; mild in the youngest to traces in matured, senescing leaves but highest in the physiologically active leaves. Even a series of single bloom families were heterozygous for the intensity of bloom varying from normal to heavy bloom. In triple or double bloom types, the presence of bloom on upper or lower side of the leaf is mostly confined to the latest emerged leaf indicating the role of penetrance and expressivity of the genes controlling the bloom character or due to multiple alleles.

3.5.3 Plant Type

The concept of plant type in castor gained importance especially with Texas stable pistillate-tenth-order revertant (TSP-10R), an exotic pistillate line introduced from USA. It was further crossed with three other inbred lines, viz. JI-15, JP-5, and 26006 at Vijapur, Gujarat in 1968 to develop an indigenous, stable pistillate Vijapur Pistillate-1 (VP-1), with distinct characters like dwarf stem, condensed nodes, cup-shaped leaves, convergent branching, long primary spike, and non-shattering character. Majority of the pistillate lines derived from VP-1 background have dwarf stem, condensed nodes, cup-shaped leaves, and convergent branching which are highly linked characters (Rao et al. 2005). The plant type of VP-1 was an instant success due to its feasibility in hybrid seed production for agronomic management and wind pollination. In addition, plant type is monogenic inheritance where dwarf plant type is recessive to the normal plant type with elongated nodes, normal plant height, and divergent branching (Moshkin 1986; Lavanya and Gopinath 2008; Gourishankar et al. 2010). Single dominant gene (*PtN*) is reported for normal, elongated plant type segregated in F_2 as 3 normal (N): 1 dwarf (Dw) in two crosses between Normal × Dwarf and Dwarf × Normal while in another Dwarf × Normal cross, F_2 segregated to fit into 45:19 ratio indicating the role of three genes for plant type (Lavanya and Gopinath 2008).

The distance between stem color (*Rst/gst*) to plant type (*PtDw*) and single gene for pistillate character and plant type was estimated as 40.2 and 47.6 centimorgans based on square root of frequency of double recessive phenotypes in F_2 data (Lavanya and Gopinath 2008).

3.5.4 Leaves

Leaves in castor are simple, small to large size and palmate with 7–11 lobes. The genotypes differ in the size and number of the leaves which is also influenced by the environmental factors like season, soil type, and water stress. Papaya leaf type, with deeply dissected leaf lobes and serrated margins, is a distinct trait, observed in germplasm and exotic collections. The trait developed in parental lines like DPC-12, DPC-15, DCS-12, DCS-59 is of monogenic, recessive control and serves as a distinct morphological marker. The petioles of castor leaves are long (30 cm to > 40 cm) restricting the adoption of high plant density. A short petiole plant (< 20 cm), was used to transfer the monogenic trait to a high-yielding cultivar FCA-PB.

3.5.5 Number of Nodes to Primary Spike

Node number is an indication of flowering initiation, and on an average, every node takes 4–5 days to develop (Shifriss 1964; Moshkin 1986). Node number varies between the locations and planting season, while it is constant for each genotype within the locations based on planting season (Lavanya and Gopinath 2008). Genotypes were classified as early (< 12 nods), medium (13–16 nodes), and late (> 17 nodes) based on the number of nodes to the primary spike. Low node number is dominant to higher node number and segregates as 9 early:6 medium:1 late types. Digenic or trigenic epistatic ratios controlled the character and varied with the parents of the crosses involved (Lavanya and Gopinath 2008).

3.5.6 Spike

3.5.6.1 Spike Compactness

In castor, spikes are classified based on the arrangement or density of capsules on the spike as loose, compact, and semi-compact (Kulkarni and Ramanamurthy 1977). Compact and semi-compact spikes are highly susceptible to fungal diseases like Botrytis gray mold under conditions of high humidity, rainfall, and cloudy weather due to poor aeration and ventilation. In local collections, the basal portion of the raceme up to 15–20 cm did not bear any capsules, while in improved varieties like HC-1 and HC-6, the first portion (of 13 cm) of raceme bore 70% of the total capsules (Kulkarni 1959).

Inheritance pattern of spike nature indicated monogenic inheritance, either incomplete dominance or dominance of the compact versus loose spike (Solanki and Joshi 2001; Lavanya and Gopinath 2008). The distinction between compact and semi-compact is not much clear while loose spike is distinct from compact or semi-compact spikes. Dominance of a single gene, *SpSc,* for compactness of the spike was indicated in 3 semi-compact: 1 loose spike in a cross between compact spike type (viz. DPC 13) and semi-compact (viz. M 574). In another cross between two pistillate lines of compact vs. semi-compact, two epistatic inhibitory genes controlled the spike type while F_2 population fit into the ratio of 13 semi-compact: 3 compact spike types. The presence of dominant gene at one locus [*SpSc*] and recessive gene at other locus [*Spll*] produced the same phenotype—semi-compact spike while presence of dominant gene at other locus [*spL*] resulted in loose spike types.

3.5.7 Capsule Color

Capsules with purple, mahogany, sulfur white and green colors were available in the germplasm. The green color of capsule was controlled by a single dominant gene (Patwardhan 1931; Sesharadri and Muhammad 1951). Similarly in a cross between green and sulfur white, the F_2 is segregated in the ratio of 15 normal green:1 sulfur white.

3.5.7.1 Capsule Spines

Spines on capsules in castor are a misnomer as they are not of pricking type. Spines vary in length, number, and distribution on capsules. The number of spines may vary from 0 to 150 per capsule. Based on the presence and distribution of spines on capsules, genotypes were classified as spiny, non-spiny, and semi-spiny. In some instances, capsules on main raceme were non-spiny while those on secondary and tertiary were spiny indicating xenia effect (Pathak et al. 1965). Capsules with long and densely packed spines as in DCH-519 provide congenial micro-climate like high humidity, retention of raindrops, moisture for the germination of spores of Botrytis gray mold. Capsules with short spines, sparsely distributed spines, or absence of spines as in, viz., DPC-9, GCH-4, and 48-1 indicated tolerance to Botrytis gray mold. The presence of spines is partially dominant to non-spininess and controlled by a single gene, while F_2 gave a good fit to the 1 spiny:2 partial spiny:1 non-spiny capsules indicating incomplete dominance of sparse spiny nature and monogenic control of spiny capsule (Narain 1961; Anjani 1997; Chandramohan 2002). In a cross between spiny (130 spines per capsule) and non-spiny, the F_1 was intermediate (68 spines) and F_2 segregated in the ratio of 1 spiny:2 intermediate:1 non-spiny (Sehardri and Muhammad 1951; Kulkarni 1959). The non-spiny capsules have either rugged, wrinkled, or smooth surface. The rugged surface of capsule was partially dominant over smooth surface and controlled by a single dominant gene. Further, a single dominant gene controlled the stalk of the capsule over sessile capsule. The stalk of the capsule may be branched; partially dominant over non-branched and F_2 segregated in the ratio of 1:2:1 indicating monogenic inheritance of capsule stalk.

3.5.7.2 Locules

Normally, the capsules are trilocular but sometimes bi- and tetralocular capsules were also noticed. Rarely, capsule with 4–8 locules were recorded (Rao and Thandavarayan 1954; Pathak et al. 1965).

3.5.8 Fruit Dehiscence

Capsules of all local varieties are shattering type, dehiscing at maturity compelling premature harvesting leading to low oil content. Breeding efforts led to non-shattering varieties where threshing became difficult. Partial dehiscence of capsules is preferred where in membranes covering the seed remains intact even though capsules dehisce preventing the shattering of the seeds on the ground (Kulkarny and Ramanamurthy 1977).

3.5.9 Seed Color

Seed color at the base varied from light chocolate, deep chocolate, red, purple, black, and white and is further modified by mottling patterns, which are of independent inheritance. Seed coat color is a distinct, stable morphological marker along with either low or high mottling pattern. Genotypes were classified based on the size of the caruncle as small, viz. GCH-2 or big, viz. DCH-177 (Chakrabarty et al. 2009).

3.5.10 Cotyledons

Being a dicot, castor has two cotyledons. A single cotyledon was observed in Cimarron variety at Berhampur (Savithri and Aiyadurai 1961; Savithri 1963).

3.6 Floral Morphology

Castor is an indeterminately determinate plant as each branch is terminated by a raceme or spike which develops in a sequential order. Unisexual flowers occur in clusters of three or more, spirally on the axis. Male flowers are protected by fused tepals, split into 3 or 5 segments, five stamens with branched, tree-like filaments, in branched clusters with distinct anther cells. Female flowers have spathaceous caducous calyx, a single superior three-celled ovary, short or long styles terminated by two or three bifid stigmatic branches, each of which is divided into two fleshy lobes with a papillose surface (Kulkarni and Ramanamurthy 1977).

The floral morphology of castor is described based on the arrangement of male and female flowers on the spike. Several classifications were given by different authors based on the number and pattern of arrangement of male and female flowers on the spike (Moshkin 1986; Kulkarni and Ramanamurthy 1977; Weiss 2000).

Castor, though a sexually polymorphic species, monoecious is still the most common floral morphology, with male flowers on the lower side while female flowers are on the upper half of the same raceme. Occasionally, both male and female flowers on either side were also observed (Joshi 1926). Normally, the male flowers occupy 30–50% of lower part of the raceme. At Kanpur, lines with 90–98% femaleness were recorded.

