A Review on the Challenges for Increased Production of Castor


ABSTRACT

Castor (Ricinus communis L.) is one of the oldest cultivated crops, but currently it represents only 0.15% of the vegetable oil produced in the world. Castor oil is of continuing importance to the global specialty chemical industry because it is the only commercial source of a hydroxylated fatty acid. Castor also has tremendous future potential as an industrial oilseed crop because of its high seed oil content (more than 480 g kg⁻¹), unique fatty acid composition (900 g kg⁻¹ of ricinoleic acid), potentially high oil yields (1250–2500 L ha⁻¹), and ability to be grown under drought and saline conditions. The scientific literature on castor has been generated by a relatively small global community of researchers over the past century. Much of this work was published in dozens of languages in journals that are not easily accessible to the scientific community. This review was conducted to provide a compilation of the most relevant historic research information and define the tremendous future potential of castor. The article was prepared by a group of 22 scientists from 16 institutions and eight countries. Topics discussed in this review include: (i) germplasm, genetics, breeding, biotic stresses, genome sequencing, and biotechnology; (ii) agronomic production practices, diseases, and abiotic stresses; (iii) management and reduction of toxins for the use of castor meal as both an animal feed and an organic fertilizer; (iv) future industrial uses of castor including renewable fuels; (v) world production, consumption, and prices; and (vi) potential and challenges for increased castor production.

CASTOR IS a member of the Euphorbiaceae family that is found across all the tropical and semi-tropical regions of the world (Weiss, 2000). Castor oil is nonedible and has been used almost entirely for pharmaceutical and industrial applications. Since castor is not a legume researchers should avoid the use of the term “castor bean” frequently found in the literature on this crop. Castor was initially believed to have four centers of origin: (i) East Africa (Ethiopia), (ii) Northwest and Southwest Asia and Arabian Peninsula, (iii) India, and (iv) China. However, Ethiopia is considered to be the most probable site of origin because of the presence of high diversity (Anjani, 2012). Earlier taxonomists also divided the genus Ricinus into several species and subspecies (R. persicus Popova, R. chinensis Thunb., R. zanzibaricus Popova, R. sanguineus Groenl., R. africans Willd. etc.); however, most botanists now believe that all castor groups belong in the same species. The division into several subspecies was probably based on eco-geographical grouping or morphological characters. Because most castor accessions readily intercross, produce fertile progeny, and have the same chromosome number, castor is now considered to be a single species (Anjani, 2012). For detailed reports on castor origin, taxonomy, history, and geographic distribution, see Moshkin (1986), Brigham (1993), Kulkarni and Ramanamurthy (1977), DOR (2003), Filho (2005), and Anjani (2012).

GENETICS

Germplasm Collection and Conservation

The major repositories of castor germplasm are located in 10 countries and contain a total of 11,300 accessions (Table 1). The USDA, ARS, Plant Genetic Resources Conservation Unit at Griffin, GA, has accessions collected or donation from 51 countries (Morris and Wang, personal communication, 2012). The Germplasm Maintenance Unit in the Directorate of Oilseed Research (India) has the largest collection with 4307 accessions, of which 365 are exotic collections from 39 countries (Anjani, 2012). Two repositories in Brazil, which in previous reports listed as Cenargen/Embrapa and Centro Nacional de Pesquisa de Algodão (CNPA), are now a single germplasm bank (Embrapa) possessing 620 accessions (Milani, personal communication, 2012). A repository with 424 accessions is maintained in Colomac by Corpoica (Navas, personal communication, 2012).

Abbreviations: DAE, days after emergence; DOR, Directorate of Oilseeds Research; ELISA, enzyme-linked immunosorbent assay; HI, harvest index.
The resources available in castor germplasm banks worldwide have been barely tapped for genetic improvement, and the majority of them have been poorly characterized (Anjani, 2012; Milani, personal communication, 2012). The use of germplasm resources by the global castor community could be increased if there were uniform characterization of accessions, consolidated reports on available resources, free access to information on banks, and uniform collection standards among repositories (Anjani, 2011). These enhancements would allow an estimate of the genetic variability with single collections without the flux of accessions between countries. Germplasm characterization would also be easier if fast, nondestructible, and reliable screening methods were developed. An example is the quick and nondestructive method for estimating ricinoleic fatty acid content from which genotypes tailored for biodiesel fuel could be developed. The accessions in the germplasm bank in Colombia were characterized using morphological descriptors as well as molecular markers (Navas, unpublished data, 2012).

Some castor germplasm repositories are at risk due to lack of consistent funding since many of these gene banks are located in countries with unstable funding. Maintenance of germplasm accessions is expensive due to the need for continuous seed regeneration. In the USDA,ARS,PGRCU repository, regeneration is initiated when the germination rate of the seed stock drops below 70% or the number of seeds in an accession drops below a preset threshold. In the regeneration process, 50 seeds from each accession are planted in 6 m rows; fruits are hand-harvested at maturity; dried at 21°C with 25% relative humidity for about 1 wk before being threshed. Phenotypic data of critical plant descriptors are recorded during regeneration. Seeds are counted, weighed, and stored at 4°C for short-term storage and at –18°C for long-term storage (Morris and Wang, personal communication, 2012). Storing seeds at –80°C is being used in Brazil without significant loss of germination potential (Milani, personal communication, 2012). When the seed does not germinate, an accession can still be regenerated using tissue culture techniques.

Under natural conditions, cross pollination in castor can exceed 80% (Filho, 2005), but the actual level of cross pollination is dependent on both genotype and environmental conditions. Since pollination occurs primarily by wind distribution of the pollen, genetic purity of an individual accession can be maintained by planting in isolation (usually 1000 m from other accessions) or covering the inflorescence with a bag (Rizzardo, 2007). This later option is labor intensive and expensive, but usually more practical. Storing pollen is another option for germplasm conservation. Vargas et al. (2009) observed that castor pollen grains were viable after being stored at temperatures of –196°C, –80°C, and –18°C for up to 30 d. There is evidence that pollen viability would be retained for long periods with cryopreservation at –80°C.

### Table 1. Major germplasm repositories of castor in the world (*Ricinus communis* L.).†

<table>
<thead>
<tr>
<th>Country</th>
<th>Repository</th>
<th>No. of accessions</th>
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<tbody>
<tr>
<td>Brazil</td>
<td>Embrapa</td>
<td>620‡</td>
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<tr>
<td>Brazil</td>
<td>Empresa Baiana de Desenvolvimento Agricola S.A.</td>
<td>528</td>
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<tr>
<td>Brazil</td>
<td>Instituto Agrônomico de Campinas (I.A.C.)</td>
<td>200</td>
</tr>
<tr>
<td>China</td>
<td>Institute of Crop Science (CAAS)</td>
<td>1,689</td>
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<tr>
<td>China</td>
<td>Institute of Oil Crops Research (CAAS)</td>
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<td>Colombia</td>
<td>C.I. La Selva–CORPOICA</td>
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<td>Ethiopia</td>
<td>Biodiversity Conservation and Research Institute</td>
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<tr>
<td>India</td>
<td>National Bureau of Plant Genetic Resources</td>
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<td>Kenya</td>
<td>National Dryland Farming Research Station</td>
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<tr>
<td>Kenya</td>
<td>National Genebank of Kenya, Crop Plant Genetic Resources Centre, KARI</td>
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<tr>
<td>Romania</td>
<td>Agricultural Research Station Teleorman</td>
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<tr>
<td>Russia</td>
<td>N.I. Vavilov-All-Russian Scientific Research Institute of Plant Industry</td>
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<td>Serbia</td>
<td>Maize Research Institute</td>
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<tr>
<td>Serbia</td>
<td>Institute of Field and Vegetable Crops</td>
<td>43</td>
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<tr>
<td>Ukraine</td>
<td>Institute for Oil Crops</td>
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<tr>
<td>United States</td>
<td>USDA,ARS, PGRCU</td>
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<tr>
<td>United States</td>
<td>USDA,ARS, NCGRP</td>
<td>679</td>
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<tr>
<td><strong>Total:</strong></td>
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<td><strong>11,300</strong></td>
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Genetics of Important Traits

Understanding the genetics of economically important traits is essential for castor breeding. Earlier studies on inheritance of phenotypic traits need to be confirmed using modern cultivars and molecular assisted techniques (Milani and Zanotto, personal communication, 2012). Many morphological and qualitative traits are controlled by one or few genes. Stem color was reported to show epistatic interaction of two genes, ‘M’ (mahogany) and ‘G’ (green). The combination ‘MG’ results in a rose coloring, ‘Mg’ a mahogany, ‘mG’ a green, and ‘mg’, a tinged coloring on the stems (Harland, 1928; Peat, 1928). Tall plants are dominant over dwarf plants due to a monogenic factor. Characters like bloom, compactness of spike, presence of spines on the capsule, and branching of the stalk appear to be controlled by partial dominance and simply inherited (Rao et al., 2009). Earlier studies indicated complete or partial dominance of presence of bloom (waxy stems) over its absence. This trait showed epistasis with either two (Zimmerman, 1958) or four genes (Moshkin, 1986). The intensity and distribution of bloom on different parts of the plant appears to be controlled by multiple genes (Lavanya and Gopinath, 2008). The long petioles on castor leaves have limited the use of high plant density. A plant with short petiole was found, and this trait that is controlled by one pair of genes was transferred to the high yielding cultivar FCA-PB (Zanotto, unpublished data, 2012).

The inheritance of sex expression is particularly important in the development of hybrids. There are three types of pistillate lines that could be used for hybrid production: N, S, and NES. In the N type, the occurrence of only female flowers is controlled by a recessive gene (ff). In the S type the production of only female flowers is controlled by a polygenic complex with dominant and epistatic effects. In the S type the plant starts as female, but a reversion to the production of dioecious flowers can occur at any time. In the NES type, the plant has the recessive gene (ff) that allows it to start as female, but when air temperatures exceed 31°C there is a sexual reversion (Zimmerman, 1958; Shiff riss, 1960; Ankinneedu and Rao, 1973).

Characteristics of primary economic importance such as seed yield and seed oil content are usually inherited in a quantitative manner. Additive genetic effects were shown to be important in determining the number of nodes before flowering, number of racemes per plant, and seed oil content in studies with inbred lines evaluated in diallel crosses (Hooks et al., 1971; Swarnlata and Rana, 1984). Traits such as the length of the primary raceme, the number of capsules per primary raceme, and the seed weight have also been shown to be additively inherited (Giriraj et al., 1974; Solanki and Joshi, 2000; Solanki et al., 2003). A high heritability was reported for earliness, seed weight, and plant height (Solanki and Joshi, 2000). An extensive report on the inheritance of the components of seed yield and oil content can be found in Moshkin (1986). Studies on the general combining ability and specific combining ability for seed yield, seed yield components, and other agronomic traits were made by Pathak and Dangaria (1987), Mehta (2000), and Nóbrega et al. (2010). Significant effects of general and specific combining ability on seed yield were found in all the studies, and in most cases even genotypes with high specific combining ability had at least one parental line with high general combining ability. These results showed that selection in a conventional breeding could enhance these traits. Patel and Pathak (2011) studied the inheritance of the resistance to wilt (Fusarium oxysporum f.sp. ricinii Nanda and Prasad) and found that both the parents should be wilt resistant for developing wilt resistant hybrids.

Several breeding programs around the world are currently focused on producing castor cultivars adapted to mechanical harvest. The perennial nature and indeterminate growth habit of castor have limited success when this crop is cultivated as an annual and mechanically harvested. Plants adapted to mechanized production would ideally be short (1.0–1.5 m), have uniform maturing racemes, and produce a minimum number of lateral branches. Baldanzi and Pugliesi (1998) were successful in increasing the frequency of nonbranching plants after four cycles of selection, although successive rounds of self-pollination reduced plant vigor. The selection for short and nonbranching castor plants usually has historically been difficult due to the high genotype vs. environment interaction (Milani, personal communication, 2012).

