36

Breeding peanut

Taxonomy

Family	Fabaceae
Genus	*Arachis* L.
Species	*Arachis hypogea* L.

36.1 Economic importance

Peanuts are an important legume crop in the warm climates of the world. The United States produces about 10% of the world's peanut crop on about 3% of the total world peanut acreage. This disproportionate share of the world's production is attributable to the high average yield per acre in the United States (2800–3000 lb/acre) compared to the world's average yield (800–1000 lb/acre). Nine states in the United States account for 99% of the US peanut crop. These states are Georgia, Texas, Alabama, North Carolina, Florida, Oklahoma, Virginia, South Carolina, and New Mexico. Georgia alone produces 39% of the US total production. In 2001, the US harvested acreage was 1 411 900 acres, a total production of 4 276 704 000 lb and an average yield of 3029 lb/acre. There are three main peanuts regions in the United States – Georgia–Florida–Alabama (southeast), Texas–Oklahoma–New Mexico (Southwest region), and the Virginia–South Carolina–North Carolina region, the southeast region accounting for about 55% of all US production.

On the world scene, peanuts are produced in Asia, Africa, Australia, and the Americas. India and China together account for more than 50% of the world's total production. Other substantial peanut producing nations include Senegal, Sudan, Brazil, Argentina, South Africa, Malawi, and Nigeria.

36.2 Origin and history

The peanut is native to the Western Hemisphere. It probably originated in South America, the center of origin most likely being Brazil, where about 15 wild species are found. The Spanish explorers are credited with its spread throughout the New World. They introduced it to Europe, from where traders spread it to Asia and Africa. Peanuts reached North America via the slave trade. Commercial production of peanuts in the United States began in about 1876. The demand for the crop increased after the Civil War, transforming it from a regional (southern) food to a national food. Production came to the Cotton Belt after 1900. The expansion of the peanut industry was driven by advances in technology that resulted in the development of equipment and machinery for planting, harvesting, and processing the crop.

36.3 Market types

There are four basic market types – Runner, Virginia, Spanish, and Valencia.

Principles of Plant Genetics and Breeding, Second Edition. George Acquaah.

36.3.1 Runner

Runners have become the predominant peanut type in the United States following the introduction of the cultivar, the Florunner, which was responsible for the dramatic yield increase of the crop in the United States. They have uniform size and are grown mainly in Georgia, Alabama, Florida, Texas, and Oklahoma. About 54% of the crop is used for making peanut butter. Runners mature between 130 and 150 days, depending on the cultivar. The seeds are medium sized (900–1000 seeds/lb).

36.3.2 Virginia

Virginia cultivar have dark-green foliage and large pods. They have the largest seeds of all the types (about 500 seeds/lb) and have a russet testa. The pods usually have two seeds (occasionally 3–4). They are grown mainly in Virginia and North Carolina. They mature in about 135–140 days and may have runner or bunch types. Large seeds are sold as snack peanuts.

36.3.3 Spanish

The Spanish group of peanuts comprises bunch types with erect, light-green foliage. The pods rarely contain more than two seeds that are short with tan testa. The seeds are small sized (1000–1400 seeds/lb). They have a higher oil content compared with other types. They are grown mainly in Oklahoma and Texas and are used mainly for making peanut candies, and also snack nuts and peanut butter. They mature earlier than the runner types (about 140 days).

36.3.4 Valencia

The Valencia types typically bear many pods with 3–4 seeds and bright-red testa color. They are erect and sparsely branching with dark green foliage. They are very sweet peanuts and are usually roasted and sold as in-the-shell or boiled peanut. Valencias are grown mainly in New Mexico.

36.4 Genetic resources

Over 10 000 peanut accessions are held in germplasm banks in various countries. In the United States, the Southern Regional Plant Introduction Station at Experiment, Georgia, maintains about 4000 accessions. The International Crops Research Institute for Semi-Arid Tropics (ICRISAT) also maintains thousands of accessions.

36.5 Cytogenetics

The cultivated peanut belongs to section *Arachis*, which consists of three series – annuals, perennial, and amphidiploids. The series amphidiploide has two tetraploids – *A. hypogeae*, and *A. monticola*. Some intersectional crosses yield fertile hybrids. Others produce meiotic problems leading to embyo abortions. The genus, *Arachis*, is classified into seven sections. The section *Arachis* includes four annual diploids ($2n = 20$), several (at least five) perennial diploids, and two annual tetraploids ($2n = 40$). The cultivated peanut is a tetraploid with two subspecies and four interfertile varieties:

Subspecies		
(i)	*A. hypogea*	- variety *hypogea* (US market types Virginia, Runner) - variety *hirsuta*
(ii)	*A. fastigiata*	- variety *fastigiata* (US market type Valencia) - variety *vulgaris* (US market type Spanish)