Based on the proportion of male and female flowers, the racemes are broadly classified as (1) mostly female: with one cluster of male flowers at the bottom of raceme; (2) partially female: upper half with female flowers and lower half with male flowers; and (3) mostly male: with female flowers on top one-third portion of the raceme. Plants either with 100% pistillate flowers (Joshi 1926) or with 100% male flowers were recorded. Presence of bisexual flowers was also reported (Joshi 1926; Seshadri and Muhammad 1951; Konwar 1960). Monoecious trait is monogenic and dominant over pistillate nature, but highly sensitive to environment and variations were also noticed with age and nutrition.

The basic sex forms in castor are monoecious, pistillate, and sex reversion either to monoecious or interspersed staminate flowers. **Monoecious (M)** spike has basal one-third to 1/2 male flowers while the top portion has female flowers. The proportion of male flowers may vary usually from 30 to 50% of lower part of the raceme to 2–10% (Lavanya 2002). In between these few whorls have both male and female flowers in an interspersed fashion. However, in few cases, both upper and lower parts of the spike had both male and female flowers. Variations like topmost male flower, lowermost female, male flowers interspersed with female flowers at the tip of the spike are common. The extreme variation of highly male or mostly male occurs with 1–5 female flowers throughout the entire spike and in different orders.

Pistillate (P) occurs as a rare recessive mutant with the spike having female flowers throughout the central and lateral spike orders. Variations like mostly female or inclined toward female produce female flowers from the base to the entire length of the spike while few staminate flowers are clustered at the base of the peduncle and sometimes dispersed at the lower end only. **Interspersed Staminate Flower (ISF)** is a variant of pistillate form with male flowers interspersed, throughout the female flowers on the spike.

Sex revertant is a female that turns to monoecious at later stage. Shifriss (1960) and Moshkin (1986) classified the sex variants based on the proportion of female and male flowers on the spike.

3.6.1 Classifications of Sex Revertants or Variants

Shifriss (1960) classified sex variants in five categories; Type A-monoecious, Type C-pistillate, Type B-sex revertant from C to A, D to A, E to A, Type D with an apically interspersed raceme as a monoecious variant, Type E uniformly interspersed raceme as a female variant. Among the above variants, A and C are developmentally persistent forms.

Moshkin (1986) classified the sex variants as stable female (female flowers from primary and later spike orders), unstable female (primary pistillate while later orders partial or fully monoecious), inclined toward female (up to ten male flowers in the lower part of the spike), interspersed (few male flowers interspersed throughout the spike) and monoecious and male with a possible occurrence of individual hermaphrodite flowers in any of the forms (Fig. 3.4).

3.6.2 Sex Reversion

Sex reversion in castor or the genetic instability of female line is the major problem in hybrid seed production in castor. Shifriss (1960) in his extensive study on sex variants in castor

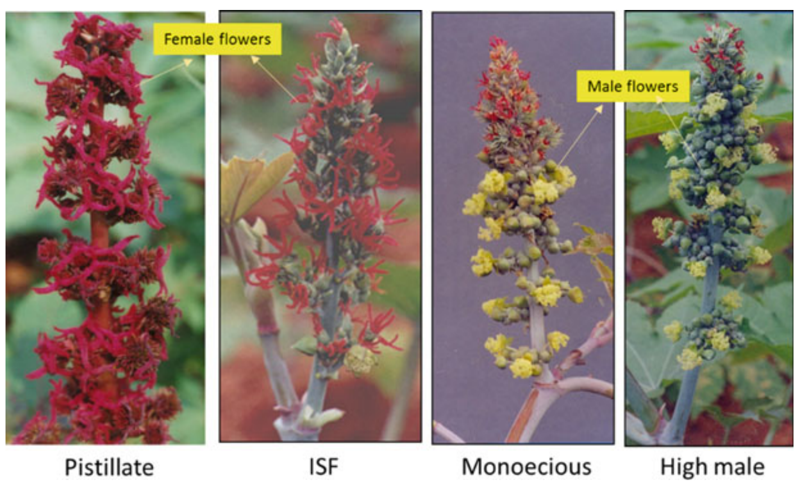

Fig. 3.4 Sex variants in castor

classified them as conventional and unconventional types. In conventional variants, qualitative genes determine the production of male or female flowers, while polygenes either accelerate or deplete a growth regulator to determine the male-to-female flower ratio (Shifriss 1960). Unconventional variants evolved as dominant spontaneous female mutants from monoecious inbreds are predominantly early-reverted. The genetic instability in all spontaneous female mutants was not linked with male sterility or meiotic abnormalities (Shifriss 1960). The time of phenotypic reversion is unstable, but reversion as such is not associated with any serious breakdown in the female producing mechanism. Reversions in later spike orders, seventh order or more, called late revertants were heritable and predictable to produce higher proportion of female plants, which in turn were late revertants. Development and maintenance of female lines in India commercially exploited the late revertants for production of quality hybrid seed while early revertants of less than third spike order are low heritable and unpredictable.

3.6.3 Inheritance of Sex Expression

Castor is typically monoecious plant, but the proportion of male and female flowers is greatly influenced by non-genetic factors. In normal monoecious varieties, the percentage of pistillate flowers on racemes is usually the highest on main raceme and decreases gradually on subsequent raceme orders. A proportionate increase in the number of male flowers is related to proportionate decrease of pistillate flowers and is highly influenced by seasons. The number of pistillate flowers and subsequent number of capsules on the main raceme have high heritability value (Sindagi 1964).

The expression of pistillate character is recessive to monoecious trait in majority of the cases and controlled by single to polygenes, depending on the material involved (Louis et al. 1986; Patel et al. 1986; Chauhan et al. 1992); additive and epistatic gene effects for the inheritance of 100% pistillate whorls in primary and later two orders (Solanki and Joshi 2000). Monogenic recessive gene control of perfect femaleness was indicated in M_2 of three female mutants of Aruna using 100-125 KR gamma rays (Weiss 1971). In 16 pistillate mutants, two pairs of closely linked recessive genes, *ppII* for pistillate expression and narrowly lanceolate functional leaves on floral axes and peduncles of inflorescences were obtained in Yong 283 (Zhou and Gu 1990).

3.6.4 Sex Expression Versus Environment

The role of environment for variation in the sex ratio of flowers within a genotype was well established and classified as female and male promoting environment. The tendency to produce female flowers in a spike increased with several environmental factors like winter season, low monthly mean temperatures (< 30 °C), young age or early spike orders, high nutrition, less difference between maximum and minimum temperatures, etc. On the contrary, summer or rainy season, high monthly mean temperatures (> 32 °C), old age or late spike orders, low nutrition, and large difference between maximum and minimum temperature promote male flowers on a spike (Lavanya 2002). The role of exogenous and endogenous growth hormones like gibberellic acid, silver nitrate, and ethylene in shifting the female and male tendency has been well documented (Ramesh et al. 2000; Lakshmamma et al. 2002, Murthy et al. 2003; Neeraja et al. 2010).

3.6.5 Inheritance of Interspersed Staminate Flowers (ISFs)

Two pairs of recessive genes, *id1* and *id2*, result in expression of ISF, while two, dominant genes, *Id1* and *Id2*, lead to the absence of ISF and are partially dominant to *id1id2* (George 1966). The highest number of ISF with homozygous recessive genes (*id1id1id2id2*) was produced irrespective of any environment. Higher peroxidase activity was detected in male flower buds, which had five isoenzymatic bands than in female flower buds, while female lacked one and had two extra electrophoretic bands in peroxidase extracts from female flower buds (Jaiswal and Kumar 1983). Pistillate with ISF expression is recessive to pistillate trait and controlled from one (P_1) or two (P_1P_2) to four genes ($P_1P_2P_3P_4$). Digenic epistatic ratios like 13 pistillate: 3 pistillate with ISF in secondary spikes and tetragenic epistatic ratios in primary (162:94) and secondary (229:27) spikes were also observed in two crosses (Lavanya and Gopinath 2008).

3.7 Genetic Parameters

3.7.1 Correlations

Seed yield, a complex trait of low heritability, is essentially dependent on the expression and correlation of different component characters. Correlation studies help in simultaneous selection of positively associated characters, correlated response, and indirect selection. Several studies on correlation in castor indicated that seed yield was positively correlated to total and effective primary spike length, weight of the primary raceme, total number of capsules per primary or plant, total number of effective spikes per plant, 100-seed weight, number of nodes and plant height (Ramesh et al. 2001, 2010; Lavanya et al. 2006; Severino et al. 2012), plant height, number of leaves, branches, stem girth, petiole length, leaf area, number of capsules per plant and dry matter accumulation (Shinde et al. 1985), while oil yield is closely and positively associated with plant height, effective length of primary raceme, number of spikes, number of capsules and seed yield on whole plant basis (Ratnakumari 1996).

Under rainfed conditions, significant and positive correlation between seed yield and number of capsules per plant was reported while days to 50% flowering and number of nodes to primary spike had negative significant correlation with seed yield (Patel and Jaimini 1991). Days to flowering recorded positive correlation with plant height, number of nodes on main stem, and number of capsules on primary raceme, while it was negatively associated with number of secondary branches and total number of racemes per plant (Bhatt and Reddy 1981). Several other yield components had negative association among themselves like seed yield with duration and node number (Dorairaj et al. 1973a), number of spikes with total and effective length, capsule number (Ratnakar 1982), and capsule number with test weight (Shinde et al. 1985).