Early maturation is another important trait for castor cultivation in regions with short growing seasons or tropical areas which produce multiple crops each year. The negative correlation between early maturity and high seed yield is the major impediment to developing very early maturing genotypes. An early maturing gene population was developed using random crosses between extra-early accessions for six generations (Anjani and Reddy, 2003). This population generated 23 accessions with high seed yield potential, and one of the accessions had 50% of the plants flowered at 26 d after planting. The early-maturity trait in these accessions appeared to be only marginally impacted by environment (Anjani, 2010b).

The genes encoding ricin have recently become an important issue because of concerns about terrorists harvesting the toxin found in the seed and meal of castor. The ricin toxin contains two subunits that are encoded by a single gene (Halling et al., 1985; Tregear and Roberts, 1992). Recurrent selection was used to develop the cultivar Brigham, a genotype with 10-fold reduction in ricin level to help address these concerns (Auld et al., 2001, 2003).

A natural mutant expressing high oleic acid and reduced ricinoleic acid in the seed was identified (Barros et al., 2004), and the high-oleic acid trait appeared to be controlled by two independent genes (ol, ML) with epistatic interaction (Rojas-Barros et al., 2005). Decreasing the ricinoleic acid content would enhance performance of castor oil as a feedstock for biodiesel.

Assessments of castor genetic and phenotypic variability through several methodologies can be found in Costa et al. (2006), Allan et al. (2008), Rao et al. (2009), Neto et al. (2010), Gajera et al. (2010), and Zheng et al. (2010). Heritability of several agronomical traits was assessed by Passos et al. (2010).

Development of Commercial Cultivars

Because castor is a cross-pollinated crop that has limited inbreeding depression, it is often treated as a self-pollinated crop in breeding programs (Moshkin, 1986; Lavanya and Chandramohan, 2003). Detailed descriptions of methods for castor breeding can be found in Kulkarni and Ramanamurthy (1977), Moshkin (1986), Lavanya et al. (2006), Auld et al. (2009), and Lavanya and Solanki (2010).

Mass selection in castor has been effective for selection of traits with high heritabilities. This technique works best with
self-fertilization of selected plants to prevent cross pollination and controlled selection techniques to reduce environmental variation (Auld et al., 2009). Mass selection with self-pollination was the most effective method for increasing the frequency of pistillate castor plants of the type NES (Bertozzo et al., 2011). Cultivars developed by mass selection included Kavkazskaya (in the former USSR), IAC-38, and BR5 Energia (in Brazil), and Conver and 'Kansaas' (in the United States) (Moshkin, 1986; Filho, 2005). Mass selection with intercrossing in isolated plots was used to develop Nila Bicentenaria, adapted to the Andean Region of Colombia (1500–2200 m above sea level) (Navas, unpublished data, 2012). The approach was also used to purify three cultivars highly variable for days to flowering and number of capsules per raceme (Reddy et al., 1999). The back cross method has been used in castor to transfer monogenic traits such as dwarf plant type, nonspiny capsules, stem color, bloom, nonshattering, plant height, and resistance to wilt.

Pedigree selection has been used for selection of high yielding families and individual plants within the families. Subsequent progeny testing for oil content and resistance to fusarium wilt resulted in the wilt resistant cultivar Violetovaya (Moshkin, 1986). Individual plant selection followed by progeny test was used in the development of the cultivar Guarany in Brazil (Amaral, 2003). Several tall-type cultivars with late maturation such as HC 1 to HC 8, EB 16 A, S-20, Junagadh 1, Punjab castor 1, EB 31, Rosy, and MC 1 were developed using this method in India (Kulkarni and Ramanamurthy, 1977). Recurrent selection has successfully reduced plant height in the cultivar Guarani by successive cycles of selection and recombination of selected lines or individual plants (Zanotto et al., 2004; Oliveira and Zanotto, 2008). In the first stage of selection, short plants were selected and self pollinated, and, in the second stage, 180 self-pollinated lines were evaluated for plant height in isolation, and 30 selected plants were self pollinated (Filho, 2005). After five cycles of selection the reduction in plant height ranged from 3.4 to 28 cm (Oliveira and Zanotto, 2008).

Three types of radiation (γ rays, fast neutrons, and thermal neutrons) were applied in castor to create variability (Kulkarni and Ramanamurthy, 1977). The cultivar Aruna was developed through thermal neutron treatment of HC-6 to reduce the apical dominance, plant height, and days to maturity (Kulkarni and Ramanamurthy, 1977). This cultivar provided significant increase in earliness of flowering (35–40 d) and fruit maturation (110–150 d). Gamma rays were also used to develop wilt resistant pistillate lines from VP-1 and double or triple bloom types from the nonflowering pistillate line DPC-9 (Lavanya et al., 2008). Several other mutagens like γ rays (40–60 kR), ethidium bromide, and diethyl sulfate (10–50 g kg⁻¹) have also been used in breeding programs (Lavanya et al., 2006).

The emphasis of current breeding programs in India is on high seed yield, increased seed oil content, and resistance to fusarium wilt, gray mold, leaf hoppers, and capsule borer (Lavanya et al., 2006; Lavanya and Solanki, 2010). Hybridization involving single, double, or triple crosses is being used to combine the traits from different sources. The pedigree method of selection of inbreds is used for five to six generations until genotypes are homozygous. Selection criteria include traits that contribute to seed yield such as long semi-compact spikes (>40 cm), number of capsules per raceme (>60), number of effective spikes per plant (>5), and seed weight (>300 mg).

Breeding to increase the harvest index (HI) is a promising avenue for improvement in castor oil yield. Castor seed HI can be as low as 0.1 (Rana et al., 2006), while in many other cultivated crops it ranges from 0.4 to 0.6. The HI can be increased by selecting for reduced structural components such as plant height, stem diameter, petiole length, capsule spines density, capsule hulls and seed coat thickness, and caruncle weight. Seed oil content could also be enhanced by reducing the protein and carbohydrate content in the extensive endosperm of castor.

The most important global challenge in the development of new cultivars seems to be the adaptation of castor plant to mechanical harvest. Although some cultivars are already suited for mechanical harvest, it is necessary to have a range of cultivars adapted to many production environments and cropping systems. Some locations will require cultivars with specialized traits such as reduced ricin content in the United States as well as tolerance to regionally prominent pests and diseases.

The development of new castor cultivars would be enhanced by improved knowledge on the genetics and molecular biology of this species. Increased interaction between plant breeders and geneticists with supporting scientists such as molecular biologists, plant physiologists, plant nutritionists, entomologists, and plant pathologists would speed the genetic improvement of castor. Recent studies on the inheritance of disease tolerance, plant architecture, cuticular wax, and use of molecular markers hold great promise in castor.

**Hybrid Production**

The development of pistillate lines has allowed breeders to successfully use heterosis (hybrid vigor) in castor. The intensity of heterosis on castor seed yield depends on both the genetic diversity and individual combining ability of the parents (Lavanya and Chandramohan, 2003; Golakia et al., 2004; Ramana et al., 2005; Lavanya et al., 2006).

Commercial exploitation of heterosis in India was almost instantly adopted after the development of VP-1, an S-type stable pistillate line derived from TSP 10 R (Texas Stable Pistillate 10R) introduced from the United States (Ankineedu and Rao, 1973). Several pistillate lines were developed using VP-1 source of pistillate expression (Lavanya et al., 2006; Pathak, 2009; Lavanya and Solanki, 2010). Other pistillate lines were developed using NES type of sexual expression, but GCH-6 is the only commercial hybrid based on that system. Several other sources of pistillate lines were identified in the germplasm bank at DOR, India (Lavanya and Solanki, 2010; Anjani, 2012). Additional studies that looked for genotypes with genetic male sterility in exiting germplasm or mutation populations were unsuccessful (Chauhan et al., 1990).

The first commercial castor hybrid, GCH 3, was developed in India. This hybrid had potential seed yields 88% higher than the existing cultivars, medium maturity (140–210 d), and high oil content (466 g kg⁻¹). Since then, a total of 15 hybrids were released in India many with resistance to fusarium wilt and high seed yield potential (Lavanya and Solanki, 2010). In the State of Gujarat the adoption of hybrid seed increased average seed yield from 350 to 1970 kg ha⁻¹. Current castor hybrids are
planted on 50 to 60% of the fields in India and up to 95% of the fields in the State of Gujarat. An alternative method for developing castor hybrids was proposed by Toppa (2011). The method of cryptic hybrids was described by Lonququist and Williams (1967) in maize (Zea mays L.) and consists of simultaneous self-pollination and crossing on the same plant followed by selection of the best progeny at each cycle. The method can be employed in castor because this plant has a limited inbreeding depression and produces more than one raceme per plant. After four cycles of selection, 12 cryptic castor hybrids had higher seed yield (1675 kg ha⁻¹) than 12 conventional hybrids (1550 kg ha⁻¹) evaluated over 2 yr in two locations (Toppa, 2011).

The rapid acceptance of commercial hybrid castor cultivars in both India and China has increased interest in future development of this technology. Improved hybrids adapted to multiple production environments with improved seed and oil yield that carry tolerance to multiple pests, diseases, and abiotic stresses represents a long-term challenge. There is also an increased demand for developing improved technology to reduce the cost of hybrid castor seed.

**Biotechnology**

Modern biotechnology offers great promise in reducing noxious compounds, enhancing seed oil content, improving seed quality, and increasing stress tolerance. Castor breeding programs could also benefit from the use of markers assisted selection in important traits. The production of oil with high levels of ricinoleic acid in other species, have been largely unsuccessful. Transgenic Arabidopsis plants expressing the castor hydroxylation gene produced oils containing <200 g kg⁻¹ of hydroxy fatty acid (Broun and Somerville, 1997). The detailed metabolism of how castor produces and stores oils with high levels of ricinoleic acid are not well understood (Lin et al., 2002; McKeon and Lin, 2002; He et al., 2004, 2005, 2007). Gaining a better understanding of castor oil biosynthesis holds promise of even higher oil contents and modified fatty acids profiles (Auld et al., 2009).

The use of genetic engineering to knock out or silence the expression of genes related to allergens and ricin could be highly productive. The genes that produce both types of proteins are highly expressed during seed development (Chen et al., 2004, 2005), but the gene expression could be suppressed up to 10,000-fold with the proper choice of promoter and application of gene-silencing techniques. However, commercial production of a transgenic castor is questionable because of the costs involved in the deregulation of a transgenic trait.

Genetic transformation of castor remains challenging because it is recalcitrant to efficient regeneration of stable, transformed plants. Regeneration of plants from callus cultures of castor has been problematic, and the lack of a protocol for plant regeneration has restricted the development of transgenic cultivars (Sujatha et al., 2008). Rapid regeneration of castor plants would also be useful for multiplication of pistillate lines for hybrid production. The use of the dihaploids in castor breeding would greatly reduce the time and expense required to generate inbred populations.

The first report of transformed castor described a vacuum infiltration technique using Agrobacterium tumefaciens vector systems and associated marker genes (McKeon and Chen, 2003). Since then, an apparently more efficient method also mediated by Agrobacterium has been developed (Sujatha and Sailaja, 2005). There are only a few reports on successful castor plant transformation and regeneration.

Most of the reported cases of successful plantlet differentiation have been obtained on apical meristems and shoot tip callus (Sujatha et al., 2008). Successful in vitro regeneration of castor stem tips was obtained on a culture medium with reduced NO₃⁻/NH₄⁺ lacking FeSO₄ (Bertozzo and Machado, 2010) together with an appropriate concentration of auxins (Lan et al., 2010). The induction of shoots on the embryo axis of castor seed was more efficient in a culture media containing thidiazuron and 300 g kg⁻¹ of glucose (Carvalho et al., 2008). Alam et al. (2010) described a protocol for in vitro induction of shoots and roots from cotyledonary nodes of castor seedlings. See Sujatha et al. (2008) for a detailed review on tissue culture in castor.