36.6 General botany

The peanut (*Arachis hypogaea*), also called the groundnut and earthnut, among other names, is technically a pea not a nut. It is an unusual plant in the sense that it flowers aboveground, but fruits belowground. The cultivated plant is an annual with a central upright stem that may stand up to about 18 inches tall. It bears numerous branches that vary from prostrate to nearly erect. It has pinnately compound leaves. The cultivars in cultivation may be grouped into two, based on the arrangement of the nuts at the base of the stem. In **bunch types**, the nuts are closely clustered about the base, while in **runner types** the nuts are scattered along prostrate branches that radiate from the base of the plant to the top. Peanuts have a strong taproot system. Most roots are

Industry highlights

*Breeding peanut (*Arachis hypogaea *L.) and root-knot nematode resistance*

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The program

The Texas peanut breeding program originated in 1939 with the principle objective being to improve yield stability of the crop. Later, objectives included development of disease (pest) resistance and, more recently, objectives to improve the edible quality of the product were implemented. Pedigree selection with and without single seed descent has been used extensively in the program but the mainstay of the disease resistance transfer has been accomplished via the backcross technique. Diseases and nematodes have been recognized as major constraints to production since the very early stages of the program. After discovery of moderate resistance in some plant introduction material in the late 1950s, a project was initiated to develop leaf spot resistance. To enhance the available gene pool, a concentrated effort began in 1970 to introduce leaf spot resistance genes from the wild species. In 1976 an international effort was initiated to collect, preserve, evaluate, and utilize wild *Arachis* from the area of origin of the genus in South America. Through this effort, more than 1500 new wild *Arachis* accessions were added to the germplasm collection, including more than 60 new species and additional representatives of the 22 previously described species. We also introduced more than 3900 land races of *A. hypogaea*.

Introgression program

Leaf spot

Our introgression program began in earnest in 1972. Abdou *et al.* (1974) had identified near immunity to two leaf spot pathogens [*Cercosporidium personatum* (Beck and Curtis) Deighton and *Cercospora arachidicola* Hori] in *A. cardenasii* Krapov. and W.C. Gregory and *A. chacoensis nom. nud.* (now classified as *A. diogoi* (Krapovickas and Gregory, 1994)), respectively. Most of the wild *Arachis* are 2n = 20 but the cultigen is 2n = 4x = 40. We had used both *A. cardenasii* and *A. diogoi* species individually in attempts to cross with *A. hypogaea* and form fertile hexaploids from interspecific triploid progenies, followed by crossing of the 6x progeny back to 4x individuals, then further backcrossing of progenies to 4x to accomplish chromosome segregation and to eventually develop tetraploid progenies that were cross-compatible with *A. hypogaea* and possessed the leaf spot resistance(s) (Simpson, 1990). With both species, widespread sterility occurred after one or two generations of backcrossing to the *A. hypogaea* recurrent parent; in several lines sterility prevented the second backcross. In 1973 we attempted to combine the two resistances into one diploid hybrid and use that hybrid to attempt the hexaploid route. A successful hybridization of *A. diogoi* × *A. cardenasii* was achieved only once in 3500 pollinations, resulting in a partially fertile hybrid with 50% pollen stain. However, that was the end of that pathway's success. Major sterility problems ensued as we doubled chromosome numbers of the triploid and attempted crosses/backcrosses to *A. hypogaea* (Simpson, 1990).

The next attempt consisted of doubling the chromosome number of the *A. diogoi* × *A. cardenasii* hybrid, then crossing with *A. hypogaea*. Even though this was a tetraploid × tetraploid, the process met with equal, if not greater sterility problems than previous attempts.

In this time-frame, Smartt *et al.* (1978a, 1978b) published their theory that the cultivated peanut was comprised of two genomes, made up of an A genome represented by *A. cardenasii* and *A. diogoi*, and a B genome represented by *A. batizocoi*. Based on this hypothesis, we crossed the *A. diogoi* × A. *cardenasii* hybrid on to *A. batizocoi* and obtained a sterile (pollen stain = 0.01%) hybrid. We doubled the chromosomes of this plant to yield a highly fertile complex amphiploid (tetraploid) hybrid with normal meiosis and a pollen stain >90%. From this point we initiated our crossing/backcrossing effort to establish fertile progenies with leaf spot resistance (the pathway is shown in Figure B36.1). Progress was slow primarily because we had not established a reliable laboratory technique for screening large numbers of plants; therefore, each cycle required more than 18 months when selections were made based on leaf spot resistance. However, we carried two sections of the program, with the hope that selection based on fertility and agronomic traits other than resistance would yield fertile plants with leaf spot resistance at an earlier date. Without selection for resistance, the program moved rapidly, with a cycle being made in 10 months or less. The initial complex amphiploid from this program was later released as the germplasm line TxAG-6 (Simpson *et al.*, 1993).