3.7.2 Path Coefficient Analysis

Majority of the characters like number of nodes to primary spike, total primary spike length, number of capsules on main spike, number of effective spikes per plant, and 100-seed weight had positive direct effect on seed yield (Lavanya et al. 2006; Omkarappa et al. 2010; Ramesh et al. 2010), while a few studies reported negative direct effect of number of nodes to primary raceme, plant height up to primary raceme, effective spike length, number of capsules on main spike, 100-seed weight, oil content on seed yield (Ananthasayana and Reddy 1981; Raju 1981; Patel and Jaimini 1991; Yadav et al. 2004).

Number of capsules on the primary spike had a positive indirect effect through other characters except 100-seed weight on capsule yield (Ananthasayana and Reddi 1981), while plant height, seed yield from primary spike, and number of lateral spikes indirectly increased yield per plant (Moshkin 1986). Majority of the traits like plant height, seed yield of primary spike, number of lateral spikes, days to flowering, number of nodes up to primary raceme, total and effective length of primary spike had an indirect effect on seed yield per plant (Ramesh et al. 2010), while oil content and 10-seed weight had a large negative direct effect on seed yield under irrigated conditions (Yadav and Raviprakash 2004).

3.7.3 Gene Action

Studies on predominant gene action and their heritability assist the plant breeders to formulate the immediate breeding methodology to be followed and further selection programs. Predominance of non-additive gene action for seed yield and many other yield components was reported by many researchers (Lavanya et al. 2003; Madariya et al. 2008; Barad et al. 2009; Patel et al. 2010). Additive gene action was predominant only for plant height, length of the raceme (Narkhede et al. 1987), and all the characters (Mehta et al. 1991). Both additive and non-additive gene actions were also reported for some of the characters (Mehta et al. 1991; Dobariya et al. 1992; Padhar et al. 2010; Ramesh et al. 2010).

Complementary epistasis was observed for days to flowering, effective branches, node number on main stem, and 100-seed weight in three different crosses, while for other characters, duplicate epistasis was recorded (Pathak et al. 1988). Tertiary racemes had the highest genetic advance under moderate stress conditions when ten genotypes with divergent plant type and duration were evaluated under early and late sown conditions. Breeding methods like mass selection for reducing the duration and improving the seed yield and biparental mating with reciprocal recurrent selection, bulk population, and mass pedigree methods of selection for improving the seed yield were suggested (AICRP on castor, DOR 2006).

3.8 Heritability

Among the several yield components, apart from morphological characters, 100-seed weight is a highly heritable trait, while other characters like total and effective primary spike length, total number of capsules per plant, number of effective spikes per plant, plant height, number of nodes to the primary raceme, days to 50% flowering and maturity are mostly influenced by local environmental conditions. However, higher narrow sense heritability estimates for maturity, flowering time, and low for seed yield were reported (Singh and Yadava 1981; Ratnakumari 1996).

Number of nodes had the highest heritability (Kaul and Prasad 1983), while all the characters except plant height showed higher heritability values (Dhapke et al. 1992). High heritability coupled with high genetic advance and genotypic variability was noted for number of branches/plant, number of capsules/main raceme, length of pistillate region, capsules/plant, and seeds/plant suggesting the influence of additive gene action (Dhapke et al. 1992).

In a study on genetic association and selection indices in three height groups of castor, plant height markedly affected trait associations and selection index (SI) of traits, including seed yield and it was more efficient than selection based on seed yield alone (Bhatt and Reddy 1986). The selection index for dwarf varieties included number of primary and secondary branches/plant and capsules/raceme, while for moderately tall varieties, number of primary branches/plant, days to maturity, and seed weight were important. Selection indexes for tall varieties were days to flowering, node number, and plant height. Seed yield and racemes/plant were included in the five-trait SI for all varieties.

Further, high heritability coupled with high genetic advance and genetic variability were found for branches/plant, capsules/plant, and seed/plant indicating the influence of additive gene action providing scope for further selection. Mass selection was effective for shortening the duration and improving the yields (Reddy et al. 1999). Estimates for heritability and genetic advance were higher for secondary over primary yield components like capsule number, weight, seed number, and 100-seed weight indicating a higher selective value for these characters.

Heritability ranged from 0.152 for seed yield/plant to 0.893 for number of nodes on main stem. Genetic advance was high for plant height and number of days to flowering. High positive phenotypic correlations were shown by all characters except for number of days to flowering and node number. Path coefficient analysis indicated that both the number of capsules/primary raceme and number of secondary branches exhibited high positive direct effects on seed yield/plant. In yet another study, Bhatt and Reddy (1986) further suggested that semi-dwarf lines with a large number of capsules on primary raceme and with a moderate number of primary and secondary branches are desirable parents in a breeding program.

3.9 Worldwide History of Castor Plant Breeding

Castor, a native of Africa and India, is a very interesting crop with all possible transitions from an uncultivated plant to a weedy type, semi-cultivated to a field crop with no gap between uncultivated and cultivated forms. Under natural conditions, castor plants show a wide variety of growth habit and seed collection was done mainly for oil extraction (through crushing) at local markets. Production of high oil content seeds in a commercial scale was difficult mainly due to the natural height of the plant and prolonged flowering period.

Crop improvement of castor was initiated in the USA long back in early 1902, at the Brooklyn Botanical Gardens, New York and Oklahoma. Initial attempts were directed toward pure line selection for higher oil content from a collection of a large number of samples (White 1918b). Later in 1940 s, intensive work was carried out in 22 different states to combine different desirable characters like earliness, short plant, and non-shattering habit in different varieties like "Conver" and "Kansas" with oil content of 53%. Techniques for emasculation, hand pollination, and hybridization were standardized for effective breeding programs (White 1918a, b; Weibel and Woodworth 1946).

The breeding objectives in erstwhile USSR were aimed to develop genotypes with early maturity and non-shattering capsules. In the initial phase (1922–1931), the objective was to introduce varieties with early maturity to escape frost and uniform maturity suitable for manual harvesting. Breeders were successful to develop, Manchurian, an early maturing (75–85 days) variety. In the second phase (1932–39), efforts were directed toward introduction of non-shattering Sanguineus types suitable for double-stage combine harvesting. In the third phase (1939–1956), the aim was to introduce varieties suitable for single-stage combine harvesting (uniform/synchronous maturity) with simultaneous hulling of seeds. The emphasis is now shifted to development of high-yielding varieties with synchronous maturity, suitable for combine harvesting and resistant to harmful diseases such as Fusarium wilt. Among the several varieties developed, "Persian" variety with a single spike was the most productive variety (Moshkin 1986).

Intensive breeding efforts for desirable characters, specifically for only seed yield, high oil content, and spike length through different breeding techniques at State Agronomic Institute, Sao Paulo, EMBRAPA, Brazil, resulted in several high-yielding promising strains like No. 14, 38, and 45 (Kulkarni 1959).

In Italy, castor is an annual crop grown under irrigated conditions during spring–summer period, while recently the possibility of unirrigated semi-perennial crop is explored in eastern coast of Sicily (Anatasi et al. 2015). Initial breeding efforts through selection and hybridization based on germplasm collection led to early maturing (100 days), small plant height, like variety M-6. A Tunisian cultivar performed better for seed yield and ricinoleic acid (89%) compared to the local RG-2 (Sicilian genotype) (Anatasi et al. 2015).

Breeding efforts in France were carried out at the Central Plant Breeding Station, Versailles. Mutants generated from pollen grains by electromagnetic treatment had non-dehiscent capsules with thin walls.

In the Transvaal area of South Africa, near Johannesburg and Pretoria, Knapp worked on a large collection of geographically diverse germplasm from Italy, India, Manchuria, Africa, Brazil, and Russia for over 20 years. Screening for drought resistance under extreme hot summer and cold winter conditions of Transvaal (1800 m above sea level) resulted in annual varieties with drought resistance and tolerance to *Alternaria* *ricini*. Other promising varieties of non-spiny, non-shattering, and short types were cultivated in several other African and Asian countries like India, Pakistan, and Iran.

Breeding work in India was initiated in early 1920 s at different places like Tindivanam, Rajendranagar, Hebbal, Raichur, Nagpur, Jalgaon, Nadiad, Junagadh, Jullandhar, and Kanpur. Crop improvement in castor was initiated as selections from populations with an emphasis on seed yield and branching habit. Later on, non-shattering character and oil content were given importance in the fifties. Selections from local populations resulted in only 10–20% improvement for seed yield and 1–2% for oil content for want of large stock of germplasm. In 1960 s, castor was the first oilseed crop to induce variability for duration, plant height, and oil content using ionizing radiations, viz. *X*- and gamma rays and chemical mutagens. Later on, with the introduction and development of pistillate lines, hybrid development took a momentum and up to 70% of the castor-growing areas are dominated by mostly public sector hybrids. The emphasis is now on development of high oil yielding, early and medium duration (90–150 days) hybrids, and varieties resistant to major pests and disease like wilt complex, Botrytis gray mold and sucking pests (Lavanya et al. 2006).

In the Philippines, the most common varieties (*tangan-tangan* in Pilipino) grown in the country are *Bangkok, Brazilian, Ethiopian, and Lamao Red* which differ in their seed color, plant height, and adaptability. Among the two types of Bangkok, Bangkok brown-spotted type is generally adapted to the Philippine conditions with 49–56% oil. Bangkok white-spotted type, on the other hand, has few small chestnut white spots scattered on its back side.

The *Brazilian* variety, commonly grown in Mindanao and Luzon, is tall (6–8 ft) with dark brown stem color and 49.3% oil content. Ethiopian is an early maturing, agronomically adaptable variety with red seed having small white dots on both the sides and 49% oil. Another variety is *Lamao Red* which is tall (6–8 ft) with reddish brown stem color. Other castor bean varieties include *Cimarron, Connex, Baker No. 1, Baker 195,* and *Iranian* variety (Anon. 2007).