**Genomics**

The recent completion of a draft genome sequence for castor was a significant step toward the accelerated improvement of castor as a model oilseed species (Chan et al., 2010). The development of additional genomic data, a more complete genome sequence, and final assembly will ensure the development of an integrated physical–genetic map as well as the gene expression (Cagliari et al., 2010) and proteomics (Campos et al., 2010) studies needed to identify genes that encode important traits in castor. The reference genome has already allowed the identification of genes involved in oil biosynthesis (Cagliari et al., 2010) and toxin formation (Chan et al., 2010) as well as facilitating the mining of sequence polymorphisms that allow rapid characterization of castor germplasm (Foster et al., 2010; Qiu et al., 2010; Rivarola et al., 2011). Molecular marker sets developed from association or linkage studies could aid in the simultaneous selection of castor plants possessing a superior combinations of several traits.

For relatively simply inherited traits such as ricin content and high-oleic fatty acid composition with already known gene candidates, genomic information can assist both genes mapping as well as the identification of the complete set of genes relevant to a particular phenotype. These candidate genes can then be targeted for inactivation using either transgenic methods or mutagenesis. Specific mutant alleles could also be pyramided through “traditional” genetic crossing with the use of molecular markers. Because there are more than two dozen ricin homolog genes and putative pseudogenes (Chan et al., 2010), detailed knowledge of the genome and target genes will be very helpful in identifying plants with no toxin. The development of a high-quality reference genome data set with associated annotation and expression data would also strongly support approaches for the improvement of important agronomic traits.

While the published draft genome sequence for castor is of immediate value, the sequence itself remains fragmented and likely incomplete. The draft sequence is distributed across 28,500 scaffold assemblies, and the overall assembled sequence span of about 350 Mb suggests a partial coverage of the estimated 420 Mb diploid genome (KEW, 2011). There is a continuing need to create the comprehensive and contiguous genome sequence of castor necessary to construct an integrated sequence assembly including physical, genetic, and transcriptional maps. A growing abundance of tools and resources are in place to support the rapid development of a detailed genome sequence and organization.
information data set for castor. Given the relatively small size of the castor genome, diploid genetics, established genetic diversity, wide range of adaptation, and tremendous potential as a plant oil feedstock, castor can serve as a model species for the emerging bio-industrial chemical and bio-energy sectors.

Agronomy

Agricultural Practices

In most of the regions of castor production, seed yield can be rapidly increased with the use of improved agronomic practices. The main technologies include selection of the appropriate cultivar combined with use of good quality seed, appropriate planting date, irrigation, soil fertilization, management of weed, pest, and diseases, optimized plant population, mechanical harvesting, and postharvest management.

Optimizing planting population is an inexpensive practice that can significantly increase castor seed yield. However, the optimum plant population varies influenced by the genotype, environmental conditions, and agricultural practices. Because environmental conditions are not constant, there is not an individual plant density that can be broadly recommended for castor. Instead, researchers should focus on determining a range of plant populations targeting the best yield across years and environmental conditions. As an example of environment influence, plant populations recommended for the cultivar BRS Nordestina (tall type) in different locations were 5000 plant ha–1 (Severino et al., 2006d), 4200 plant ha–1 (Severino et al., 2006a), and 12,500 plant ha–1 (Carvalho et al., 2010). In the cultivar Guarani (tall type), plant populations ranging from 10,000 to 22,222 plant ha–1 did not affect seed yield (Bizinoto et al., 2010). In the cultivar FCA-PB (short type), the seed yield was 22% higher (4100 kg ha–1) using an optimized plant population in the range of 55,000 to 70,000 plant ha–1 and row spacing of 0.45 to 0.75 m (Soratto et al., 2011).

Planting date can also influence castor seed yield. Castor seed yield varied from 89 to 1954 kg ha–1 among four locations and six planting dates in the States of Mississippi and Tennessee (Baldwin and Cossar, 2009). The greatest yields were obtained with early spring planting. Planting date also impacted the occurrence of pests and diseases in the State of Rio Grande do Sul, Brazil (Zuchi et al., 2010a).

Studies on seed yield components suggested that the increase of one yield component does not always result in a proportional increase in seed yield because other components compensate (Fanan et al., 2009; Zuchi et al., 2010c). Studies vary regarding the impact of first, second, and third racemes on final seed yield because of the genotype and environmental factors (Fanan et al., 2009; Neto et al., 2009; Zuchi et al., 2010b; Silva et al., 2010c). In castor plants subjected to repeated defoliations, the seed yield component with the widest adaptation was the number of racemes (Severino et al., 2010).

It has been historically believed that plants with a higher proportion of female flowers in relation to male flowers would produce higher seed yield (Severino et al., 2006c; Bertozzo et al., 2011). However, the ratio of female to male flowers is highly sensitive to environmental conditions. The proportion of female flowers is reduced by temperatures above 30°C, increasing plant age, higher raceme position, inadequate mineral nutrition, and sudden changes in temperature (Lakshmamma et al., 2002; Lavanya, 2002; Neeraja et al., 2010). Consequently, the proportion of female flowers ratio influence on seed yield needs to be further investigated. Recent research indicates that castor seed yield does not appear to be sink-limited but source-limited (Severino, unpublished data, 2012). Therefore, increasing the proportion of female flowers would not necessarily increase seed yield if assimilates and nutrients were in fact the factor limiting seed production.

India has been successful in the development of high yielding hybrids, but further seed yield increases can be achieved. In the State of Tamil Nadu (India), a 72% seed yield increase was obtained with adoption of hybrids, better weed management, and pest control (Manickan et al., 2009b). The average seed yields in India range from 1864 kg ha–1 in the State of Gujarat to 371 kg ha–1 in the State of Andra Pradesh, where the crop has been predominantly grown without irrigation on marginal soils (Basappa, 2007).

In Brazil, seed yields have averaged 667 kg ha–1 over the last 10 yr (CONAB, 2011). The State of Parana has the highest average seed yield in the country (1600 kg ha–1) due to better soil fertility and agronomical practices (Silva et al., 2009). The use of high-yielding castor genotypes has been very limited because of not-mechanized production, limited use of fertilization, and the lack of good agronomic practices (Santos et al., 2001). Hence, 90% of the castor is grown in Brazil on small farms of <5 ha, with the use of low quality seed, poor management, insufficient technical assistance, primitive agronomical practices, and scarcity of credit (Queiroga and Santos, 2008; Silva, 2009).

Propagation of castor using seedlings started in plastic bags or root plugs has been studied as an alternative for regions with short-growing seasons (Lima et al., 2006a, 2006b, 2007b). While castor production is feasible under such conditions, it is limited by the fragile castor roots, malformed root systems, and the high costs of production.

In a no-till system, the highest castor seed yield was obtained when the previous crop was a mix of sunhemp (Crotalaria juncea L.) and pearl millet (Pennisetum glaucum L.). It seems that the high N content of sunhemp and the high biomass volume of pearl millet created an ideal environment for castor production (Silva et al., 2010a). However, chopping the mulch before planting castor caused a quick decomposition of the covering biomass and reduced castor seed yield (Silva et al., 2010a).

Castor plants can lose leaves because of pests, diseases, wind, hail, machinery traffic, and inappropriate use of herbicides and defoliants. A castor plant can recover from a drastic defoliation; however, damage to leaves always causes a reduction on seed yield. For each 1 m² of lost leaf area, production is reduced by 37.8 g of seed and 24.4 g of oil (Lakshmamma et al., 2009a; Lakshmi et al., 2010; Severino et al., 2010).

Two systems for castor production differing in the degree of mechanization were compared for energy returned over the invested energy (EROI) (Silva et al., 2010b). The system with less intensive mechanization consumed less energy and had a higher relative energy gain. This low-mechanization system produced less net energy and required more cropping area to produce a similar amount of net energy. The production of 1000 GJ of net energy required an area of 66.2 ha with low-mechanization compared to 37.5 ha with highly mechanized crop production (Silva
The EROIs of both production systems showed that castor was not very efficient as an energy source. This area needs further study if castor is to be considered as a viable biofuel feedstock.

Although mechanized harvest is a priority for expanded castor production, there is no study on mechanization of castor production besides breeding for appropriate plant architecture. Some topics for future research on mechanization include the optimization of harvesting machinery, development of options for mechanized harvest of small fields, managing fruit maturation and dehiscence to optimize harvest, influence of harvest on seed quality, postharvest seed quality, necessity of dedicated castor machinery, and the cost of mechanical harvesting.

Seed

An issue that deserves attention from scientists is the slow, irregular, and cold-sensitive germination of castor seed. Minimum temperature required for germination is 14 to 15°C, the optimum temperature is 31°C, and the maximum temperature is 36°C. Often low soil temperatures delay germination and seeding emergence resulting in irregular stands (Moskkin, 1986). Bianchini and Pacini (1996) suggested that the caruncle in castor seed could have some role in the germination process. Some studies showed that removal of caruncle does not affect germination, and it can even make the germination occur faster (Lagoa and Pereira, 1987; Martins et al., 2006; Sousa et al., 2009). Removing the caruncle had no influence on the germination of castor seed under several levels of soil moisture and salinity (Severino et al., 2012). The caruncle (also called elaiosome) is a dispersion mechanism commonly found in species of the Euphorbiaceae family. Many ant species attracted to the nutrients present in the caruncle carry the seed to their nests to feed on the caruncle. Once in the nest chambers, the seeds can germinate under near optimum conditions (Martins et al., 2006, 2009; Pikart et al., 2010).

Mendes et al. (2010) compared many tests for determining the vigor of castor seed and found that often the germination rates observed in laboratory tests do not correlate well with emergence rates under field conditions. The best estimates of seed emergence in soil was found with tests of emergence after accelerated aging (41°C, 72 h, 100% relative humidity) or under cold tests (seeds were put to germinate in wet paper at 10°C for 7 d, followed by 25°C for 5 d). Accelerated aging at 45°C and 100% relative humidity caused almost complete seed deterioration and prevented the measurement of seed vigor. Electrical conductivity tests were also shown to have limited application for castor seed (Mendes et al., 2010). There was also a low correlation between the tetrazolium test and other tests for seed germination, emergence, and vigor. Nevertheless, the tetrazolium test is useful in assessing the viability of castor seed (Gaspar-Oliveira et al., 2010).

The quality and vigor of castor seed have also been analyzed by X-ray images (Carvalho et al., 2010b). The seeds were classified according to the internal morphology and apparent level of reserves. The opaque and full seeds had higher germination, emergence, and vigor than those seeds that were empty or had a malformed embryo.

Postharvest seed dormancy has been reported in some castor genotypes, but it has not been seen as a major constraint for most of the current commercial cultivars (Lago et al., 1979; Weiss, 2000). Machado et al. (2010) observed that 9.3% of seeds were dormant just after harvest, which decreased to 5.5% when stored for 12 mo at room temperature. The seed stored for 1 yr suffered no reduction in germination and produced seedlings with higher dry matter and longer roots. After storage for 5 yr at ambient temperature, the seed had a maximum survival of 65 to 70% (Pandey and Radhamani, 2006). No difference on seed germination and vigor was found among primary, secondary, and tertiary racemes (Machado et al., 2010). Scarification with sulfuric acid caused a drastic reduction in germination rate of castor seed (Sousa et al., 2009). Accelerated aging of castor seed did not cause reduction in height, stem diameter, or leaf area of the resulting plants (Lopes et al., 2008).

The process of water absorption in castor seed consists of a 24-h phase of fast water absorption that slows after the moisture content reaches 350 to 400 g kg⁻¹. The rate and maximum level of water absorption was influenced by the physiological quality of castor seed. Castor seed can germinate at a moisture level of 40% field capacity or less but quick swelling and germination occurs in soils at 60 to 80% field capacity (Sousa et al., 2008). The castor seed germination was null in a soil with 22% of field capacity, but increased to 44.8% when the soil had 29% of field capacity (Severino et al., 2012). Castor seed coat was found to be impermeable to many organic chemical compounds, when compared to soybean (Glycine max L.) and switchgrass (Panicum virgatum L.) seeds that are considered permeable and semi-permeable, respectively (Salanenka and Taylor, 2009).