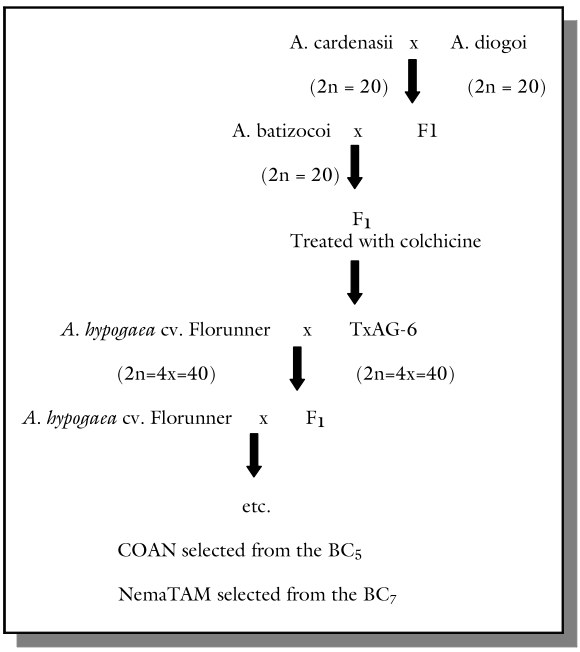

Figure B36.1 Tetraploid pathway for introgression of root-knot nematode resistance into *Arachis hypogaea*. Figure courtesy of Charles Simpson.

Nematodes

Root-knot nematodes (*Meloidogyne arenaria* (Neal) Chitwood) became a serious pest of peanut in the major growing area of Central Texas (as well as many other places in the USA and the world) by the early 1970s. However, no useful level of resistance had been identified in the cultigen, so we began testing for resistance in the wild species. Banks (1969) had demonstrated some resistance to *M. hapla* in the *Rhizomatosae*, but since the rhizomatous taxa would not cross with the cultivated peanut or its sectional relatives (Gregory and Gregory, 1979) these genes were unavailable. In 1989 numerous accessions of wild peanut were identified with resistance (near immunity) to the root-knot nematode (Nelson *et al.*, 1989). Fortunately one of those accessions was *A. cardenasii*, the primary A genome parent we had been working with in the leaf spot resistance program. Our next effort was to test the advanced backcross generation materials from the leaf spot program in hopes that the gene(s) for nematode resistance might have been retained. Unfortunately, the only materials that proved to be resistant to the root-knot nematode were TxAG-6 and the F_1 from the first backcross to *A. hypogaea*. Even so, the availability of a high level of resistance to root-knot in genotypes that were readily cross-compatible with the cultigen was a tremendous benefit to the effort to develop a nematode resistant cultivar (Simpson, 1990).

We then initiated an intense backcross breeding program with a selection from the BC_1F_1 materials, subsequently released as the germplasm line TxAG-7 (Simpson *et al.*, 1993), to transfer the gene(s) to the most desirable cultivated peanut available, which at that time was Florunner. Florunner, a revolutionary peanut because of its large increase in yield, was released from University of Florida in 1969 (Norden *et al.*, 1969) and by 1986 had become the most successful peanut variety ever developed, worldwide.

Backcross program

Our backcross effort (Simpson, 1990) consisted of: making crosses in the fall of the year at the Texas A&M University Research and Extension Center in Stephenville; harvesting and then planting the F_1 seeds as soon as they were mature enough to germinate (usually mid-December); harvesting seeds (F_2 or BC_nF_1) from these plants in late April; and sending the seeds to the Plant Nematology laboratory in College Station for resistance screening. Seeds were planted in 10 cm pots and the seedlings inoculated with 10 000 root-knot nematode eggs per pot. Plants were harvested eight weeks after inoculation and highly resistant plants were identified based on low levels of nematode reproduction (Starr *et al.*, 1990, 1995). Stem cuttings from resistant individuals were then sent back to Stephenville to be used as male parents in the next backcross generation that were initiated in September and October. In each cycle, the primary selection criterion was the nematode resistance, especially in the earlier generations. After the BC_3 generation we also began making selections based on the plant characters of pod shape and seed per pod. We continued this process through seven backcrosses. The pathway is shown in Figure B36.1 (Simpson, 1990).

At about the third backcross generation we determined that at least two resistance genes were present in the early generation materials but at this stage it was not certain that more than one dominant gene controlled the trait (Starr *et al.*, 1990) in our more advanced generation lines. At this time we also initiated a collaboration with A.H. Paterson and M.D. Burow to develop molecular markers linked to the resistance loci (Burow *et al.*, 1996).