3.10 Breeding Methodology

3.10.1 Selection from Germplasm or Introduction

Castor, a cross-pollinated crop with limited inbreeding depression, is often treated as a self-pollinated crop in breeding programs (Severino et al. 2012). Castor, being a monotypic genus, subspecies and local germplasm collection were the base material for selection program. At V.S. Pustovoit All-Union Scientific Research Institute (VNIIMK), USSR, high-yielding, non-shattering varieties like Donskaya 172/1 and Kruglik 5 were selected from Persian subspecies, while early maturing Saratovskaya 66 and Ceripi Wild were selected from *ruderalis* subspecies of African and Asian countries (Moshkin 1986). In USA, tall and late maturing *zanzibarian* subspecies were used for selecting early, short, non-shattering, and high oil content varieties like Cimarron, Baker 296, Lynn, Dawn, Hale, Campins with high yield, short internodes, and better foliage (Moshkin 1986; Hegde and Lavanya 2012). In India, selections from local germplasm led to selection of several medium to late maturing, medium plant height, non-shattering, high oil lines like HC-1 to HC-9 in India (Lavanya et al. 2006).

3.10.2 Mass Selection

Mass selection is an effective breeding method in case of heterogeneous local landraces with highly heritable qualitative and quantitative characters. In castor, it is used mainly for selection of female plants, long primary spike, and reduced plant height. Mass selection followed by progeny row selection was effective to select wilt-resistant plants and improvement of local selections (Moshkin 1986). Significant achievements by mass selection included Kavkazskaya from VNIIIMK, USSR, IAC-38 from Brazil, Conver and Kansas from USA (Kulkarni and Ramanamurthy 1977).

A revised mass selection or family selection was also used to select high-yielding families and individual plants within the families. The method includes random-mating in isolation between new and unimproved old varieties followed by selection of the best plants along with parental types coupled with negative or reverse selection of low yielding, late and shattering plants. About 15–30 families and 100–150 individual plants within each family were selected. Mass selection along with progeny testing was effective for oil content and resistance to Fusarium wilt, viz. Fioletovaya, a variety improved for wilt resistance (Moshkin 1986). The method was also used to select early, short, annual types in place of perennial types.

Initial selection criteria like yield and branching habit were gradually replaced by other traits like non-shattering capsules and oil content (Kulkarni and Ramanamurthy 1977). Three varieties were purified for two variable characters like days to flowering and number of capsules after three cycles of mass selection (Reddy et al. 1999). A population CCP-1 was developed by inter-breeding with free flow of genes among selected lines of the varieties, viz. HC-6, HC-8, JI-35.

3.10.3 Single Plant Selection with Progeny Tests

The method was followed initially in germplasm collections having natural genetic variability for several heritable traits. Single plant selections for highly heritable traits followed by progeny row testing unravel the hidden, recessive genes. Several heritable traits can be simultaneously dealt by selecting highest possible number of self-pollinated lines. The method is similar to Pustovoit method of recurrent selection in sunflower and followed both after selfing and hybridization to reveal the hidden genotypic variability behind the phenotypic expression of heritable traits.

Half of the seed of the best plants within a family are sown and evaluated by progeny row testing method. Remnant seeds of the best plants within the progeny rows are sown in the next season and are allowed to cross-pollinate. Selection for specific characters like non-shattering capsules, plant height, sparse or less branching suitable for combine harvesting was practiced in VNIIMK, USSR (Moshkin 1986).

In open-pollinated populations, individual selections were made between and within families to maintain genetic diversity, while bulk selections between families are quantitatively restricted to 1–2% of the total number of plants. In the initial stages of selection, pistillate spikes which are prone to high cross-pollination are selected. Selection in segregating populations is initiated in F_2 but may be delayed up to F_4–F_6 when the homozygosity increases. In case of breeding for Fusarium wilt resistance, selections started in F_1 itself when incomplete dominance was involved.

Selection needs to be based on phenotype alone with minimum interference of environmental conditions. Precautions need to be taken for a leveled field with crop rotation and application of fertilizers to the preceding crop. Selection of plants is more effective under wider spacing (70 × 70 cm in USSR, 90 × 60 cm in India) for maximum phenotypic expression and yield potential of individual plants. Single seed per hill is most ideal for selection of plants with productive spikes, increased oil content, and low hull percent in seeds. However, the evaluation of varieties and hybrids needs to be done under good agronomic conditions with required fertilizer and irrigation conditions.

3.10.4 Development of Inbred or Pure Lines

Inbreeding or induced self-pollination is essential to develop homozygous and homogenous pure lines for morphological and quantitative characters. Due to minimum inbreeding depression on selfing, inbreeding was used to develop and maintain varieties or inbreds or pure lines.

At VNIIMK, USSR, inbreds for several traits like duration, seed yield, oil content, plant height, and morphological characters like stem color, intensity, and distribution of bloom and presence of spines were separated. Successful examples include red-stemmed inbreds from green Kruglik 5, non-spiny and tall inbreds from Sanguineus 401, purification of Kruglik 5 for plant height, spike compactness, and maturity through inbreeding (Moshkin 1986). Inbreeding was also essential for recessive characters like non-shattering capsules, shortened internodes, and single spike. Wilt resistance of varieties, viz. Chervonnaya, VNIIMK 165, improved; Fioletovaya and VNIIMK 360 improved by selfing wilt-resistant plants in wilt sick plot (Moshkin 1986). The percentage of female plants was also increased by selfing or sibbing plants with highly female spikes (Moshkin 1986; Lavanya et al. 2006).

Inbreeding was practiced either from germplasm or working collection or interspecific breeding material. Segregation for plant height, length of spike, arrangement of capsules, maturity, and other morphological characteristics in addition to transgressive segregation was high in F_2 and fixed in later generations by selfing. Majority of the inbred varieties in India were developed by selection from the existing types followed by sibbing until homozygous condition is retained and evaluated in trials as inbreds (Kulkarni and Ramanamurthy 1977; Lavanya et al. 2006).

3.10.5 Hand Pollination and Selfing

Parental lines are sown in a crossing block, and morphological off-types are removed from them. Spikes with majority of unopened female buds and a few buds with extended stigma of yellowish green or light red color are selected either for selfing or crossing. The spikes, measuring 8–10 cm, are tagged one day prior to the pollination after removing male flowers, if any and covered with butter paper cover. Male flowers, which have just opened, from male parent are collected in a petri dish early in the morning, and the burst out pollen is used to pollinate female spike early in the morning from 6 AM to 9 AM on alternate days. Pollination has to be repeated 5–6 times depending on the spike length and opening of female flowers. Pollen is applied by brush or rubbing the male flowers pollen on the stigma of the female flowers. Details of crossing like parents, dates of pollination need to be mentioned on a separate tag instead of butter paper cover, as it need to be changed, minimum 3–5 times during the pollination period.

Sibbing is done with a mixture of pollens from plants of the same line. Selfing of highly female spikes is done either by inducing or forced selfing. At the beginning of the flowering, opened or fertilized female flowers were removed and enclosed in butter paper covers. Nipping induces male flowers within the whorls of female flowers and contributes to forced or induced selfing.

3.11 Hybridization and Selection

3.11.1 Intra- and Inter-generic Hybridization

The six subspecies within the monotypic genus, with $2n = 20$, are inter-crossable without any barriers or meiotic abnormalities. Each subspecies has its own strengths and limitations, and thus, intra-generic hybridization was successful in the initial stages of breeding program. In USSR, *communis* (earlier *sanguineus*), Persian and Chinese subspecies, were used as the initial breeding material.

3.11.1.1 Subspecies *Communis* (Sanguineus)

Originated from South west Asia, widespread near Mediterranean Sea and American continent. Plants are characterized by specific traits like large seed size, drought resistance, high seed yield, oil content, and indehiscent capsules but late maturing and unsuitable for mechanized harvesting due to their excessive vegetative growth.

3.11.1.2 Subspecies *Persicus* (Persian)

Originated from Asia Minor region, requires less heat, faster growth during vegetative period but susceptible to Botrytis gray rot due to its dense spikes and Fusarium wilt. Plants are characterized by small seed, productive, uniform maturity with dehiscent capsules. Varieties of Persian subspecies like Donskaya 172/1, Kruglik 5, Kavkazskaya improved were introduced in USSR (Moshkin 1986).

3.11.1.3 Subspecies *Sinensis* (Chinese)

Developed in East Asia under high humidity, has specific traits like early ripening, indehiscent capsules, drought resistant but low yielding, low oil content. Plants have higher number of lateral spikes, loose and weakly attached capsules resulting in losses during harvesting.

3.11.1.4 Subspecies *Indicus* (Indian)

Originated from India, tropical, prolonged vegetative period, tall, high yielding, indehiscent capsules, resistant to drought. Two small-seeded forms, variety indicus and variety griseofollius, were used to develop medium maturing varieties like SA-1 and SA-2.

3.11.1.5 Subspecies *Zanzibarian* (Zanzibarinus)

Is also tropical with slow growth rate, high yielding under optimum moisture conditions, and occurs in three tall and late types.

3.11.1.6 Subspecies *Ruderalis* (Ruderal)

Poorly developed, late maturing, low productivity and includes common, wild cultivated varieties (var. ruderalis) also includes wild growing varieties of Ethiopia and Asia Minor (var. Spontaneous), shattering local types from Sudan, Egypt, Mediterranean coast and huge tall forms from Mexico, Colombia, and Guatemala.