The dynamics of water and seed dry weight accumulation is equal among raceme position in the plant, but it does differ among genotypes. Physiological maturity is attained when seeds had a water content of 21.8 ± 2.4% (Vallejos et al., 2011). The impact of drying during maturation on germination of castor seed was studied by Kermode and Bewley (1985). They found that beginning at 25 d after pollination (midway in the seed development) castor seed can germinate if they are dried slowly while only completely mature seed can be fast dried and still develop into normal seedlings.

Castor seeds were divided in five classes according to seed coat color during maturation ranging from black to yellow. The immature seeds with a lighter colored coat are smaller, lighter, and contain less oil. The N and P content in these seeds were proportional to seed weight. However, the amount of potassium in the seed keeps constant while the seed weight increases due to dry matter accumulation (Lucena et al., 2010).

Physical properties and the fine structure of castor seed were studied by microscopic techniques to provide information for industrial processing. True seed density was 1458 ± 27 kg m⁻³, bulk density was 538 ± 11 kg m⁻³, and thickness of seed coat was 281.97 ± 13.21 μm. The lipid bodies in castor seed’s endosperm were also bigger (12.63 ± 1.30 μm in diameter) than other oilseeds such as peanut (Arachis hypogaea L.) (Perea-Flores et al., 2011).

Fertilization and Plant Nutrition

A castor field yielding 2000 kg ha⁻¹ of seed will remove 80 kg ha⁻¹ of N, 18 kg ha⁻¹ of P₂O₅, 32 kg ha⁻¹ of K₂O, 13 kg ha⁻¹ of CaO, and 10 kg ha⁻¹ of MgO from the soil (Filho and Freire, 1958). If husks are not returned to the soil after crushing, this removal is even higher (Severino et al., 2006b).
A detailed review on uptake, translocation, and partitioning of nutrients in castor can be found in Peuke (2010).

In Brazil, maximum seed yields were obtained with an application of 59 kg ha\(^{-1}\) of N, while no effect of additions of P, K, or minor nutrients was observed (Severino et al., 2006c). Mineral fertilizers were more effective than bovine manure for supplying N due to slow mineralization of organic materials in a semiarid environment (Severino et al., 2006b). Silva et al. (2007) observed increased castor seed yield when N-rich fertilizers were added up to 80 kg ha\(^{-1}\). The best time for N application for two hybrids cultivated as second crop in a non-till system varied according to the genotype and environmental conditions (Moro et al., 2011). The application of P increased castor seed yield in a soil with high levels of K and organic matter (Pacheco et al., 2008), and in an acidic soil in the State of Alagoas, Brazil (Silva et al., 2012). When water was a more limiting factor than soil nutrients, castor seed yield showed only a limited response to N, P, and K fertilizers (Neto et al., 2009). When castor was cultivated in rotation after sugarcane, seed yield was increased by 90% when the soil was fertilized with 10 t ha\(^{-1}\) of sewage sludge (Chiaradia et al., 2009). In India, seed yield increases in irrigated castor hybrid GCH-4 were observed after fertilization with N and K (Hadvani et al., 2010).

In semiarid regions of India where deficiency of S, B, and Zn are widespread, the fertilization with these three nutrients increased the seed yield of rain-fed castor in commercial fields from 757 to 1043 kg ha\(^{-1}\) over 3 yr of study. When N and P were also applied, seed yields were increased an additional 15% (Sahrawat et al., 2010). In an acidic (pH 4.2), dystrophic, Red Latosol, the addition of lime increased castor seed yield, but addition of Zn had no effect on plant growth or production (Leles et al., 2010). Castor seed immersed in solutions containing the micronutrients Fe, Zn, and Mo before germination exhibited increased germination rates and seedling dry mass but a reduced germination rate when treated with B (de Oliveira et al., 2010).

Boron is usually considered immobile in the phloem of castor. Consequently, a foliar application of B is not expected to be effective. However, Eichert and Goldbach (2010) demonstrated that the phloem mobility of B is high if the xylem flow rate is low (i.e., under high relative humidity of air or dry soil conditions). Under these conditions, it appears that B can be taken up and translocated from the leaves to the developing seeds. Description and illustration of the symptoms of macronutrients and micronutrients deficiency in castor can be found in: Lavres et al. (2005), Lange et al. (2005), Lakshmamma and Lakshmi (2005), Severino et al. (2009), and Lavres et al. (2009).

**Irrigation**

Castor plants have high levels of drought tolerance, but seed yields are reduced under limited water supply. Castor can produce a low seed yield under low water availability where some species would not make a crop; however, only with an adequate water supply seed yield can be optimized, particularly with genotypes with high yield potential. Under an optimized irrigation level, a seed yield of 3780 kg ha\(^{-1}\) was obtained in India with the hybrid GCH-5 (Raj et al., 2010). In Greece, the seed yield of 1080 kg ha\(^{-1}\) observed on the hybrid Pronto with 147 mm of rain was increased to 4040 kg ha\(^{-1}\) due to the addition of 363 mm of water through irrigation (Koutrubas et al., 1999).

Seed yields of rain-fed castor fields can be increased by small amounts of supplementary irrigation (Sharma et al., 2010). The seed yield of BRS Nordestina increased from 873 to 1301 kg ha\(^{-1}\) with early planting and irrigation of 130 mm before the regular rainy season (Neto et al., 2010). A castor field produced 1774 kg ha\(^{-1}\) of seeds without irrigation, 2199 kg ha\(^{-1}\) with a supplementary irrigation at the end of the growing season, and 4252 kg ha\(^{-1}\) with supplementary irrigation before and after the rainy season (Souza et al., 2007).

**Weed Management**

Because the growth of the castor leaf area is slow in the early phases of development, weeds are able to grow quickly and cover the soil. The critical period of weed control varies according to environmental conditions and cultivar. The most critical period was 21 to 56 days after emergence (DAE) for a tall genotype planted at 5000 plants ha\(^{-1}\) (Azevedo et al., 2001), 9 to 41 DAE for an early maturing and short hybrid (Maciel et al., 2007a), and 14 to 42 DAE for a short hybrid planted at 45,000 plants ha\(^{-1}\) (Tropaldi et al., 2009).

There are some selective pre-emergence herbicides for castor, such as Trifluralin, Pendimethalin, and Clomazone. These herbicides are effective against monocotyledons, but they are less effective against broad-leaved plants (Maciel et al., 2007b; Manickan et al., 2009a). Chlorimuron-ethyl is the only post-emergence herbicide effective against broad-leaved plants reported to be selective in castor (Sofatti et al., 2012). A program for weed management which included a pre-emergence herbicide (Trifluralin, Pendimethalin, or Clomazone) followed by a post-emergence herbicide (chlorimuron-ethyl) applied at 20 DAE was effective in controlling weeds and increasing seed yield without causing phytotoxic effects on castor plants (Sofatti et al., 2012). The herbicide halosulfuron is efficient against many sedge species (Cyperus spp.) and has no phytotoxic effect when sprayed on castor leaves with application rates up to 112.5 g a.i. ha\(^{-1}\) (Silva et al., 2010d).

ACCase-inhibiting herbicides specific for controlling monocotyledon weeds are also safe to be sprayed in castor fields (Martins et al., 2004). Nonselective herbicide mixes, such as Paraquat + Bentazon and Paraquat + Diquat can be used in castor fields as long as care is taken to avoid spraying the herbicide on the castor leaves (Maciel et al., 2008). However, only weeds located between rows of castor plants can be reached by this spraying method.

Castor as a volunteer plant needs to receive more attention from research, particularly when castor fields are rotated with edible crops because castor seeds can be harvested and mixed to those products. Volunteer occurrence needs to be assessed and strategies for preventing contamination must be proposed. Consequences of contamination of food or feed with volunteer castor seed are also an important research demand.

**Diseases**

Castor is affected by several diseases; however, only a few are regarded to be of economic importance. The three major diseases affecting castor are: gray mold (Botryotinia fuckeliana G.H. Godfrey or Amphobotrys vicini N.F. Buchw., in its anamorphic), vascular wilt (Fusarium oxysporum f.sp. risci Nanda and Prasad), and charcoal rot (Macrophomina phaseolina [Tassi] Goid.).
Several others diseases can sporadically cause severe outbreaks depending on genotype and climatic conditions, such as the leaf spots caused by the fungus *Alternaria ricini* (Yoshii) Hansf. and *Cercospora ricinellae* Saccardo and Berlese and the bacteria *Xanthomonas axonopodis pv. ricini* Hasse. Among these, *A. ricini* deserves more attention because it is a seed-borne fungus that can also cause seedling blight and pod rot with seed yield losses reaching 70% (Holliday, 1980).

Gray mold is probably the most serious castor disease worldwide. A meticulous study of gray mold was conducted in the early 20th century (Godfrey, 1923), but only a few studies on this disease have been conducted recently (Soares, 2012). Consequently, there have been only a few advances in the management of gray mold. Breeding programs have failed to develop resistant genotypes, but genotypes with moderate levels of tolerance have been identified (Araújo et al., 2007; Anjani, 2012). There has also been the development of diagrammatic scales to assess disease severity in the field (Sussel et al., 2009; Chagas et al., 2010) and a technique to screen germplasm resistance under controlled conditions (Soares et al., 2010). Studies are still needed on the control of *B. ricini* with fungicides and application timing for management of this disease. Although *B. ricini* is a seed-borne fungus, the initial inoculum source of the disease is not likely to be the seed because there is a large time between planting and flowering (Soares, 2012). Under tropical conditions, the initial inoculum source is probably the conidia produced on wild castor plants. The fungus infection on the first flowers produces abundant sporulation allowing multiple rounds of re-infection as this pathogen is spread by wind, rain, and probably insects. Additionally, *B. ricini* has a wide host range within the Euphorbiaceae family, including both weeds and ornamentals, such as *Caperonia palustris* L. (*Euphorbia supina* Raf., *E. milli* Des Moul., *E. pulcherrima* Willd. ex Klotzsch, *E. heterophylla* L., *E. inarticulata* Schweinf. *Acalypha hispida* Burm., and *Jatropha podagrica* Hook. (Soares, 2012).

Vascular wilt is regarded as the most important disease of castor in India (Desai and Dange, 2003). The incidence of this disease in other regions is probably underestimated because symptoms are easily confused with charcoal rot. The use of varietal resistance, seed treatment, and crop rotation are the best practices to manage this disease. Several commercial hybrids and breeding lines resistant to vascular wilt have been developed in India (Anjani et al., 2004; Anjani, 2005a, 2005c, 2012; Patel and Pathak, 2011).

Charcoal rot, also known as macrophomina root rot, is a major disease in most countries where castor is cultivated (Araújo et al., 2007; Rajani and Parakhia, 2009). Bisset et al. (1996) defined the criteria for developing castor resistance to charcoal rot, and some tolerant genotypes have been recently developed (Anjani et al., 2004, Anjani, 2005b). Management of charcoal rot is primarily based on cultivar resistance, but crop rotation and organic matter amendments can reduce the severity of this disease (Rajani and Parakhia, 2009).

There are several plant parasitic nematodes reported on castor, but usually these pests do not cause serious damage (Kotle, 1995). The reniform nematode (*Rotylenchulus reniformis* Linford and Oliveira) is considered the most important one because it predisposes castor to the infection of *F. oxysporum* (Dange et al., 2005). Castor is considered resistant to *Meloidogyne paranaensis Carneiro, M. javanica Treub, M. incognita* Chitwood (Arieira et al., 2009), and *M. ethiopica* Whitehead (Lima et al., 2009a).

The development of tolerance to multiple diseases of castor will require studies on the inheritance of disease resistance because the selection of tolerant genotypes without adequate information on its genetics base can be erratic. Standardization of screening procedures among plant pathologists and more international cooperation would enhance both the understanding of the basic interactions of the host, the pathogen, and the impact of the environment necessary for disease development in castor (Soares, personal communication, 2012).