Releases

After the fifth backcross, we also initiated seed increases of lines that appeared to have most of the plant, pod, and seed characteristics of Florunner and nematode resistance. Field tests for yield potential began in 1995 and from these tests we identified five lines with reasonable yield and excellent resistance. Following a second year of testing we made a winter increase of numerous sister seed rows in Puerto Rico from one line; from this material we released the world's first root-

knot resistant peanut cultivar, COAN, in 1999 (Simpson and Starr, 2001). This release was rushed through the process and had one major flaw; the plant size was too small, limiting the seed production of the plants. Even though the yields under heavy nematode pressure had yields that were 150–200% better than susceptible cultivars, the total yields were still too low to be profitable for grower acceptance.

During this time the molecular marker work was progressing and preliminary tests with several restriction fragment length polymorphism (RFLP) loci indicated that we would be able to use this technology for more efficient screening for resistance. We would even be able to identify plants homozygous for the one major dominant gene that appeared to control resistance (Burow *et al.*, 1996).

After the BC_7 was made, selection and seed increase resulted in lines that performed much better than COAN in yield tests and still contained the resistance gene. After one year of testing we decided to do a Puerto Rico winter increase of three of the best lines in the hope of being able to select a line for release as a cultivar with greater yield potential.

In the second testing year we space planted 300 individual seeds from the winter nursery of the three lines in the field at Stephenville. We collected tissue for DNA analyses from the 900 plants and at harvest we had molecular data to identify the homozygous resistant plants which had the dominant (RR) gene (Church *et al.*, 2000). These data were utilized when we were evaluating the individual plants for plant, pod, and seed characters and selecting individual plants for a breeder seed increase. We selected numerous desirable plants that were homozygous resistant from each line. The seeds from these were planted as plant rows in a Puerto Rico winter nursery to gain another generation.

After a third year of yield testing and extensive other evaluations, the cultivar NemaTAM was released in 2001 (Simpson *et al.*, 2003). NemaTAM has about 30% greater yield potential than COAN and the same high level of root-knot resistance. Two major benefits of these resistant cultivars are that (i) the resistance will eliminate the need for use of nematicides, even at very high nematode population densities, and (ii) the inhibition of nematode reproduction due to the resistance results in lower nematode population densities such that a susceptible crop plant in rotation with the resistant cultivar will be subjected to less nematode disease pressure (Starr *et al.*, 2002).

The resistance in COAN and NemaTAM to *M. arenaria* is controlled by a single dominant gene (Burow *et al.*, 1996; Choi *et al.*, 1999; Church *et al.*, 2000), but evidence for additional genes in the same species used to form TxAG-6 indicates that we have the opportunity to pyramid genes for more stable resistance (Burow *et al.*, 1996; Garcia *et al.*, 1996; Choi *et al.*, 1999).

Further testing indicates that the resistance in TxAG-6 is conditioned by at least two genes, one dominant and one recessive (Church, 2002) We also discovered that COAN and NemaTAM are resistant to *M. javanica*, which is also parasitic on peanut and especially prevalent in India and northern Africa. This resistance to *M. javanica* has been confirmed in an independent study (Timper *et al.*, 2003). At present we can only assume the resistance is conditioned by the same gene; we have not tested this hypothesis.

The future

The program continues to try to identify, characterize, and locate flanking molecular markers for the second resistance gene so we can pyramid the genes. It would be desirable to move from the current RFLP marker assisted selection system to one based on polymerase chain reaction (PCR), which would increase the efficiency of the system. We are also continuing our efforts to identify genes and markers resistance to *M. hapla* as well as *M. javanica*. However, now our major efforts are to combine the nematode resistance gene(s) with other characters to develop cultivars with multiple traits, including high O/L (ratio of oleic free fatty acid to linoleic free fatty acid), tomato spotted wilt virus resistance, sclerotinia resistance (*Sclerotinia minor* Jagger) and leaf spot resistance.

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nodulated for biological nitrogen fixation. The branching pattern in peanut may be alternate or sequential. Virginia types have alternate branching, a trait that is generally believed to be dominant over the sequential branching of Spanish and Valencia peanuts. Aerial podding is conditioned by dominance or partial dominance.

The flowers arise in the leaf axils above the ground. They are self-pollinated. Upon fertilization, the ovary begins to enlarge while the section behind it, called the **peg** or **gynophore,** elongates to push the ovary into the soil for fruit development. The fruit is an indehiscent pod that may contain 1–6 (but usually 1–3) seeds. The pods form predominantly underground. However, mutants with aerial podding have been developed. Consequently, it is critical that the pegs reach the soil. The seed has a thin papery testa that varies in color – brick red, russet, light tan, purple, white, black or multicolored. Some cultivars exhibit seed dormancy. Well-developed nuts have a shelling percentage of 70–80%.