3.11.2 Examples of Intragenic Hybridization

A small-seeded variety microspermus developed by intercrossing the large-seeded communis subspecies with small-seeded Persian subspecies at VNIIMK, USSR, was the base material to develop the female line, CNES-1 at USA, and k-1182 at France. Nebraska 145/4, the female line of green stemmed variety was further used to develop high-yielding varieties like Pacific-6 at USA (Moshkin 1986). Varieties like VNIIMK 165, Stepnaya 6, large-seeded Donskaya, were also interspecific derivatives with majority of Persian characteristics. VNIIMK 165 is double-cross-derivative involving four subspecies, Persian (Kruglik 5), Chinese, communis, and Indian subspecies, and has non-shattering capsules and single spike for mechanical harvesting. Similar hybridization between early maturing, non-shattering, and drought-resistant Chinese or *sinensis* subspecies and local collections at VNIIMK led to dove colored, early maturing varieties like early hybrid, kubanskaya 9. Other interspecific derivatives include American variety Cimarron, suitable for irrigated conditions and varieties with condensed internodes of 1–3 cm, like Baker 296, Lynn, Dawn, Hale, Campinas with higher foliage and rapid growth of dry matter and yield. Dwarf female line, TSP-10R, is another widely used pistillate parent for development of hybrids in USA, Brazil, India, with a potential of 25–30 q/ha under irrigated conditions.

Initial attempts on inter-generic hybridization with related genera in the Euphorbiaceae family like *Euphorbia lathyris* were not successful (Moshkin 1986). Recently, putative hybrids were developed by using castor and cassava hybridization, and molecular tools were standardized to prove the hybridity of the material (Gedil et al. 2009).

3.12 Handling of Segregating Generations

3.12.1 Pedigree Method of Selection

The method is most commonly used to select simultaneously several heritable and morphological traits after hybridization. The possibility of recombinants is usually high, when parents are genetically diverse. Selection criteria and detailed description of each selected plant are maintained in the registers. In castor, three highly heritable characters, viz. stem color and presence, and distribution of bloom and spines on the capsules of individual selected plants are maintained in the registers. Promising selected hybrids were selfed to generate a large F_2 population. Individual desirable plants from F_2 s were selected, selfed, and advanced to $F_{3,}$ F_4 to derive uniform lines based on highly heritable characters. Continuous selfing will lead to a high degree of homozygosity in F_5 and F_6 generations where selection is based on quantitative characters. In F_6, selfed seed of individual best plants with uniform characters within a family is bulked.

Several such inbred lines are evaluated in preliminary varietal trials in unreplicated augmented randomized block design with standard checks replicated after every ten entries in each block. Simultaneous screening for resistance to pests and diseases either under natural or artificial inoculation conditions resulted in several high-yielding varieties with pest or disease resistance.

Pedigree method was used to transfer polygenic controlled character like long raceme. A number of long-duration (240–270 days), tall plant-type varieties like HC-1 to HC-8, EB-16 A, S-20, Junagadh 1, Punjab castor 1, EB 31, Rosy, MC 1 were developed by hybridization and selection methods prior to inception of All India Coordinated Research Project (AICRP) on castor. High-yielding varieties, viz. SA-I, SA-II, TMV-1, TMV-2, TMV-3, TMV-4, and TMV-5 developed at Tindivanam center were recommended for Tamil Nadu (Lavanya et al. 2006).

Major drawback in pedigree method of selection is that generation of diversity is limited to the initial population size in F_2 which is essential to produce F_3 inbred lines. The F_2 population size is determined by the diversity of the parents, number, and heritability of the characters involved; greater the diversity, larger the F_2 population size.

3.12.2 Bulk Method

Segregating populations are allowed to open pollinate without any artificial selection until the later generations, F_5 or F_6 or F_7, attain homozygous and homogenous populations. The method is more successful for selecting segregating generations both under abiotic and biotic stress conditions like drought, salinity, acidity, and disease resistance followed by preliminary yield evaluations.

3.12.3 Backcross Method

This method is most successfully used to transfer monogenically inherited qualitative characters in an otherwise highly adaptable, high-yielding background. Fixation of the various desired characters in the breeding material allowed the use of backcross method to transfer simply inherited characteristics, viz. short internodes, non-spiny capsule, stem color, presence or absence of wax on the stem, seed shattering, plant height, and disease resistance.

3.13 Recurrent Selection

The efficiency of recurrent selection breeding procedure for reducing the plant height or altering the plant stature of Guarani cultivar for mechanical harvest was established after four cycles of recurrent selection in three locations at Brazil (Auld et al. 2009). In the first stage of selection cycle, short plants were selected and self-pollinated. In the second stage, 180 self-pollinated lines were evaluated for plant height in isolation and 30 plants were selfed (Filho 1999). The selected lines were gone through five cycles of selection, and the 30 selected lines were intercrossed and the seed bulked to generate the cycle 1 seed. The procedure was repeated for four additional cycles of selection, and reduction in plant height ranged from 3.4 to 28 cm for the five cycles of selection, while seed yield was not influenced by reduction in plant height (Oliveira and Zanotto 2008).

3.14 Population Improvement

The method was initiated as a random-mating population involving hybrids, F_2 populations, improved varieties, inbred lines in a population and sown in 0.1–0.2 ha area under isolation for 2–3 years. Negative and mass selection was done to remove the unwanted plants and bulk the productive, healthy plants for evaluation in preliminary and multi-location trials, viz. Sovkhoznaya and Stepnaya 6 varieties (Moshkin 1986).

Breeding programs aim to combine high seed yield and oil content and thus need to exploit both non-additive and additive gene actions simultaneously through parental mating and recurrent selection. A population improvement program was initiated with an objective to isolate high oil lines with 6–25 nodes to flower. Single crosses involving three high oil lines, CO-1 (58.6%), HO, HC 8 (56%) and 15 other diverse male lines, viz. Pb-1, T-3, T-4, 411, Baker, 4-4, Sowbhagya, 413 A, 1-21, Aruna, 239, 279, Bhagya, VI-9, JI-44 formed the base material. Part of the F_1 seed was used to raise the segregating population. Biparental mating was attempted in each segregating population by crossing 50–100 selected plants from promising crosses to broaden the genetic base. Promising recombinants of the crosses were crossed in F_3 generation to generate base material for further improvement (Lavanya et al. 2006). Similar efforts initiated in major All India Coordinated Research Project (AICRP) castor centers, through construction of gene pools for monoecious and pistillate trait to generate diverse parental material.

3.15 Mutation Breeding

Creation of variability in castor is limited to intra-genetic, inter-varietal hybridization in absence of wild species and related genera. Mutation breeding was resorted to induce variability for morphological characters, sex expression, and resistance to Fusarium wilt. Basic studies on relative efficiency of chemical and physical mutagens, standard doses, and genotypic variability of mutagen sensitivity were studied in detail during 1970 s (Kulkarni and Ramanamurthy 1977).

In castor, three types of radiations, viz. gamma rays 20 to 45 KR, fast neutrons 2.5×1012, 5×1012, 1×1013 and 5×1013, and thermal neutrons 0.87×1013, 1.75×1013, 2.62×1013, 3.49×1013 were used to induce variability. Irradiations of HC-1 by castor breeders resulted in several morphological variants, viz. chlorotic leaves, distorted ovaries, sex variants, and cytological abnormalities like inversions, translocations, anaphase bridges, and ring chromosomes. Other mutagens like X-rays (50–1100 R) resulted in variants for zero and single bloom from triple bloom. Irradiation of HC-6 with thermal neutron treatment of 0.87×1013 mh/cm^2 led to isolation of a short duration mutant, NPH-1 and later released as Aruna variety. The variety is early flowering (35-40 DAS), maturing (110-150 DAS), short height (75 cm) with 11 nodes to primary raceme. It was popular in several south Indian states like Andhra Pradesh, Tamil Nadu, and Karnataka under rainfed conditions.

Three female mutants obtained using 100-125 KR gamma rays confirmed monogenic and recessive nature of the pistillate trait (Chauhan et al. 1992). Other mutagens like gamma rays, ethidium bromide, diethyl sulfate were also utilized to induce variations for plant type, growth duration, female spikes, etc. Gamma ray irradiation at 55-60 KR gamma rays, of VP-1, a wilt susceptible stable S-type pistillate line led to several wilt-resistant pistillate lines like M-574 and M-619 (Lavanya et al. 2001) which were used in the development of hybrids like DCH-519 and YRCH-2. Recent example includes, DPC-23, a triple bloom, wilt- and leafhopper-resistant, early pistillate with less than ten nodes from DPC-9, a zero bloom, wilt-resistant but leafhopper susceptible pistillate line (Lavanya et al. 2008).

3.16 Varietal Breeding

In castor, monoecious lines or male lines were also used as varieties initially before the development and popularization of hybrids. Conventional breeding programs like mass or pure line selection, recombination breeding followed by pedigree and backcross method led to the release of several varieties in erstwhile USSR, USA, Brazil, India, and several other countries.