### Pests

In India, insect pests of economic importance are castor semilooper (*Achaea janata*), castor shoot borer (*Conogethes punctiferalis*), capsule borer (*Dichocrocis punctiferalis*), tobacco caterpillar (*Spodoptera litura*), red hairy caterpillar (*Amsacta* spp.), and leafminer (*Liriomyza trifolii*) (Basappa, 2007; Anjani et al., 2010). In Brazil, the major pests are stink bug (*Nezara viridula*); leafhopper (*Empoasca* spp.); defoliators including armyworm (*Spodoptera frugiperda*), *A. janata*, and black cutworm (*Agrotis ipsilon*); and the mites *Tetranychus urticae* and *Tetranychus ludeni* (Soares et al., 2001; Ribeiro and Costa, 2008). In Colombia, cotton lace bug (*Bemisia tabaci*) was reported as a pest of castor plants (Varón et al., 2010).

Defoliation of castor plants by *A. janata* was shown to cause greater reduction in seed yield when the attack started early in the growing season (30 DAE). When the attack started later (i.e., 60, 90, or 120 DAE) the damage was progressively less (Basappa and Lingappa, 2001).

Castor farmers in Andhra Pradesh, India increased the seed yield by 28% when they used an Integrated Pest Management program with pesticides and crop rotation, insect traps, and neem extract (Basappa, 2007). Purple leaved cultivars of castor (with high levels of anthocyanins) were found to be tolerant to leafminer. The presence of epicuticular wax (blooming) on castor leaves reduced infestation and defoliation caused by *A. janata* and *S. littoralis* (Sarma et al., 2006).

### Abiotic Stresses

Tolerance to environmental stresses, particularly to drought stress, is one of the strengths of castor as a crop. Because castor oil is an only-industrial product, there is a possibility that the competition for land with food crops moves castor production into marginal soils. In that scenario, tolerance to abiotic stresses would be particularly important.

Castor plants are more sensitive to water stress in the early stages of growth. At the cellular level, water stress reduced callus initiation, nitrate reductase activity, and chlorophyll content (Manjula et al., 2003a, 2003b). Drought stress increases cuticular wax load (Lakshmamma et al., 2009b) and abscisic acid concentration in the phloem sap (Zhong et al., 1996).

Osmotic adjustment is an important mechanism for drought tolerance in castor. Nine genotypes of castor subjected to drought demonstrated osmotic adjustments in the leaves but with a wide variability in the intensity of the effect. Among the osmotically active compounds accumulated soluble sugars were by far the most important (61%), followed by free amino acids (17%), proline (12%), and K (2.8%). The seed yield of genotypes...
with higher osmotic adjustment was 53% greater compared to genotypes with low osmotic adjustment (Babita et al., 2010).

Under limited water supply, castor plants maintained efficient stomatal control while keeping a high level of net CO₂ fixation. Water loss by transpiration was minimized by an early stomatal closure (Sauser and Rosa, 2010). It has been observed that under drought stress the photosynthetic apparatus of castor plants was preserved and that photosynthetic limitations were mostly due to diffusive resistance (Sauser and Rosa, 2010).

Castor plants were able to partially recover photosynthetic functions while experiencing stress due to severe drought. When the stress was removed, the plants completely recovered their normal photosynthetic function within 24 h. For comparison, the species California brittlebush (Encelia californica Nutt.) and tree tobacco (Nicotiana glauca Graham) took 7 d to achieve the same level of recovery. However, castor showed high levels of sensitivity to limited light (Funk and Zachary, 2010).

Growth and production of castor were also inhibited by high salinity (Na) in the either the irrigation water or in the soil (Silva et al., 2008). Plants were most sensitive in the early stages of development (Pinheiro et al., 2008). Increasing salinity delayed and reduced total emergence of castor seed, but the genotype CSRN 367 was notably less sensitive to the effects of salinity than BRS Paraguaçu (Silva et al., 2005). The threshold of Na salinity for castor emergence and growth is 7.1 dS m⁻¹ while the emergence rate was delayed by 9 d and was 50% lower at a salinity of 13.6 dS m⁻¹. Sixty percent of the seedlings did not survive when subjected to the same salinity level for 11 d (Zhou et al., 2010). Increasing levels of Na salinity apparently damaged the photosynthetic apparatus and induced proline accumulation in castor plants (Li et al., 2010).

Castor is extremely sensitive to soil hypoxia. Within 2 to 6 h after subjecting castor plants to soil flooding, Else et al. (2001) observed a reduction in stomatal conductance, transpiration, CO₂ uptake, leaf elongation, root hydraulic conductance, and production of abscisic acid from flooded roots. Castor plants subjected to continuous flooding were permanently damaged after 3 d and died after 4 d (Severino et al., 2005). Leaves of plants subjected to hypoxic condition had increased β-amylase activity; increased concentration of starch, protein, and soluble sugars; and reduced activity of nitrate reductase (Beltrão et al., 2003, 2006). Baldwin and Cossar (2009) also observed reduction in seed yield on castor fields subjected to flooding.

Soil acidity can also impair castor growth. The growth of castor plants was reduced in a soil with 6.5 mmol cm⁻³ of Al, but the addition of wood ash or bovine manure reduced the effect of acidity (Lima et al., 2009b). Increased exchangeable Al content was also less harmful to the growth of castor plants when the soil had a high content of organic matter (Lima et al., 2007a).

Temperature in the root zone can influence leaf growth, water status, and carbohydrate transport in castor plants. When air temperature was kept at 22°C for 34 d, plants with root-zone temperature at 20°C had 881 cm² of leaf area, while plants kept at 10°C had only 288 cm² of leaves. The shoot and root biomass production was three times smaller in the plants subjected to cold soil temperatures (Poire et al., 2010). When temperatures increased in the root-zone plants resumed normal leaf growth within a few days.

**Industrial Uses of Castor Oil**

Castor oil is unique among vegetable oils because it is the only commercial source of a hydroxylated fatty acid (ricinoleic acid). This unique fatty acid comprises around 90% of the castor oil (Fig. 1). No other commercial vegetable oil produces such a high predominance of a single fatty acid. There appears to be a very low influence of production environment on ricinoleic acid concentration. Consequently, the castor oil industry expects low variability in the fatty acid profile of castor oil grown at different locations or in different years (Ramos et al., 1984; Ogumnjii, 2006; Xu et al., 2008; Mutlu and Meier, 2010).

Hydroxylated fatty acids (ricinoleic and lesquerelic) can also be found in seeds of plants belonging to the genus Lesquerella. However, these species have not yet been commercially cultivated on a wide scale. The content of ricinoleic fatty acid can reach 100 g kg⁻¹ in Duck River bladderpod (L. densipila Rollins), Lescur’s bladderpod (L. lescurrii (A. Gray S. Watson) lyreleaf bladderpod (L. hyrata Rollins), and Spring Creek bladderpod (L. perforata Rollins). The content of lesquerolic acid can reach 800 g kg⁻¹ in white bladderpod (L. pallida (Torr. & A. Gray) S. Watson) (Goodrum and Geller, 2005; Jenderek et al., 2009).

The high concentration of ricinoleic acid in castor seed allows the production of high purity derivatives. The hydroxyl group in ricinoleic acid is an uncommon and important point of chemical reaction that complements the double bond and the carboxyl group (Fig. 1) (ICOA, 1992; Ogumnjii, 2006). Another important characteristic of castor oil is its high solubility in alcohols at room temperature which also facilitates several chemical reactions (da Silva et al., 2006). The high viscosity over a wide range of temperatures makes castor a valuable ingredient of lubricants. Mutlu and Meier (2010) stated that “castor oil is one of the most promising renewable raw materials for the chemical and polymer industries due to its manifold uses and to a series of well-established industrial procedures that yield a variety of different renewable platform chemicals.”

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**Fig. 1. Reaction points in the molecule of ricinoleic acid: carboxyl group (1), double bond (2), and hydroxyl (3).** Adapted from Mutlu and Meier (2010).
Identifying all of the products containing castor oil derivatives would result in an extensive list of items. Important groups of products based on castor oil include: oil-based formulations of lubricants and grease; functional fluids and process oils; oleochemicals; reactive components for paints, coatings, and inks; polymers and foams; textile finishing agents; emulsifiers; stabilizers in vinyl compounds; and wetting agents (Budavari, 1989; Oggunniyi, 2006; Mutlu and Meier, 2010). Johnson (2007) identified a broad list of castor derivatives considered safe as cosmetic ingredients. Certain characteristics of castor oil derivatives, like high lubricity, high melting point, and insolubility in aliphatic petrochemical fuels and solvents, make it useful as a lubricant for equipment operating under extreme conditions (Mutlu and Meier, 2010; Yao et al., 2010).

Production of bio-based polyurethanes is a significant use for castor oil. Polyurethanes are one of the most important classes of polymers, with wide applications and properties that have been traditionally produced from petroleum-based polyols (Oprea, 2010). Use of renewable and biodegradable materials for production of polyurethanes is increasingly demanded by both industry and society due to energy and environmental concerns (Sharma and Kundu, 2006; Xu et al., 2008). Castor oil is also the only commercially available natural oil polyol. For a comprehensive review on castor oil extraction, refining, and major reactions used in the processing of castor oil, see Oggunniyi (2006) and Mutlu and Meier (2010). For a review on polymers made from castor oil, see Sharma and Kundu (2006).

Biodiesel

Castor oil is considered an option for biodiesel production in several countries. In Brazil, governmental policies promoted castor as a biodiesel feedstock in an attempt to bring social benefits to small farmers in the semiarid region of the country (Hall et al., 2009; César and Batalha, 2010). However, 7 yr after the Brazilian biodiesel program was launched, negligible amounts of castor oil have been used for biodiesel production. The main raw materials used in the production of 2.32 billion liters of biodiesel in 2010 were soybean oil, tallow, and cottonseed oil (MME, 2010). Some biodiesel industries in Brazil promoted and supported castor cultivation by small farmers as a government requirement for accessing the biodiesel market. However, the castor oil produced in this program was not used for biodiesel but sold for higher prices to the chemical industry (César and Batalha, 2010).

Production of biodiesel from castor oil is technically feasible. Transesterification of castor oil into biodiesel can be optimized by adjustments in the types and ratio of catalysts and reagents, reaction time, catalytic system, temperature, and the purification process. The temperature, alcohol ratio, and quantity of catalyst for optimized transesterification of castor oil were determined for ethanol by da Silva et al. (2006) and for methanol by Jeong and Park (2009). The purification phase has some additional difficulties when compared to other vegetable oils (Meneghetti et al., 2007; França et al., 2009; Peña et al., 2009). Alternative technologies and methods for producing biodiesel from castor have been reported, such as using ethanol instead of methanol (Meneghetti et al., 2006b), using acid catalyst instead of the traditional base catalyst (Meneghetti et al., 2006a), blending castor with other vegetable oils (Meneghetti et al., 2007), using microwave heating (Perin et al., 2008), and using co-solvents (Peña et al., 2009).

The major constraint for using castor oil as feedstock for biodiesel has been the high price paid for the oil as industrial oil rather than its physical and chemical properties. Because castor oil is in high demand by the chemical industry to manufacture very high value products, it is not economical to use this oil as a replacement for diesel.

Pure castor biodiesel cannot be used to replace diesel in internal combustion engines because of its high density, viscosity, and hygroscopicity (Scholz and Silva, 2008; Albuquerque et al., 2009; Peña et al., 2009; Refaat, 2009; Canoira et al., 2010; Berman et al., 2011). However, castor biodiesel can meet biodiesel specifications if blended with regular diesel or biodiesel made with other lipid feedstocks (Meneghetti et al., 2007; Canoira et al., 2010; Berman et al., 2011). Castor oil should be blended up to 200 g kg–1 with cotton seed or soybean biodiesel to ensure compliance with the viscosity standards (Albuquerque et al., 2009) and up to 400 g kg–1 with diesel to meet the specifications of EN 590 (Canoira et al., 2010).

Biodiesel produced from castor has a remarkable advantage regarding lubricity. The reduction of S content in diesel aiming to limit exhaustion pollutants causes a diminished fuel lubricity. While any biodiesel can enhance diesel lubricity, biodiesel derived from castor can achieve the required lubricity at concentration as low as 2 g kg–1; for comparison, rapeseed (Brassica napus L.) and soybean biodiesel have to be added at concentrations above 7.5 g kg–1 to have an equivalent effect. Castor biodiesel has an additional advantage over traditional lubricity additives because of its high energy value and positive fuel properties (Drown et al., 2001; Goodrum and Geller, 2005; Knothe, 2005; Refaat, 2009; Berman et al., 2011). Two other positive characteristics of castor biodiesel are a high oxidative stability (44 h) and low cloud point (–14°C) which is particularly important in cold weather (Berman et al., 2011).