36.7 Reproductive biology

36.7.1 Floral morphology

The peanut inflorescence occurs in clusters of three or more flowers in the axil of the cataphyll of foliage leaves. Inflorescence may occur on either the main stem or lateral branches. Spanish and Valencia cultivars bear their inflorescence on the main stem, whereas the inflorescence of Virginia cultivars occurs on lateral branches. A flower is subtended by a bract and occurs on a minute branch of the inflorescence, which arises in the axil of a second bract. The calyx and corolla are borne at the top of the hypanthium, which surrounds the staminal column. The calyx has

five lobes, whereas the staminal column is usually composed of ten filaments, eight of which are normally anther bearing. About 50–75% of the bottom parts of the filaments are fused.

36.7.2 Pollination

Normally, only one of the flowers in an inflorescence matures to anthesis. Anthesis generally occurs before flower opening. Bud opening occurs at the beginning of the light period. The stigma remains receptive for about 12–24 hours after flower opening. It takes only about 5–6 hours for an opened flower to stay open.

36.8 Common breeding methods

The common approaches to breeding peanuts include the use of plant introductions. Introductions of peanut germplasm can be a beginning point for crop improvement. Selections from introductions may provide a parental material for breeding. Selection may also be used to isolate pure lines from hybrid populations.

A widely used method of breeding peanut is hybridization of superior parents to create opportunities for transgressive segregation to occur. Pedigree selection may be used to advance generations. However, the use of single seed descent is more rapid when used in conjunction with winter nurseries. Backcross breeding may be used to incorporate specific genes of interest.

36.9 Establishing a breeding nursery

Peanut crossing is often done in the greenhouse using potted plants. However, wild species are more successfully hybridized in the field than in the greenhouse. The success of hybridization, whether under field or greenhouse conditions, depends on proper humidity. Drought causes low success. Breeders may emasculate the flowers in the evening and pollinate the next morning.

36.10 Artificial pollination

36.10.1 Materials and equipment

Equipment use includes forceps, sharp knife, scalpel, razor blade, magnifier (2–3x) attached to a head band, camel hair brush, bottle of alcohol.

36.10.2 Preparation of female plant

Flowers near the main stem are preferred for emasculation. Further, one flower in each inflorescence is selected for emasculation. The flower is emasculated in the bud stage. To emasculate, the bud is grasped between the thumb and index finger of the hand. Next, the petal in front of the keel and the sepal on the side of the standard are folded down. The standard petal is opened with the forceps and the wing petals pulled out and down. The standard is held back with the thumb and index finger while the operator pulls the keel free of the stigma and anthers. Alternatively, the keel and wing petals may be removed altogether. The anther and the stamens are removed to complete the emasculation. If an emasculated flower is not be immediately pollinated, the hypanthium is tagged (e.g., with a small thread).

36.10.3 Pollination

Pollen collected between 5 and 7 a.m. is the most viable. Flowers are artificially pollinated in the morning to early afternoon. The keel may be detached and used as a brush to directly deposit the pollen unto the stigma. Some operators transfer the pollen with a camel hair brush or the tip of the forceps. The environment may be humidified, but care should be taken not to dislodge the pollen. Pollen may be collected and stored under desiccated condition in a cool place (6 °C) for up to about a week without losing viability.

Fertilization occurs between 12 and 16 hours after pollination, after which the ovary elongates as the intercalary meristem at its base grows. The peg eventually penetrates the soil where it develops into a mature peanut fruit. An identification wire may be tied to the peg from the emasculated flower before it penetrates the soil.

36.10.4 Seed development and harvesting

Seed is mature for harvesting after about 55–65 days, depending on the environment and cultivar. Peanuts are ready to be harvested when 65–70% is mature. Early harvesting results in shriveled kernels. At proper maturity, the kernels display the distinct texture and color of the variety, the inside of the shell is beginning to color and show dark veins. Harvesting it is easier in sandy soils and occurs with less loss of pods with small-podded than large-podded varieties.

36.11 Common breeding objectives

Some of the major objectives in peanut breeding are:

- **Yield potential and stability.** Breeders are interested high crop yield *per se* and also stable yield with adaptation to various agroecological zones. High shelling percentage is important. Early maturity is desired in some production areas.
- **Disease resistance.** Important diseases of peanut include foliar ones such as leaf spot (caused by *Cercospora* spp). Stem and peg rots (caused by *Sclerotium rolfsii*) and charcoal rot (by *Rizoctonia* spp.) are economic diseases in some production area.
- **Insect resistance.** Important insect pests include leafhoppers, corn earworm, cutworms, and tobacco thrips.
- **Product quality.** Peanuts consist of 40–48% oil and 25–30% protein, making the crop a major source of vegetable oil and plant protein. Breeding high oil content is an important objective.

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Outcomes assessment

Part A

Please answer the following questions true or false.

1 The cultivated peanut is a diploid.
2 Peanut is self-pollinated.
3 Virginia variety of peanuts is characterized by small pods.

Part B

Please answer the following questions.

1 Give the four basic market types of peanuts.
2 Give the scientific name of peanuts.
3 Distinguish between a runner and bunch type of peanuts.