Selection criteria for varietal development in erstwhile USSR varied from non-shattering, early maturing, short plant height, high seed yielding, synchronous maturity suitable for combine harvesting. The variety VNIIMK 165 developed in 1952 at VNIIMK gained popularity for its high seed yield, suitable for combine harvesting, non-shattering capsules, and uniform maturity. Since 1957, the emphasis has shifted to development of wilt-resistant varieties resulting in Chervonnaya, VNIIMK 165 improved, Donskaya long-spiked, and Donskaya early. The major donor for wilt resistance was small-seeded Sanguineus. Three major groups of varieties were identified for their high seed yield and wilt resistance (Table 3.1, Moshkin 1986). Breeding efforts were also directed toward varieties with shortened internodes like Karlik heterozygotic (Moshkin 1986), Dawn, Lynn (Brigham 1967, 1993), dwarf female lines like CNES-1, TSP-10R in USA, and Frantsiya 301 M. The variety SA-2 has outyielded VNIIMK 165 by 3 q/ha under Russian conditions.

Varietal development in India intensified after the initiation of seven AICRP castor centers, mainly to reduce duration, plant height, non-shattering, high seed yield, and oil content. Available varieties like Aruna, JI-44, GCH 3 were evaluated in seven centers, and breeding program was initiated by recombination breeding between available material and local selections, viz. RC-7, RC-12, RC-8, L.448.57, HC, 413 A, T3, 6501, Kalpi 6, 6501, Tarai-4, and TMV 2, in individual centers and selected for seed yield and important yield components. Consistent plant breeding efforts led to the release of two high yielding vaieties in 1974. Bhagya (65), a cross of high oil line (HO) and MI 415, which is earlier and shorter than Aruna and Sowbhagya (157-B) from a double cross involving Aruna and a short mutant, Mauthner's dwarf. Sowbhagya was suitable for intercropping systems due to its convergent plant type and slightly longer duration than Aruna. RC 8, an induced mutant from RC 1188 (a tall plant type from Tamil Nadu) is a medium maturing (150–180 days) variety with 1200–2000 kg/ha yielding ability, was released in Karnataka. Other promising varieties like AKC 1 for Maharashtra, GAUC-1 or VI-9 for Gujarat (a selection from S 20) were released under State Varietal Release Committees. GAUC-1 variety has an average productivity of 1200–1500 kg/ha with an oil content of 46–47%. SKI 73 is another early maturing (150 days) variety released for all irrigated areas of the country as GC 2.

Intensive cultivation of improved varieties without crop rotation and/or cultivation of castor in poorly drained soils led to increased buildup of Fusarium wilt and susceptibility of all the above selections. The breeding objectives were modified to develop high-yielding varieties resistant to Fusarium wilt or wilt complex.

Natural and artificial screening of available germplasm, crossing between wilt-resistant

Table 3.1 Promising varieties in USSR (1974–1978)

S. No.	Group	Specific characters	Varieties
1.	I	High seed yield, uniform maturity, suitable for combine harvesting, resistance to Fusarium wilt	VNIIMK 360, 3218, 4280, Sizaya 7, Chervonnaya, VNIIMK 165 improved
2.	II	High yielding, moderately resistant to Fusarium wilt	Donskaya long-spiked, Donskaya 39/44, Donskaya early, Stepnaya 6, VNIIMK 165
3.	III	Average yield, highly susceptible to Fusarium wilt	Early hybrid and Kruglik 5

Source Moshkin (1986)

sources and agronomically superior and high-yielding genotypes led to development of wilt-resistant varieties like 48-1 and DCS 9 from diverse wilt-resistant sources (Mauthner's Dwarf and 240). Variety 48-1 (Jwala) is the male parent of GCH 4 hybrid and recommended for endemic areas like Karnataka. It has non-spiny capsules, medium maturing 110–120 days to first picking with very high branching potential. The variety DCS 9 (Jyothi), recommended for rainfed areas of peninsular India, is an early maturing (90–100 days to first picking), wilt-resistant variety with high yielding capacity (1200 kg/ha) under rainfed conditions. Another popular variety, Kranti (PCS 4), was released from Palem center for rainfed areas of Andhra Pradesh which has early maturity 90–100 days to first picking with good branching potential. Other varieties like Haritha (PCS 124), a wilt-resistant variety, and Kiran (PCS 136), a non-spiny variety from Palem center, were also recommended for rainfed areas of Andhra Pradesh. Some of the promising varieties along with their yield potential, suitable areas for cultivation, and specific features are given in Table 3.2.

3.17 Heterosis Breeding

Exploitation of heterosis in castor was initiated since 1960 s even before the development of pistillate lines. Due to its inbuilt self-pollination nature and limited inbreeding depression on selfing, it was considered that heterosis may not be as high as in other cross-pollinated crops but it varied from < 20 to > 100% over the standard checks (Lavanya et al. 2006). Heterosis was observed for non-economical characters like plant height in early seedling stages, leaf number, and leaf area index. Attempts to exploit hybrid vigor through monoecious lines were not successful due to laborious process of emasculation. Heterosis was high for seed yield followed by number of capsules on the main raceme and 100-seed weight. Heterosis and heterobeltiosis for seed yield per plant were due to heterosis for capsules on main raceme, length of pistillate region of main raceme, effective branches per plant, and seed yield of main raceme while heterosis for seed yield was associated with number of effective spikes per plant (Lavanya et al. 2006). However, heterosis for seed yield, as

Table 3.2 Promising castor varieties in India

Variety	Yield potential (kg/ha)	Oil content (%)	Recommended states/regions	Salient features/traits
Kiran (PCS 136)	1200–1500 (R)	51	Rainfed areas of Andhra Pradesh and also late sown *kharif* conditions with one or two irrigations.	Tolerant to Botrytis gray mold
Haritha (PCS-124)	1400–1600 (R)	49	Light soils of Southern Telangana, Rayalaseema, and Prakasam district.	Resistant to wilt
Jwala (48-1)	1000 (R) 1800 (I)	50	All castor-growing areas under both rainfed and irrigated	Resistant to Fusarium wilt; tolerant to Botrytis gray mold, salinity
GC-3	2340 (I)	49	Irrigated areas of Gujarat	Resistant to wilt
Chandra prabha			Uttar Pradesh	Suitable for intercropping
DCS-107	1500–1700	49	Identified for both rainfed and irrigated areas of the country	Resistant to wilt and tolerant to leafhopper
JI-273 (GC-3)	2340	49.6	Irrigated areas of Gujarat	Resistant to wilt, tolerant to Macrophomina root rot
Pragathi (PCS-262)	1500–2500	48	Rainfed areas of Telangana	High seed yield and wilt resistant

per Atsmon (1989), may be due to the highly female expression inherited from the dominant female nature of the S-type pistillate line. Genetic basis of heterosis of seed yield is due to the factors other than heterosis per se like the improved parental lines for spike density, highly female spikes, earliness, and short stature (Atsmon 1989).

Heterosis was mainly manifested in parental lines of contrasting morphological characters like dwarf plant type with condensed nodes, cup-shaped leaves in pistillate lines vs. normal tall plant type, elongated nodes, flat leaves in male lines (Lavanya et al. 2006). Per se performance and average heterosis in dwarf × tall crosses were higher to the parents involving moderately tall × tall and tall × dwarf crosses. Heterosis for seed yield was correlated with heterosis for main spike length and capsules/primary spike when one of the parents was tall. The first-generation hybrid between Kruglik 5 and Sanguineus gave 1400–1900 kg/ha higher seed yield than both the parents in USSR (Moshkin 1986). Heterosis has increased up to 18–23% when parents were of diverse origin and upon emasculation of pistillate lines. Heterosis breeding gained its momentum due to the identification of pistillate lines and suitable male lines.

3.17.1 Types of Pistillate Mechanism Used in Hybrid Development

3.17.1.1 N-Type

The N-type pistillate lines, viz. Nebraska 145-4, CNES-1, were initially used in USA for development of castor hybrids. The pistillate character in N-type, governed by a recessive sex-switching gene and maintained by sib-mating, is similar to conventional rare recessive female mutants proposed by Shifriss. It is similar to genetic male sterility system as the progeny from female plants segregate into 1 monoecious: 1 pistillate in hybrid seed production plots. Seed production is laborious as normal monoecious plants have to be rouged out before anthesis leading to low genetic purity and high cost of rouging. The female line is maintained by allowing 20–25% monoecious plants in foundation seed production plots. The progeny of spontaneous sibbing of pistillate plants of four varieties, TMV-2, S-20, D-3, and HC 6, which segregated in the ratio of 1 monoecious: 1 pistillate was grouped under the N-type. CNES-1, the N-type pistillate line, developed at Davis, California, was also used in the development of pistillate lines at AICRP (castor) centers.

3.17.1.2 S-Type

S-type pistillate line was obtained by selection within sex reversals at the Weizmann Institute, Israel, and governed by dominant and epistatic effects. Sex reversals are plant variants, which begin as female and revert to normal monoecism at any time after the first raceme and ten or more racemes when grown as perennials. These perennial plants were considered as females, if grown only as annuals. Sex reversion is ontogenetically irreversible and is variegated where a part of the plant may still be pistillate, while the other half is reverted to monoecious.

Selection for femaleness within sex reversals is carried out by growing the plants as perennials and choosing the late revertants. Selection within a graded series of unconventional dominant female variants led to the development of S-type pistillate lines. Selfed plants of the second and third orders of reversion yielded more number of pistillate plants than sibbed pistillate and first selfed order revertants (Gopi et al. 1996) while fourth-order revertants gave significantly more number of pistillate plants than the early revertants (Patel and Joshi 1972). Selfed plants of the tenth order of reversion yield nearly hundred percent pistillate plants in their progenies. The rate of reversion in a female progeny is decreased from 79.2% in first-order revertant to 12.2% in fourth-order revertant. The highest number of capsules and seed yield was obtained when the fourth-order revertant was crossed with the male line having 50% flowers. Depending on the genetic background, the selection pressure, and number of cycles of selection, female plants varied from 60 to 95% in the progenies from sex revertants when grown as annuals.