The energy required for production of biodiesel from castor oil was estimated at 56.8 GJ ha–1. The production of castor seed consumed only 19% of the total energy, while most of the energy was consumed in oil extraction and refining (39%) and on biodiesel production (42%). If the energy present in the by-products (field residues, husks, and meal) is not taken into account, biodiesel production has a negative energy balance (Chechetto et al., 2010).

Noxious Compounds

Ricin

Ricin is a protein found only in the endosperm of castor seed (Lord et al., 1994). Castor oil does not contain ricin because this protein is insoluble in oil, and any residual ricin is eliminated in the refining process. Ricin comprises 1 to 5% of the weight of the castor meal remaining after oil extraction (Balint, 1974; Greenfield et al., 2002). Ricin content varies among genotypes. The ricin concentration varied from 1.9 to 16 g kg–1 among 263 accessions from the USDA germplasm bank (Pinkerton et al., 1999) and from 3.5 to 32.2 among 20 accessions from Embrapa germplasm bank (Baldoni et al., 2011).

During seed development, ricin can first be detected 28 d after pollination, and its concentration rapidly increases up to...
complete development at 44 d. When germinating, ricin can still be detected in the endosperm tissue for up to 6 d after radicle protrusion, but no ricin can be detected in root, hypocotyls, or cotyledons of developing seedlings (Barnes et al., 2009b).

Ricin is a Type II ribosome-inactivating protein belonging to the A-B family of toxins (dimeric) consisting of two functionally different subunits: an enzymatically active A-moiety and a receptor binding B-moiety. The two ricin polypeptide chains have molecular weights of 30 kDa (A) and 33 kDa (B), and they are normally linked by a single disulfide bond (Lin and Li, 1980; Olsnes and Kozlov, 2001).

The B-chain is a lectin that acts by inserting the A-chain into the cell. It binds to glycoproteins or glycolipids containing galactose on the surface of target cells and triggers a receptor-mediated endocytosis of the A-chain (Rutenber and Robertus, 1991). The A-chain acts by inactivating ribosomes (Olsnes and Kozlov, 2001). Once inside the cell, a single ricin A-chain molecule can inactivate more than 1500 ribosomes per minute which ultimately results in cell death (Franz and Jaax, 1997).

Outside the cell, the separated A-chain is harmless (Olsnes and Kozlov, 2001). Many plant species produce seed storage proteins that are very similar in structure to the ricin A-chain, but they are not as toxic as ricin due to the lack of an efficient B-chain. Wang et al. (2006) found a ricin A-chain to a cinnamonin B-chain and compared its cytotoxicity to the native cinnamonin. They found that the native cinnamonin was 138 times less cytotoxic than ricin. However, when the cinnamonin A-chain was bound to a ricin B-chain the cytotoxicity of the hybrid protein was similar to the native ricin found in castor.

Sehgal et al. (2010) observed the existence of three isoforms of ricin. The isoforms were fractionated into ricin I, II, and III by chromatography. Their molecular weights lie between 60 and 65 kDa. All three of the isoforms were cytotoxic to Vero cell line with IC50, but with different toxicity levels in the range of 8 to 60 ng mL⁻¹.

In its crude form, ricin is often found in association with a protein called ricinus communis agglutinin (RCA-I or RCA₂₁₀). RCA₂₁₀ has a greatly reduced toxicity and consists of two A-chains and two B-chains very similar in structure to the A- and the B-chains of ricin. RCA₂₁₀ can cause agglutination of mammalian red blood cells (Harley and Bevers, 1986; Pinkerton et al., 1999; Olsnes and Kozlov, 2001; Audi et al., 2005). The homology between RCA₂₁₀ and ricin is 90% in the A-chain and 84% in the B-chain (Butterworth and Lord, 1983). Consequently, RCA₂₁₀ cross-reacts with nearly all anti-ricin antibodies (Harley and Bevers, 1986).

Tregear and Roberts (1992) found six to eight sequences with substantial similarity (51–93%) to the gene encoding ricin in the genome of Ricinus communis. Leshin et al. (2010) searched for sequences specific for the A-chain in the draft genome of castor. When these sequences were expressed in Escherichia coli Migula they synthesized ricin-like proteins confirming that they had a ricin-A-chain-like activity of inactivating ribosomes. Chan et al. (2010), in the most recent castor draft genome, found 28 potential genes encoding ricin-like proteins.

Ricin toxicity depends on the type of exposure. The mean lethal dose (LD₅₀) in mice (Mus musculus L.) is approximately 1000-fold lower by injection or inhalation than by oral administration (Audi et al., 2005). The lethal dose for an adult human is about 0.35 to 0.7 mg kg⁻¹ of body weight by inhalation, whereas the lethal oral dose has been estimated to be between 1 and 20 mg of ricin kg⁻¹ of body weight. Ricin is less toxic through ingestion due to immune barriers present in the intestinal track and the harsh digestive conditions found in the stomach and epithelial (Nagler-Anderson, 2001). Ruminal microbiota is able to degrade ricin in vitro conditions although the toxin inhibits the growth of those microorganisms (de Oliveira et al., 2010b). Ricin is also more toxic to animal cells than to plant cells and bacterial (Olsnes and Kozlov, 2001).

Animals can develop immunity to ricin. In a study performed by Tokarnia and Döbereiner (1997), bovines that had previously ingested low doses of ricin tolerated higher doses of ricin with limited symptoms of intoxication. However, animals not previously orally immunized did not survive the same doses of ricin. Hewetson et al. (1993) observed that immunized mice tolerated the inhalation of ricin in doses that would kill 99% (LD₉₉) of non-immunized mice. Anti-ricin vaccine has been developed using a ricin A-chain with substitution of two critical amino acids that reduced toxicity (Legler et al., 2011). A protocol for production of polyclonal antibodies in rabbits was described by Furtado et al. (2011).

Major symptoms of ricin intoxication in rabbits (Oryctolagus cuniculus L.) were first noticed 8 h after ingestion with death occurring between 12 and 68 h. Symptoms included: diarrhea, low appetite, anorexia, cramps, weakness, and dark soft feces. Necropsy disclosed that the organs primarily affected were the small intestine and the cecum (Brito and Tokarnia, 1996).

The high toxicity of ricin and potentially large quantities of raw material containing ricin generated by commercial castor production have made this protein a major bioterror concern in the United States (Franz and Jaax, 1997; Doan, 2004; Audi et al., 2005). Ricin was considered a potential weapon of bioterrorism because a crude ricin-rich preparation with a high level of toxicity can be easily produced in a simple laboratory (Olsnes, 2004). Several methods can be used for purification of ricin including acid extraction; precipitation with sodium chloride and ammonium sulfate; and chromatography in DEAE-cellulose, Sephadex, and hydroxyapatite (Silva, 1974; Woo et al., 1998).

Due to both the perceived and actual risks associated with the ricin toxin, research efforts have been focused on the development of sensitive methods for the detection of this toxin in complex matrices, such as castor meal, food, and human biological samples. Historically, methods based on the survival rate of animals exposed to different doses have been the preferred standard for the detection of ricin (Godal et al., 1984; He et al., 2010a). However, tests with live animal are not practical for use in most laboratories because they are expensive, time-consuming, require special animal care facilities, and cannot process large number of samples. The accuracy of live animal tests are also questionable because the LD₅₀ values are influenced by factors such as the animal species, the injection route, observation time, age, sex, and feeding conditions (Godal et al., 1984; Zhan and Zhou, 2003; He et al., 2010a).

Cell-free and cell-based cytotoxicity assays offer promising alternatives to in vivo methods. The cell-based assay is a method to determine the number of viable cells through the quantitation of the ATP present as an indicator of metabolically active cells (Neal et al., 2010). The cell-free translational assay uses luciferase
activity as a reporter for protein translation (Hale, 2001; He et al., 2008). These assays are designed for use with multiwell-plate formats making them efficient for automated screening and conducting toxicity assays on many samples.

There is a variety of immunological methods for ricin detection. Enzyme-linked immunosorbent assay (ELISA) has proven to be one of the most versatile techniques (Koja et al., 1980; Poli et al., 1994; Shyu et al., 2002a). However, this method sometimes can detect antigens that have cross-reactivity which are not ricin. ELISA can also underestimate actual ricin content when antigens are in high concentration, what is called the hook effect (Garber et al., 2005). Immunological methods cannot distinguish a toxic ricin molecule from a nontoxic ricin molecule (Kumar et al., 2010; Furtado et al., 2011). Among several methods evaluated by Kumar et al. (2010), only SDS-PAGE was able to differentiate native from denatured ricin molecules. In addition, ELISA may not be sensitive enough for the detection of ricin in biological samples such as: sera, animal waste, or intentionally contaminated food samples (Kumar et al., 2010).

An immuno-polymerase chain reaction assay was developed to combine the advantages of immunoassays with the power of the immune-polymerase chain reaction (He et al., 2010b). This assay can detect as little as 10 fg mL⁻¹ of ricin in saline solution buffer, 10 pg mL⁻¹ in liquid eggs and milk, and 100 pg mL⁻¹ in ground beef extracts. While this method is extremely sensitive, it has a disadvantage because the presence of very low concentrations of nonspecifically bound DNA marker molecules can lead to strong background signals.

Other methods for detecting ricin, such as chemiluminescence ELISA (Poli et al., 1994), fiber optic-based sensor (Narang et al., 1997), mass spectrometry (Na et al., 2004), and radial immunodiffusion (Pinkerton et al., 1999) have also been proposed. O’Brien et al. (2000), Taitt et al. (2002), and Delehanty and Ligler (2002) developed methods for the simultaneous detection of several potential biological threat agents, including ricin. Shyu et al. (2002b) developed a sensor in which A-chain specific antibodies are linked to gold particles and B-chain specific antibodies are linked to a matrix in a way that ricin moieties can be measured when linked to both antibodies. Wannemacher et al. (1992) compared the accuracy and sensitivity of several methods for detecting ricin. They found sensitivity of 0.04 mg L⁻¹ for in vivo tests in rats, 0.01 mg L⁻¹ with Vero cells, 0.002 mg L⁻¹ by ELISA, 5 mg L⁻¹ by HPLC, 20 mg L⁻¹ by gel electrophoresis, and 25 mg L⁻¹ by high-performance capillary electrophoresis. When assessing the same castor seed extract, the results were 4.1 mg L⁻¹ by rat toxicity, 4.9 mg L⁻¹ by cytotoxicity of Vero cells, 1.3 mg L⁻¹ by ELISA, 9.3 mg L⁻¹ by HPLC, 3.3 mg L⁻¹ by gel electrophoresis, and 2.9 mg L⁻¹ by capillary electrophoresis. It was concluded that all of the methods can detect ricin but the quantification can vary widely among them.

Breeding for ricin-free castor genotypes are highly dependent on the development of efficient, accurate, and reliable tests for ricin toxicity measurement. It is likely that many methods currently employed are detecting nontoxic ricin and overestimating the toxicity of individual samples. Therefore, the measurement of relative ricin toxicity remains a challenge for the scientific community working on this protein. Because lectins such as ricin play an important role in plant protection against insect pests the development of ricin-free castor genotypes must consider the risk of increased incidence of pests (Vandenborre et al., 2011).

**Allergens**

Allergens are an important concern for all who handle castor seed or meal in storage and oil extraction facilities. Castor seed and pollen contain potent allergens that can cause medical problems such as conjunctivitis, rhinitis, and urticaria (Garcia-Gonzalez et al., 1999). Sensitive persons living near to castor processing facilities can suffer from allergies caused by the dust generated during seed cleaning or oil extraction (ICOA, 1989). In the air of Chenai, India, castor pollen was identified as an important allergen (Raju et al., 2005).