Part C

Please write a brief essay on each of the following topics.

1 Discuss the reproductive biology of peanuts.
2 Discuss the common breeding methods for peanuts.
3 Discuss the emasculation of peanut flower.

37

Breeding potato

Taxonomy

Family	Solanaceae
Genus	*Solanum* L.
Species	*Solanum tuberosum* L

37.1 Economic importance

Potato is among the top five crops that feed the world, the others being wheat, corn, sorghum, and rice. In 1998, potatoes ranked as the fourth most important food crop in the United States. The total harvest in 1998 was 1.388 million acres and a total yield of 475.8 million cwt. About 35% of the production was processed into frozen products (primarily fries). Per capita consumption of potatoes in the United States in 1999 was 144.7 lb. The top five producing states in 1998 were Idaho, Washington, Oregon, Wisconsin, and North Dakota, with Idaho leading all production with about 450 million cwt, followed by Washington.

On the world scene, 293 million tons of potatoes were produced on 18 million hectares worldwide in 1998. With the break-up of the former Soviet Union, China becomes the world's leading producer of potatoes. Developing countries accounted for 36% of total production in 1998. In Asia, the key producers include China, India, Indonesia, and Nepal; in Africa, Egypt, South Africa, Algeria, and Morocco account for 80% of the region's total production. Latin American countries that produce a substantial amount of potatoes include Ecuador, Peru, Brazil, and Mexico. In Europe, the leading countries include the former Soviet Union, Poland, West Germany, and France.

37.2 Origin and history

Potato originates in the Andes mountains of Peru and Bolivia where the plant has been cultivated for over 2400 years. The Aymara Indians developed numerous varieties on the Titicaca Plateau, some 10 000 feet above sea level. The first written account of potato was made in 1553 by the Spanish Conquistador Pedro Cieza de Leon in his journal, *Chronicle of Peru*. The Spanish introduced the potato to Europe between 1565 and 1580. It was taken from England to Bermuda and later to Virginia, USA, in 1621. It was also introduced into Germany in the 1620s where it became a part of the Prussian diet by the time of the Seven Year War (1756–1763). Antoine Parmentier, a prisoner of war in Prussia, introduced the crop to France after the war. Potato was introduced into North America when Irish immigrants (hence the name "Irish potato") brought it to Londonderry, New Hampshire, where large-scale production occurred in 1719.

By the 1840s, the devastation by the fungus *Phytophthora infestans* (causes late blight) and heavy rains brought untold hunger and starvation to Ireland. This sparked a mass immigration of about two million Irish, mostly to North America. In America, Luther

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Burbank was first to undertake improvement of the plant, subsequently releasing the "Burbank" potato to West Coast states in the late 1800s. A mutation of the Burbank potato was discovered in Colorado that was disease resistant. It had reticulated skin and became known as the Burbank Russet and is grown on most farms in Idaho.

37.3 Adaptation

Potato is a cool-season crop. The optimum temperature for shoot growth and development is 22 °C. In the early stages, soil temperature of about 24 °C is ideal. However, in later stages, a cooler temperature of about 18 °C is desired for good tuberization. Tuber formation and development is slowed when soil temperature rises above 20 °C and ceases at 29 °C. Above this temperature, the effect of respiration exceeds the rate of accumulation of assimilates from photosynthesis.

Potatoes are sensitive to hard frost that may occur in fall, winter, or early spring. Tubers will freeze at about −2 °C and loose quality upon thawing. Tuberization is best under short photoperiod, cool temperature, and low nitrogen, while vegetative shoot production is favored by long days, high temperature, low light intensity, and high amounts of nitrogen. However, tuberization can occur at 12 °C night air temperatures. Tuber yield decreases by 4% for each 0.6 °C above optimal temperature. The best potato production occurs in regions with daily growing season temperatures averaging between 15.5 °C and 18 °C. High soil temperatures result in knobby and malformed tubers. Potato flowers and sets seed best when long days and cool temperatures prevail. Consequently, potatoes set seed when grown in the northern states but not the southern states.

37.4 Genetic resources

Potato diversity is maintained in a number of germplasm banks in various parts of the world. The major repositories include the International Potato Center (CIP) in Peru (has the best collection of cultivated potatoes, especially, andigena, phureja, and "bitter potatoes"); the Commonwealth Potato Collection at Pentlandfield, Scotland, and the German–Dutch Potato Collection at Braunschweig, Germany. In the United States, the IR-1 project at Sturgeon Bay, Wisconsin, is important to US breeders.

37.5 Cytogenetics

The genus *Solanum* contains about 2000 species, of which only about 150 bear tubers. The cultivated potato, *Solanum tuberosum*, is a tetraploid (2n = 4x = 48). Five cytological groups of potato have been identified, with somatic numbers of 24, 36, 48, 60, and 72. About 70% of tuber-bearing potatoes are diploids, while 5% and 8% are tetraploids and hexaploids, respectively. Most of the diploids are self-incompatible, producing seed only when fertilized by pollen containing a different *S* allele.