The development of a stable pistillate line, TSP-10R (Texas stable pistillate tenth-order revertant) in 1962, with 100% pistillate raceme on a high percentage of plants brought the momentum to the castor hybrids. The exotic line was further utilized to develop a stable pistillate line VP-1 in Gujarat, India.

VP-1 was the first stable pistillate line developed in Gujarat, India, from the segregation of a double-cross between F_2 of JHB 48 (JP 5 × 26006) × JHB 67 (TSP-10R × 719/1) with distinct morphological characters like green stem, triple bloom, cup-shaped leaves, condensed nodes, long primary spike with spiny capsules. Majority of the commercial hybrids were generated from S-type pistillate lines, viz. LRES-17, DPC-9, SKP-84, MCP-1-1, M-574, and M-619.

3.17.1.3 NES Type

In NES system, pistillate character is governed by a homozygous recessive gene, while interspersed staminate flowers (ISF) were manipulated by environmentally sensitive genes, but not confined to any particular raceme order (Ankineedu and Rao 1973). Temperatures of above 31 °C promote ISF, while lower temperatures result in fully female racemes. A pistillate line “240” of NES background was developed by a cross between non-revertant pistillate progeny of the cross 625-4 × HC 6 with US3 415-9. The male parent, US3 415-9, is an “E”-type sex variant with ISF from base to top. The pistillate population has 56% strictly pollinate and 44% pistillate with few ISFs that mature later than the topmost female flower appearing on the spike. Later, few pistillate lines like NES-6, NES-19, NES-22, JP-65 were developed in India.

3.17.2 Pistillate Lines

Prior to the development of pistillate lines, inbred lines having highly female spikes were used as female lines. Initial research by Sidorov and Sokolov led to the identification of a heterozygous female line K-57, which segregated into 1:1 female: male plants (Moshkin 1986). In USA, plants with partial or total femaleness were selected from the collection of Gilmore. Classen and Hoffman (1950) developed an N-type pistillate line Nebraska 145-4. A three-way inter-line hybrid was also developed using the female plants of the hybrid between N 145-4 and Brazil 330 with a male line.

The NES system of pistillate line 240 was developed by a cross between non-revertant pistillate progeny of the cross 625-4 × HC 6 with US_3 415-9. The male parent, US_3 415-9, is an “E”-type sex variant with ISF from base to top. The pistillate population has 56% strictly pistillate and 44% pistillate with a few ISFs that mature later than the top most female flower appearing on the spike (Kulkarni and Ankineedu 1966). Yet, another NES type from segregating generations of the cross (high oil mutant from HC 6 × Mauthner’s dwarf) × (Aruna × Mauthner’s dwarf) with desirable attributes such as low node number on main stem (12), normal plant type, medium tall, red stem, double bloom, non-spiny, and non-shattering habit with an oil content of 55% was identified (Ankineedu and Rao 1973). Temperatures above 31 °C promote ISF, while lower temperatures (< 31 °C) result in fully female racemes. The NES system is advantageous due to easy transfer and maintenance of a single recessive gene for femaleness in contrast to polygenic, dominant, and epistatic gene complex in S-type. JP-65, a NES-type pistillate line, was utilized for the development and release of a high-yielding hybrid, GCH-6 at Junagadh. Several other sources were identified by screening of 1250 germplasm accessions at ICAR-Indian Institute of Oilseed Research (formerly DOR, Directorate of oilseed Research) Hyderabad, viz. EC 153132, EC 169761, EC 169803 for pistillate character and used in hybridization program (1986–87). Four pistillate lines NES 15, NES 16, NES 17, and NES 18 were derivatives of these pistillate selections.

Diversification of pistillate base through hybridization, selection, and generation advancement for early-to-medium duration, stable pistillate character, wilt resistance, and economic characters was taken up at ICAR-IIOR in collaboration with AICRP castor centers at SK Nagar, Junagadh, Mandor, and Palem. At Hyderabad, seeds of VP-1 were subjected to irradiation (55 KR gamma rays) and selections stable pistillate behavior and wilt resistance by screening in wilt sick fields five mutant VP-1 selections, viz. M-574, M-619, M-568, M-571, and M-591, were stable for pistillate behavior and resistance to wilt (Lavanya et al. 2000). Among the 20 pistillate lines developed at ICAR-IIOR, M-619, DPC 9, and DPC-11 showed resistance to wilt. In addition, pistillate lines NES 6, DPC 9, and 10 were stable for pistillate nature up to sixth order of spike irrespective of seasonal conditions. Genotypic variation for production of ISF was highest in NES-22, DPC-9, DPC-10, and M-568 during May to June. Good combiners for seed yield, 100-seed weight, oil content (DPC-12), number of effective spikes per plant (NES-6, DPC-11, and M-568) were identified (Rao et al. 2000). Stringent selection pressure for the maintenance of non-reversal and ISF nature of pistillate lines were the key factors for pistillate line stability (Chakrabarthy and Banu 1999). DPC-9, the most promising pistillate line with high femaleness, late revertant nature, and high seed yield (279 g/pl), was the female line of several hybrids like DCH-177, PCH-111, YRCH-1, and HCH-6. Clustering pattern indicated five groups of pistillate lines.

Majority of the pistillate lines are developed from VP-1 or S-type of stable pistillate line source, which is originated from an exotic source –TSP-10R from USA. This has been converted to suitable agronomic types of Indian conditions like LRES 17, DPC 9, DPC 10, DPC 14, DPC-15, DPC-16, DPC-17 to DPC-29 through conventional breeding techniques like intraspecific or inter-varietal hybridization followed by pedigree selection and mutation breeding.

A diversified source of pistillate character, i.e., 240, was introduced to local genotypes like Bhagya, CO-1 and selected for very early, dwarf, normal plant, good branching pistillate line called NES 6. The early nature of pistillate line resulted in very early hybrids with low seed yield and thus converted to a new agronomic background like TMV-5, using pedigree method of selection and a new pistillate line-DPC 16 with purple stem, zero bloom, spiny capsules with medium duration (12–14 nodes), unlike NES 6 (> 10 nodes) having a unique trait like hermaphrodite flower at the tip of the pistillate line was developed. A list of sources along with the pedigree and the pistillate lines developed in India is given in Table 3.3.

DPC-18, a medium duration, non-VP-1 based pistillate line, was generated by inter-varietal hybridization involving a triple-cross-derivative 163-1-10-2 (Bhagya × CO-1 × HC-8) and a wilt-resistant variety 48-1. IPC-23 (DPC-23), a mutant pistillate line developed from a zero bloom, leaf hopper susceptible DPC-9 pistillate line, with green stem, triple bloom, low node number (7–8), short plant height (40–50 cm), early flowering (30–40 days to 50% flowering), was resistant to leaf hopper and Fusarium wilt and good combiner for early flowering and maturity (Lavanya et al. 2008, 2018). Inter-varietal hybridization involving different castor hybrids, pistillate lines helped to generate

Table 3.3 Diversified sources of pistillate character in castor (ICAR-IIOR, Hyderabad)

Source	Pedigree	Pistillate lines developed
S-type	TSP-10R × VP-1	LRES-17, DPC-9, DPC-10, DPC-14, DPC-21, DPC-25
NES type	240	NES 6, DPC 15, DPC 16, JP-65
	163-1-11 × 1501-4	DPC 11
Mutant VP-1	VP-1 with 55 Kr gamma rays	M 571, M 574, M 619, M 584
Hybridization	163-1-10-2 × 48-1	DPC 18 (new)
	M 619 × JI 225 F_4	DPC 17 (new)

Table 3.4 Pistillate lines registered by PGRC, ICAR-NBPGR for unique traits

Pistillate line	Registration No.	Pedigree	Special features
LRES 17	INGR 01010	VP-1 × HC 8	Green, triple bloom, spiny, dwarf, condensed nodes, cup leaves, resistant to Jassids
DPC 9	INGR 01009	87-V-2-1	Non-revertant, S-type pistillate, green, zero bloom, spiny, resistant to Fusarium wilt
M 619	INGR 03095	Mutant of VP-1 (55 Kr gamma rays)	Green, triple bloom, spiny, dwarf, condensed nodes, cup leaves, resistant to Fusarium wilt
MCP 1-1	INGR 04121	Selection from VP-1	Mahogany, triple bloom, spiny, dwarf, cup leaves, resistant to leaf hoppers
DPC-16	INGR 14003	NES-6 × TMV-5	Pistillate line unique for hermaphrodite flower at the tip of the spike, purple stem, zero bloom

new pistillate sources through recombinants or transgressive segregates and about 15 diverse pistillate lines were stabilized after 12–15 generations of selection pressure for pistillate character. Table 3.4 is a list of five pistillate lines registered for their unique or specific traits by Plant Germplasm Registration committee (PGRC), ICAR-NBPGR.

Evaluation of pistillate lines in different sowing seasons indicated variation in the expressivity of the ISF character with either one or two male flowers or > 10 male flowers per spike in all the pistillate lines irrespective of the sowing season. Variation is due to a complex phenomenon of both genetic and environmental factors like monthly mean day temperatures at the time of spike initiation, triggering mechanisms or the role of modifying genes. Sowing in the months of July and August leads to high ISF production in female lines and low genetic purity of hybrid seed produced. September and October are ideal months for sowing of certified hybrid seed production while January is ideal for sowing of foundation seed production of pistillate lines.