The castor allergens were discovered when Spies and Coulson (1943) isolated a protein fraction and called it CB-1A. Youle and Huang (1978) concluded that CB-1A belong to a family of storage proteins named 2S Albumins that is present in seeds of a wide range of dicotyledonous plants. Members of the 2S albums family are 12 to 15 kDa in size and contain eight conserved cysteine residues; they generally consist of two polypeptide chains covalently linked by two disulphide bonds.

Because the 2S albums found in castor are similar to the proteins found in other species, it appears that their role is not limited to storing energy for seed germination and early development. It has been suggested that castor allergens may play a role in plant defenses based on their inhibition of insect α-amylase (Nascimento et al., 2011).

Thorpe et al. (1988) detected specific IgE antibodies to the 2S storage albums in most (96%) castor sensitive patients, confirming these as the major allergens. Irwin et al. (1990) proposed that a single preprotein could be processed into two different heterodimeric storage proteins. Sharief and Li (1982) determined the complete primary structure of one isoform of allergenic 2S albumin, and named it Ric c 1. Machado and Junior (1992) and da Silva et al. (1996) isolated and characterized another protein named Ric c 3 which is thought to be the third allergen characterized from *R. communis*. Bashir et al. (1998) verified the phylogenetic relationships between Ric c 1 and Ric c 3. Other allergenic isoforms present in a *R. communis* 2S albumin pool, were characterized by Machado et al. (2003). The three-dimensional structure of recombinant Ric c 3 in aqueous solution has been determined by nuclear magnetic resonance methods (Pantoja-Uceda et al., 2003).

An allergy response requires the existence of at least two binding sites (epitopes) on the surface of the allergen as well as antibodies specific for each of these epitopes. Felix et al. (2008) demonstrated the existence of at least two different IgE recognition sites on Ric c 1 and four epitopes on Ric c 3. Two residues of glutamic acid on each epitope were identified as amino acids involved in the IgE–allergen interaction (Deus-de-Oliveira et al., 2011). The identification of glutamic acid residues with critical roles in IgE-binding to Ric c 3 and Ric c 1 supports the potential use of free amino acids as IgE-blockage drugs in allergy treatment. Treating castor meal with Ca salts changed lateral groups of these amino acids and reduced the meal’s allergenicity (Deus-de-Oliveira et al., 2011).

Continued research on castor allergens is fundamental for developing strategies for allergy treatments or allergen inactivation. It is equally important to determine if castor fields can...
cause allergy in nearby population centers, to develop less allergenic genotypes, and to define potential ecological implications of growing a less allergenic castor plant.

Ricinine

Ricinine (C_{8}H_{8}O_{2}N_{2}) is an alkaloid found in all organs of castor. It can be detected early in the seedling stage. Ricinine concentration can be influenced by environmental factors, such as salinity and drought and varies according to phenological plant stages. Ricinine is high in young leaves but disappears in senescing leaves. Ricinine content also varies among organs: 2.3 to 32.9 g kg\(^{-1}\) on leaves, 10.7 g kg\(^{-1}\) in flowers, 2.4 g kg\(^{-1}\) in stems, 0.16 g kg\(^{-1}\) in shoots, 3 g kg\(^{-1}\) in roots, and 0.43 to 7.0 g kg\(^{-1}\) in seeds (Waller et al., 1965; Waller and Skursky, 1972; Moshkin, 1986; Holfelder et al., 1998; Ali, 2002; Leite et al., 2005; Xu et al., 2007; Wen et al., 2008; Cazal et al., 2009).

Ricinine is a central nervous system stimulant that can induce seizures but also improves memory retention in low dose (Ferraz et al., 2000). It can be lethal if ingested in high doses (Döbereiner et al., 1981). In mice, the LD\(_{50}\) was estimated to be 0.34 g kg\(^{-1}\) by intra-peritoneal administration and 3.0 g kg\(^{-1}\) by intra-gastric administration (Ferraz et al., 1999). The LD\(_{50}\) for both bovines and rabbits is about 5 g of pericarp per kg of body weight. Major symptoms of intoxication include: lack of equilibrium, inability to walk, muscle tremors, salivation, and mastication. In bovines, the first symptoms appeared <2 h after ingestion with death occurring after 5 to 8 h. In rabbits, the symptoms and death occurred slightly faster with lesions forming in internal organs such as the lung, liver, and brain (Döbereiner et al., 1981; Rezende et al., 2011).

The function of ricinine in the castor plant is unclear. Some believe that it acts as a toxin or repellent against insects. It is lethal to the aphid Myzus persicae Sulzer (Olifá et al., 1991), to the caterpillars Spodoptera frugiperda (Löpez et al., 2010) and S. exigua (Rizwan-ul-Haq et al., 2009), and to the leaf-cutting ant Atta sexdens rubropilosa Forel (Bigi et al., 2004). The ricinine present in castor pollen can be toxic to social bees (Apis mellifera L. and Saptotrigona postica Latreille) (Rother et al., 2009; Assis et al., 2011). When extracts and powders derived from castor leaves were found to suppress parasitic nematode growth, ricinine was thought to be the active compound (Radwan et al., 2007; Amaral et al., 2009; Katooli et al., 2011; Lopes et al., 2011).

Ricinine seems to play the dual role of plant defense and N storing and translocation. That is why it can be found in high concentration in young leaves when N is stored, but it is absent in senescing leaves when the N has been translocated to growing leaves and seeds. The concentration of two alkaloids produced in important crops (caffeine in Coffea arabica L. and nicotine in Nicotiana tabacum L.) is influenced by N fertilization just like other N-rich compounds (Ascione et al., 2011; Gonthier et al., 2011).

A survey of plants that were potentially toxic to cattle (Bos taurus) in the semiarid region of Brazil revealed that intoxication due to ingestion of castor leaves or seed has been rare. The assessment was made by interviewing farmers and veterinarians covering an area of 12,500 km\(^{2}\) with an estimated population of 451,000 animals (bovine, sheep [Ovis aries], goat [Capra hircus], and horses [Equus caballus]) in which wild castor plants are often found. Cases of intoxication were found to be very common with other plant species. However, few occurrences of intoxication with castor were reported, and they occurred only in bovines. In one case, 15 individuals in a herd of 180 bovines were intoxicated and showed symptoms of ricinine ingestion after grazing in an area containing castor plants. All of the intoxicated cattle recovered without any death. In another case, 2 bovines in a herd of 30 died with symptoms of ricinine intoxication, and a large amount of castor leaves was found in both animals (Silva et al., 2006; Assis et al., 2009). Surprisingly, six farmers stated that they had successfully fed cattle with castor leaves by gradually increasing the amount consumed (Silva et al., 2006).

Ricinine could potentially be used as an organic insecticide if it were available in large quantity. A high-speed counter-current chromatography was proposed as a method to be scaled up for extracting ricinine in large volume. Highly efficient extraction protocols have been demonstrated to be effective in recovering 81 to 100% of ricinine from various types of samples (Leite et al., 2005; Cazal et al., 2009). Ricinine can be detected in very low concentrations. The limit of detection for ricinine was found to be 6 pg mL\(^{-1}\) in a feed containing castor meal (Wang et al., 2009), 83 pg mL\(^{-1}\) in urine (Johnson et al., 2005), 1 μg kg\(^{-1}\) in a gastric sample (Mouser et al., 2007), 10 to 50 pg in Coca-Cola (Coca-Cola Company) (Melchert and Pabel, 2004), and 0.5 μg kg\(^{-1}\) in vegetable oil (Chen and Jin, 2009).

The detection of ricinine in human urine at very low concentrations suggests that it can be used as a biomarker of exposure to unpurified ricin (Darby et al., 2001; Johnson et al., 2005). Several cases of human intoxication with ricin or ricinine were confirmed with base on the ricinine detected in the urine (Coopman et al., 2009; Smith et al., 2009; Sutaraya and Cortisidis, 2009). Ricinine is stable in urine after heating at 95°C for 1 h and during storage at 25, 5, and –20°C for 3 wk (Johnson et al., 2005). It was also stable during extraction with methanol at 70°C and storage at low concentrations (0.01–50 μg mL\(^{-1}\)) for 72 h at room temperature (Wang et al., 2009).

Ricinine is not toxic against microorganisms. A stimulatory effect of ricinine on lactic acid fermentation by Lactobacillus leichmannii Henneberg was observed (Singh et al., 1996). Certain fungi can degrade ricinine (ca. 94%) after a 15-d fermentation process (Xu et al., 2007).

The importance of ricinine as a potential useful agronomic tool has been largely neglected by the scientific community. It is important to assess the variability on ricinine content among genotypes, the effect of environmental factors and agronomic practices on ricinine concentration, the importance of this compound in conferring resistance to pests and diseases of castor, and the risks of human and animal intoxication from ricinine.

Detoxification of Castor Meal

Castor meal can be easily detoxified in small quantities, but no small-scale process has been successfully scaled up to industrial level yet. As early as 1934, it was demonstrated that castor meal could be detoxified by boiling for 2 h. Since then, several methods for castor meal detoxification have been investigated. These include short but repeated boiling; autoclaving; steam heating; fermentation; ionizing radiation; mixing castor meal with the tannin-rich meal of sal seed (Shorea robusta Roth); and the addition of sodium hypochlorite, alkali, or acid substances (Gardner et al., 1960; Freitas, 1974; Kling,
Simultaneous detoxification of both ricin and the allergens was obtained with the addition of calcium hydroxide followed by extrusion (Horton and Williams, 1989).

Presently, the simplest but effective method for ricin detoxification is addition of lime. The elevated pH is probably responsible for ricin denaturation (Anandan et al., 2005; Oliveira, 2008; Barnes et al., 2009a; Diniz et al., 2010). Boiling for 10 min was also effective for ricin denaturing ricin. However, the addition of lime before boiling did not increase the rate of denaturation. Even the addition of urea 8 M and guanidine in 6 M HCl were not effective agent in the denaturation of ricin (Barnes et al., 2009a).

The development of an industrial process for castor detoxification would greatly improve the economics and perception of commercial castor production. The barriers for an industrial process are the high energy costs for processing the meal, the lack of adequate methods to quickly and cheaply quantify the residual ricin in the meal (Kling, 1974; ICOA, 1989).

Castor Meal as an Organic Fertilizer

When castor meal was used as an organic fertilizer, the high N content, fast rate of mineralization, and anti-nematode effect were advantageous. Castor meal contained 75 g kg⁻¹ of N. The mineralization of this organic material as measured by microbial evolution of CO₂ was seven times faster than bovine manure and 15 times faster than bagasse of sugarcane (Saccharatum officinarum L.). Castor meal contained 75 g kg⁻¹ of N. The mineralization of this organic material as measured by microbial evolution of CO₂ was seven times faster than bovine manure and 15 times faster than bagasse of sugarcane (Saccharatum officinarum L.). Castor meal contained 75 g kg⁻¹ of N. The mineralization of this organic material as measured by microbial evolution of CO₂ was seven times faster than bovine manure and 15 times faster than bagasse of sugarcane (Saccharatum officinarum L.). Castor meal contained 75 g kg⁻¹ of N. The mineralization of this organic material as measured by microbial evolution of CO₂ was seven times faster than bovine manure and 15 times faster than bagasse of sugarcane (Saccharatum officinarum L.). Castor meal contained 75 g kg⁻¹ of N. The mineralization of this organic material as measured by microbial evolution of CO₂ was seven times faster than bovine manure and 15 times faster than bagasse of sugarcane (Saccharatum officinarum L.). Castor meal contained 75 g kg⁻¹ of N. The mineralization of this organic material as measured by microbial evolution of CO₂ was seven times faster than bovine manure and 15 times faster than bagasse of sugarcane (Saccharatum officinarum L.).
survival or other undefined factors (Rich et al., 1989). Addition of 10 mL L\(^{-1}\) of castor meal did not reduce Meloidogyne javanica Kofoid gall number in tomato (\textit{Lycopersicon esculentum} L.) roots, but the number of eggs per plant were reduced by 48% (Lopes et al., 2009). Tomato plants growing in a soil infected with \textit{M. incognita} benefited from the addition of 24 kg ha\(^{-1}\) of ground castor fruits (Mashela et al., 2007). Castor meal also had a synergistic effect with the nematicide carbofuran, on the reduction of root-lesion nematode (\textit{Pratylenchus delaterris} Luc.) and on the increased growth of crossandra (\textit{Crossandra undulafolia} Salis.) plants (Jothi et al., 2004). Castor leaves and fruits added to the soil increased yield of tomato and reduced root galling and reproduction rate of \textit{M. incognita} (Kaskavalei et al., 2009).