A cultivated diploid that is used in South American production is the *S. phureja*. It is used in bridge crossing and other genetic studies. Triploid potato is sterile; a few are cultivated. Producing triploid potato by crossing 2n × 4n is seldom successful because of the so-called "triploid block". Hexaploids are self-fertile. A widely used hexaploid is *S. demissum*. It is the sources of the major *R* gene that confers resistance to late blight.

37.6 Genetics

Potato genetics is complex because of its autotetraploid origin. There can be four different alleles at a locus. Intralocus interactions (heterozygosity) and interlocus interaction (epistasis) occur and can be exploited by using the appropriate breeding procedure.

37.7 General botany

Potato (*Solanum tuberosum*) is an annual plant with short (1–2 feet), erect, and branched stems. Its compound leaves can be 1–2 feet long with a terminal leaflet. The flowers are borne in compound, terminal cymes with long peduncles. The flower color may be white, rose, lilac, or purple. The plant bears fruits (berries) called **potato balls**. The underground commercial part is a modified stem (or tuber) that is borne at the end of a stolon. The "eyes" on the tuber are actually rudimentary leaf scars favored by lateral branches. Each eye contains at least three buds

Industry highlights

The breeding of potato

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Evolution of the modern potato crop

Potatoes were domesticated between 7000 and 10 000 years ago in the Andes of South America (Bradshaw and Bonierbale, 2010), their wild species progenitors having been the subject of much discussion. Spooner *et al.* (2005) have provided molecular taxonomic evidence for a single domestication in the highlands of southern Peru from the northern group of members of the *S. brevicaule* complex of diploid species, such as *S. canasense*, *S.multidissectum* and *S. bukasovii*. The result was diploid *S. stenotomum*, also referred to as a form of *S. tuberosum* (Group Stenotomum), from which other cultivated species were derived; including diploid *S. phureja* (or Group Phureja), tetraploid *S. tuberosum* subsp. *andigena* (or Group Andigena) and tetraploid *S. tuberosum* subsp. *tuberosum* (or Group Tuberosum). Andigena potatoes became the most widely grown form in South America. Tuberosum potatoes were selected from Andigena types for tuber production in long days in coastal Chile and are referred to as Chilean Tuberosum. Phureja potatoes were selected from Stenotomum for lack of tuber dormancy, so that up to three crops per year could be grown in the lower, warmer, eastern valleys of the Andes.

Potatoes were introduced from South America into the Canary Islands around 1562 and from there to mainland Europe in the 1570s (Hawkes and Francisco-Ortega, 1993). It has often been assumed that these early introductions were Andigena types that evolved into Tuberosum types as the growing of potatoes spread north-eastward across Europe. However, it now seems safest to assume that the early introductions came from both the Andes and coastal Chile, as analysis of DNA from 49 herbarium specimens confirmed the presence in Europe of Andean potatoes from around 1700 and Chilean potatoes from 1811 (Ames and Spooner, 2008). Starting in the seventeenth century, potatoes were taken from Europe and cultivated in many other parts of the world. Today potatoes are grown on 18.5 million hectares of land in 149 countries from latitudes 65 °N to 50 °S and at altitudes from sea level to 4000 m (Hijmans, 2001). The potato is now the third most important food crop after wheat and rice,with annual production of over 300 million metric tons fresh weight of tubers (http://faostat.fao.org). As well as being a staple food, the potato is grown as a vegetable for table use, is processed into French fries and crisps (chips), and is used for dried products and starch production.

Potato breeding and the need for new cultivars

Potato breeding

The reproductive biology of potato is ideal for creating and maintaining variation. Potatoes flower and set true seed in berries following natural pollination by insects, particularly bumble bees. Outcrossing is enforced in cultivated (and most wild) diploid species by a gametophytic self-incompatibility system. Whilst this system does not operate in *S. tuberosum* because it is a tetraploid, 20% natural cross-pollination was estimated to occur in an artificially constructed Andigena population (Glendinning, 1976). This sexual reproduction creates an abundance of diversity by recombining the variants of genes which arose by mutation, and potatoes are highly heterozygous individuals which display inbreeding depression on selfing. The genetically unique seedlings which grow from true seeds produce tubers which can be replanted as seed tubers, and hence distinct clones can either be established and maintained by asexual vegetative reproduction or discarded. Domestication involved selection of less bitter and, hence, less toxic tubers and Andean farmers certainly retained a much wider variety of tuber shapes and skin and flesh colours than seen in wild species (Bradshaw and Bonierbale, 2010).