3.17.3 Male Lines

Male or inbred line in castor is a monoecious line with a balanced proportion of both male and female flowers. The criteria for selection of an inbred line as a male line for testing its combining ability are based on several characters like earliness compared to the female parent, desirable agronomic characters, closely maturing secondary and third-order spikes, resistance to Fusarium wilt, non-shattering, balanced proportion of male and female flowers on the raceme, high 100-seed weight (28–35 g), and high oil content (48–55%). A dominant marker gene to estimate the hybridity in the F_1 especially a seedling character like stem or hypocotyl color is useful in early detection of rogues or off-types before flowering (Atsmon 1989). The ideal combination would be contrasting stem color characters like red and green for the male and female parents (Lavanya and Solanki 2010).

Several inbred lines were developed by intraspecific hybridization involving pest- and disease-resistant germplasm accessions in combination with agronomically suitable cultivars, parental lines, etc., either in single-, double-, triple-, or backcross followed by pedigree method of selection. Male lines with early or medium duration (150 days), short-to-medium height, high oil content, resistance to wilt complex, and insect-pests were evaluated for their combining ability in a series of line × tester crosses. Among more than 1000 inbred lines available in the country, some of the inbred lines like DCS-5, DCS-9, 48-1, DCS-78, DCS-89, DCS-107, TMV-5, and TMV-6 were repeatedly used in the hybrid development programs. Male lines with good agronomic adaptability, per se performance, and combining ability are ideal for male lines (Costa et al. 2006; Lavanya and Varaprasad 2012).

3.18 Hybrids

The first castor hybrid in the world, GCH 3 (TSP-10R × JI-15), was an instant success due to its high yielding ability (88% yield increase over S-20), drought resistance, medium maturity (140–210 days), high oil content (46.6%) and was popular even in the rainfed castor-growing area. The problem of non-shattering was overcome in another early maturing hybrid, GAUCH-1 (VP-1 × VI-9) with 16% yield increase over GCH 3 and drought escape mechanism due to efficient root system than the varieties under receding moisture conditions (Reddy et al. 1999). Another hybrid GCH 2 (VP-1 × JI 35) was released in 1985 for irrigated areas of Gujarat with tolerance to root rot, 13% yield increase over GAUCH 1. The hybrid has spikes with interspersed male flowers increasing the number of capsules in higher-order spikes (Lavanya et al. 2006).

Among the 18 hybrids released so far in the public sector system, GCH-4 is high yielding (1200–2200 kg/ha), suitable for rainfed and irrigated conditions, tolerant to wilt and still the most popular hybrid even after 32 years of release. It also gave the world's highest seed yield (9 tons/ha), as a perennial crop under intensive cultivation with high inputs near riverbanks of Khisurpuri regions of Ahmedabad district (Lavanya et al. 2006). It was replaced by the latest high-yielding hybrid GCH-7 (3000 kg/ha), which is resistant to both Fusarium wilt and reniform nematode complex. Table 3.5 represents three early duration, high-yielding, wilt- and leaf hopper-resistant hybrids, viz. DCH 32, DCH 177, DCH 519, suitable for rainfed and irrigated conditions which were developed from ICAR-IIOR, Hyderabad. Hybrids like YRCH-1, PCH-111, PCH-222 were released for rainfed conditions of Tamil Nadu and Telangana states of Southern India. More than 70% area of castor is under hybrid cultivation with a seed replacement rate (SRR) of 100%. However, for remaining area SRR is about 28–30% with varietal cultivation. Castor, being a commercial crop in Gujarat, about 43 private seed companies registered 88 experimental hybrids for commercial sale during 2010 (agri.gujarat.gov.in). More than 95% of the castor-growing area in Gujarat is occupied by castor hybrids, and the rise in productivity is spectacular from 350 to 1970 kg/ha (Damodaram and Hegde 2010).

3.19 Resistance Breeding

3.19.1 Resistance to Fusarium Wilt

Fusarium wilt caused by *Fusarium oxysporum* f. sp. *ricini* (*F.o.ricini*), a soil-borne fungus, is a destructive disease causing 39–77% loss in production (Pushpavati et al. 1998). The success of any resistance breeding program relies upon the basic information on etiology of pathogen, inheritance pattern of resistance, and development of standard screening procedures, availability of resistant sources, and reliable breeding methods for incorporation of the disease resistance (Lavanya and Solanki 2010). Standard screening procedures through development of sick plot and artificial inoculation in pot culture conditions were developed in AICRP castor system (Santha et al. 2014). A large number of germplasm accessions, breeding lines, varieties, and hybrids were identified in sick plots developed at three AICRP castor centers (Table 3.6). Several inbred lines were developed by intraspecific hybridization, involving wilt-resistant sources either in single-, double-, triple-, or backcross followed by pedigree method of selection.

The inheritance and genetics of resistance to Fusarium wilt varied with each cross and controlled either by recessive genes (Sviridov 1988; Podkuichenko 1989; Lavanya et al. 2011; Rao et al. 2005), dominant genes (Reddy et al. 2010, 2011), interaction of duplicate genes (Sviridov 1988); polygenes (Desai et al. 2001), or oligogenes with epistatic interactions (Lavanya et al.

Table 3.5 Salient features of castor hybrids in seed chain

Hybrid	Mean seed yield (kg/ha)	Areas recommended	Salient features
GCH 4	1200 (R) 2200 (I)	Both rainfed and irrigate areas, all over country	Resistant to leafhoppers, tolerant to Fusarium wilt
GCH 5	1800 (R) 2800 (I)	Rainfed and irrigated areas of Gujarat	Red, double bloom, medium duration (120–180 days), semi-spiny, wilt tolerant.
DCH 177	1550 (R) 2130 (I)	Rainfed areas of Andhra Pradesh, Karnataka, Tamil Nadu, Maharashtra, and Orissa	Red single bloom, spiny, early duration (90–150 days), resistant to Fusarium wilt, both parents are resistant to wilt
DCH 519	1740 (R) 2130 (I)	All over the country	Green, triple bloom, spiny, resistant to Fusarium wilt, leaf hoppers, and both parents are resistant to wilt.
GCH 7	3000 (I)	Irrigated areas of Gujarat	Resistant to nematode-wilt complex
HCH-6	1800 (R)	Karnataka	Resistant to wilt and white fly
GNCH-1	2500–3000 (I)	Late kharif, rabi Gujarat	Resistant to wilt and leaf hopper
GCH-8	1895 (R) 3590 (I)	All over the country	Resistant to wilt and leaf hopper
YRCH-2	2100 (R)	Tamil Nadu	Resistant to wilt

R Rainfed; *I* Irrigated

Table 3.6 Parental lines and hybrids resistant to wilt complex

Disease	Male lines	Pistillate lines	Hybrids
Fusarium wilt	SKI 232, 271, 291, 293, 252, 263, JI-273, 274, 296, 298, 299, 303, 314, 315, 319, 320, 322, 326, 327, 331, 338, 340, 342; DCS 5, 9, 33, 57, 84, 85, 86, 86-1, 89, 97, 98, 100, 102, 103, 104; PCS 124, 171, M-36-03, 35-03, 3-04 (PVT 16-03), 7-04 (F6-235-3-03).	SKP 23, 42, 72, 84, 106, 112, 117, 118, 119, Geeta, JP 81, 83, 85, 86, 88, 90, 93, 96, DPC 9, 11, M 584, 571, 619	GCH 4, 5, 7, DCH 177, 519
Macrophomina root rot	JI-220	JP-81, 86, 88, 89, 93 and 96, M-584, 619	GCH 6
Reniform nematode	–	M-619	GCH-7

2011). However, for the development of a wilt-resistant castor hybrid, both the parents should be wilt resistant (Desai et al. 2001; Lavanya et al. 2011). The inheritance of resistance in 48-1, a highly resistant variety is governed by two recessive genes (Rao et al. 2005). In a cross between susceptible and resistant parents, hybrids have a tendency toward susceptible parent (Golakia et al. 2005). Breakdown of resistant cultivars is a serious problem, especially in high-intensive cultivation without proper crop rotation. Heterotic and wilt-resistant hybrids should be further exploited through recurrent selection and inter se mating in segregating generations for developing wilt-resistant parental lines (Patel and Pathak 2011).

Several sources of resistance to Fusarium wilt were incorporated in high-yielding, agronomic background leading to the development of several inbreds, pistillate lines, and hybrids (Lavanya et al. 2006). Prominent among them were DCS-9, 48-1, Haritha, DCS-107, DPC-9, M-574, M-619, DCH-177, DCH-519, GCH-7, etc.

Several preliminary hybrids, advanced breeding material, parental lines were identified as wilt-resistant consecutively for two years while DCS-86, DCS-105, DCS-107, DCS-118, DPC-23, and M-571 were the ideal wilt-resistant parental lines with consistent wilt reaction (9–18%) compared to susceptible check, JI-35 (94–96%) in the sick plot (Santha et al. 2016).

3.20 Summary

The present chapter on classical genetics and traditional plant breeding methods is an attempt to consolidate the scattered information available on different aspects. A brief history of genetics of different morphological characters and the complexity of sex expression provides the base for the future breeding programs. Several gaps in traditional plant breeding methods like development of a stable CMS system, resistance to Botrytis gray mold rot, and the complexity of sex reversion can only be addressed through collaborative and multidisciplinary approach.

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