The control of the nematode \textit{Nacobbus aberrans} Thorne was more effective when castor meal was added to the substrate 10 d before transplanting tomato seedlings (Navarro et al., 2002). \textit{Bacillus} species did not increase the castor meal anti-nematode effect against \textit{M. incognita} in tomato plants (Jithiya and Nthangeni, 2002). The effect of castor meal against \textit{M. arenaria} Chitwood was not dependent on the dose of the meal (Ritzinger and McSorley, 1998a). Castor meal anti-nematode efficiency was comparable to the nematicides aldicarb and carbofuran in the reduction of \textit{M. incognita} population and promotion of growth of \textit{Hyoscyamus muticus} L. plants (Butool et al., 1998). Castor meal reduced parasitic nematodes infecting pigeon pea plants (\textit{Cajanus cajan} L.) and promoted free-living beneficial predatory nematodes. In the same experiment, fertilization with similar quantity of mineral N did not produce the same benefits (Akhtar and Mahmood, 1996). Rice plants (\textit{Oryza sativa} L.) infested with \textit{Gymnopus poae} Golden and Birchfield benefited by the addition of 5 g of castor meal kg\(^{-1}\) of soil (Prasad et al., 2005).

Castor leaves which do not have ricin also have anti-nematode effects although the seeds are more effective (Vinuza et al., 2006). Castor leaves increased the effect of castor meal against \textit{M. incognita} attacking lentil (\textit{Lens culinaris} Medikus) and okra (\textit{Abelmoschus esculentus} L.) plants (Wani, 2006). An extract of castor leaves killed 86% of \textit{M. exigua} juveniles J2 in coffee plants (\textit{Coffea arabica} L.) (Amaral et al., 2009). Castor leaf extract was more effective than carbofuran against \textit{M. incognita} attacking tomato plants (Radwan et al., 2007). Castor leaves used as mulch were able to reduce the population of \textit{M. arenaria} infecting okra plants (Ritzinger and McSorley, 1998b). Leaves were more effective against \textit{M. javanica} if a powder was mixed in the soil than if chopped leaves were placed in the soil surface (Lopes et al., 2011).

Castor husks are another castor by-product that can be used as organic fertilizer. They have high K content (45 g kg\(^{-1}\)) but low N content (18.6 g kg\(^{-1}\)). Consequently, the husks needs to be blended with a N-rich organic material to provide a better nutrient balance for plant growth (Lima et al., 2006a, 2006b, 2008, 2011).

**Other Uses of Castor**

Many phytochemicals found in the plant tissue and seeds of castor have potential medicinal uses (Morris, 2004). Castor oil has been used as a purgative since ancient times and it is still considered to be safe and effective laxative (FDA, 2003). The ricin A-chain has also been linked to antibodies able to target cancer cells while not harming normal cells (Olsnes and Pihl, 1981; Lam et al., 2004). These immunotoxins have been reported to have many potential uses in modern medicine (Scadden et al., 1998; Longo et al., 2000; Schnell et al., 2000, 2003; Sandler et al., 2006). Experimental medicines containing castor oil were also shown to be effective treatments of evaporative dry eye (Khanal et al., 2007) and meibomian gland dysfunction (Goto et al., 2002). Castor oil combined with balsam of Peru (\textit{Myroxylon balsamum} L.) and trypsin reduced edema and scabbing of wounds (Gray and Jones, 2004). Castor oil mixed with cashew nut essential oil (Essential- Oligobasics, Oligo Basics Agro-industrial Ltd.) was evaluated as a rumen feed additive for replacing banned ionophores additives. This product was effective for increasing apparent digestibility without reducing feed intake or ruminal ammonia production (Congelion, 2009).

Castor fields can be used for honey production. Castor nectar is located in the leaf petioles, and it is regularly visited by honey bees (\textit{Apis mellifera}). When honey bee colonies were placed in a large castor field, the hives produced normal yields of 18.8 kg of honey in 49 d, and 80% of the honey was made from castor nectar (Milfont et al., 2009). Castor pollen was also found in honey in India (Paliwal et al., 2009). Castor seed production was not increased by bee activity because of the predominant wind pollination (Rizzato, 2007).

Castor meal was used as substrate to the fungus \textit{Penicillium simplicissimum} Oudem. for producing lipases by solid-state fermentation. The process generated a lipase activity of 155,000 U kg\(^{-1}\) while the allergenic potential was reduced by 16%, and all ricin was eliminated from the meal (Godoy et al., 2009, 2011). Castor meal has also been used for producing ethanol by acid or enzymatic hydrolysis (Melo et al., 2008).

Castor historically has been used as an ornamental plant (Murin, 1993; Zoltan et al., 2006; Coopman et al., 2009; Krenzelok, 2009). The plant is an attractive addition to many landscapes due to its big leaves, fast growth, drought tolerance, and diversity of colors in stem and fruits.

This species may also provide an option for phytoremediation of soils contaminated with heavy metals since castor is tolerant to several heavy metals and does not produce food products. Castor is a hyperaccumulator of Pb (Romeiro et al., 2006; Liu et al., 2008), an effective accumulator of Ni (Sherene, 2009), and moderately tolerant to Cd (Niu et al., 2007; Shi and Cai, 2009). Castor also grew well in a soil with
high content of Zn (Shi and Cai, 2010). While castor growth was not inhibited by high doses of Ba and As, these elements did not accumulate in castor vegetative tissue (Coscione and Berton, 2009; Melo et al., 2009). Castor growth was inhibited when several heavy metals (Cd, Pb, Cu, Ni, and Zn) were all added to the soils at the same time (Zeitouni et al., 2007).

Supply and Demand

Castor oil accounts for 0.15% of the world production of vegetable oils (Scholz and Silva, 2008). World consumption of castor oil increased more than 50% during the past 25 yr, rising from around 400,000 t in 1985 to 610,000 t in 2010 (Fig. 2). Most of the consumption growth occurred in the European Union and China. In the European Union (including the 27 state members), castor oil consumption increased from 88 to 127 thousand ton and in China from 40,000 to 240,000 t. The United States had only a moderate growth in consumption while usage declined in both Japan and Brazil. A few reductions in annual consumption occurred in the last decade during recessionary periods when a decline in industrial production reduced the demand for castor oil. But on average, the worldwide consumption of castor oil increased at a rate of 7.32 thousand t per year (Fig. 2).

The world production of castor seed increased 12.3 thousand tons per year between 2000 and 2009 (Table 2). In that period, India was responsible for 54.0% and China for 23.4% of the castor seed produced in the world. Because castor production was reduced by 12.2 thousand tons per year, China became a net importer of castor oil. Brazil ranked third in world castor production (11.9%) followed by Mozambique (4.3%), Paraguay (1.1%), and Thailand (1.0%). Other countries producing minor quantities of castor are Angola, Cambodia, Colombia, Ecuador, Ethiopia, Haiti, Indonesia, Kenya, Madagascar, Pakistan, Peru, Philippines, Russia, South Africa, Sudan, Syria, Tanzania, Uganda, and Vietnam (FAO, 2011; Navas and Severino, personal communication, 2012).

European Union countries were the main importers of castor oil. Their importation increased 18.1% in the period of 2003 to 2010 (Table 3). Meanwhile, China increased castor oil imports by 592%, and became the main importer in the world. Castor imports into the United States increased by 16.2% while imports by Japan were reduced by 42.4%. Despite significant domestic production, Brazil has imported significant amounts of castor oil since 2007.

The price of castor oil is influenced by the price of other agricultural products, particularly vegetable oils. The price of castor oil was 66% higher than soybean oil from 2003 to 2011 (Fig. 3). The difference observed between castor and soybean oil prices was the greatest in September 1999 (214%) and smallest in February 2009 (7%). Castor oil prices fluctuated from a minimum of 650 US$ ton⁻¹ (February 2002) to a maximum of 2700 US$ ton⁻¹ (February 2011).

The price that farmers receive for castor seed production has been highly volatile and shown a wide range of variation. During the period between 2002 and 2008, the price of a 60 kg bag of castor seed in the main producing region of Brazil (Irecê, Bahia) varied from a low value of US$10.89 to the highest of

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<th>Table 2. Production of castor seed in the main producing countries, 2000 to 2009.†</th>
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<th>Table 3. Imports of castor oil (10⁶ kg) by country, 2003 to 2010.†</th>
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An Integrated Research Strategy for Castor

Future research efforts will play a critical role on the global production of castor. The scientific community working on castor should cultivate increased international cooperation in the development of solutions to the main constraints to castor production, processing, and marketing. There were few examples of international collaboration among researchers in the published literature on castor. Neglected areas of research identified by this paper include: (i) characterization and sharing of genetic resources; (ii) studies on the inheritance of important agronomic traits; (iii) development of technologies for completely mechanized castor production; (iv) development of strategies for integrated pests and weed management; (v) improved tools to estimate ricin toxicity; and (vi) development of a global understanding of the technical, economic, and marketing factors that impact castor production. Despite the previous success of breeding programs in the development of several locally adapted cultivars and hybrids, an integrated plant improvement strategy could lead to further progress. The castor genome draft should be used as map for introducing molecular markers into castor breeding. Improved coordination of germplasm banks would allow standardization of evaluation methods and an increased exchange of accessions among breeding programs. Additionally, closer interaction among breeders, molecular biologists, plant physiologists, entomologists, and plant pathologists would speed research and reduce redundant research.

In 2008, three countries (India, China, and Brazil) produced 93% of the world’s supply of castor. Because production is concentrated in only three countries, total castor production varies widely from year to year due to fluctuation in both rainfall and the area planted. This concentration has led to cyclic castor production. Diversification of castor production regions and production under irrigation would reduce the climatic impact on castor supplies. Global consumption of castor oil would be increased if the oil were available at a consistent and competitive cost. However, current castor production is not increasing at a sufficient rate to meet even the anticipated increases in demand. Consequently, the castor oil market will continue to be limited by supply rather than by demand for several years.

Mechanized castor production is rapidly becoming mandatory to sustain or increase global castor production. Because the three main countries producing castor are experiencing fast economic development, the hand labor necessary for conventional castor production has become scarce and expensive. Currently, only limited areas of castor production of castor are fully mechanized because of the lack of nonshattering, dwarf internode, commercial cultivars (Baldan et al., 2003). Development of these cultivars with additional improvements in machinery and agronomic practices will allow the rapid transition of castor to mechanized production.

In the United States, the hazardous chemical products found in the castor plant, especially ricin, has been seen as a major concern (Olsnes, 2004; Audi et al., 2005; Doan, 2004; Franz and Jaax, 1997). The development of low ricin or ricin-free castor cultivars will probably be needed to allow commercial castor production in this country. However, in historic production regions, ricin has not been perceived as a limiting factor in castor cultivation. Nevertheless, research to develop low-ricin, low ricinine, and low allergen cultivars should include parallel studies of increased potential susceptibility to pests and diseases.

Recent studies on the use of castor meal for feeding ruminant livestock indicate that this product has a manageable risk. Again the development of low toxin castor cultivars will facilitate the use of castor meal in animal rations. Castor meal should also be promoted as a rich source of organic N and nonpesticide-based nematode control.

The use of castor oil for biodiesel production has been difficult due to its cost and to its high viscosity. However, castor also has tremendous future potential as a bioenergy and industrial feedstock because of its high oil content, potential modifications in fatty acid composition, very high oil yields, wide range of adaptation, and ability to be grown on marginal sites subject to drought and saline conditions. Consequently, most of the international scientific community working on castor, believe this crop will become a major crop used for production of plant lipids for both energy and industrial applications.

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