Modern potato breeding began in the nineteenth century when, as early as 1807, Knight in England (Knight, 1807) was advocating the use of artificial hybridization in the breeding of new cultivars. It flourished in Britain and elsewhere in Europe and North America during the second half of the nineteenth century when many new cultivars were produced by farmers, hobby breeders and seedsmen. A single Chilean Tuberosum cultivar, Rough Purple Chili, was introduced into the USA in 1851 (Goodrich, 1863); North America's most popular potato cultivar, Russet Burbank, was derived from it by three generations of open pollination with selection and released in 1914 (Ortiz, 2001). The descendents of Rough Purple Chili were widely employed as female parents in crosses with European Tuberosum at the end of the nineteenth century. Modern potato breeding started later in India and China but with rapid expansion since 1948 and 1978, respectively; furthermore, these countries are now two of the leading potato producers in the world. By 2009, the World

Catalogue of Potato Varieties (Pieterse and Hils, 2009) was able to list more than 4500 cultivars from 102 countries. This is a remarkable achievement since the genetic base of this potato breeding must be considered narrow, despite some introgressions of disease resistance genes from wild and cultivated relatives of Tuberosum potatoes and some base broadening with Andigena and Phureja/Stenotomum (Bradshaw and Bonierbale, 2010).

Need for new cultivars

Despite the large number of cultivars currently available there is a continuing need for new ones. At least two contrasting scenarios can be seen. In the European Union the potato industry is trying to increase potato usage in an economically and environmentally sustainable way. New cultivars must give more yield of saleable product at less cost of production. They must have inbuilt resistances to pests and diseases, and increased water and mineral use efficiency that allow reduced use of pesticides and fungicides and better use of water and fertilizers. Furthermore, they must have the quality traits demanded by processors and supermarkets. Finally, new cultivars must help meet consumer demands for convenience foods, improved nutritional and health benefits, improved flavor and novel products. In contrast, in Asia, Africa, and Latin America there is a need for increased and stable potato production to meet increased demand for food from human population growth. New cultivars must deliver higher yields under low inputs, disease and pest attacks, and environmental stresses such as drought, heat, cold and salinity, with water stress affecting potato production in most areas of the world. If possible, new cultivars should have improved nutritional and health properties, such as higher levels of micronutrients (biofortification). However, the greatest need is to raise fresh weight yields from a world average of 17 t/ha to European and North American levels where over 40 t/ha is achieved. Finally, the most important consequence of climate change is likely to be the need for cultivars that make better use of water, and either avoid drought (faster tuber bulking) or are tolerant of drought (Bradshaw and Bonierbale, 2010).

Breeding finished cultivars

Parents and crossing

Potato breeding worldwide has traditionally involved making crosses between pairs of parents with complementary features and this is still the main route to new cultivars. The aim is to generate genetic variation on which to practice phenotypic selection over a number of vegetative generations, for clones with as many desirable characteristics as possible for release as new cultivars. The choice of parents is all important as breeding can never simply be a numbers game. Crossing the 4500 cultivars in the world catalogue in all possible combinations would generate over ten million progenies and raising 500 seedlings of each would give a staggering total of over five billion for evaluation, an impossible task. In contrast, a phenotypic assessment of 4500 cultivars is feasible, and so is a genotypic assessment of diversity with molecular markers. Hence, breeders can now think in terms of capturing allelic diversity in a smaller core set of parents and of using association genetics to choose parents genotypically as well as phenotypically. They can also use genetic distance based on molecular markers to complement coancestry/pedigree analysis (Sun *et al.*, 2003) in order to avoid closely related parents, and hence inbreeding depression, and to ensure genetic variation for continued progress.

As genetic knowledge accumulates, it will be possible to choose parents for use in pair crosses so that one or both parents have the desired major genes and alleles of large effect at quantitative trait loci (QTLs). Major genes have been mapped for flesh, skin, and flower color, for tuber shape and eye depth, and for resistances to late blight, nematodes, viruses (PVY, PVA, PVX, PVM, PVS and PLTV), and wart. QTLs of large effect have been mapped for total glycoalkaloid content, maturity and resistances to late blight, Verticillium wilt, cyst nematodes. and PLRV. In contrast, many economically important traits are still best viewed as complex polygenic traits, despite a number of QTLs being found, and these include tuber dormancy, dry matter and starch content, fry color, resistance to *Pectobacterium*, tuberization, and yield. For these traits, breeders will still have to rely primarily on phenotypic data and use knowledge of offspring–mid-parent regressions to determine crossing strategy. A statistically significant regression is evidence of heritable variation and the slope of the regression line is a measure of heritability. With a highly heritable trait like fry color the mid-parent value is a good predictor of the mean performance of the offspring and a few carefully chosen crosses can be made (Bradshaw, 2007). In contrast, with only a moderately heritable trait such as yield, offspring mean is less predictable and more crosses need to be made to ensure that they include the best possible.

Clonal generations

Potato breeding at the Scottish Crop Research Institute (SCRI) from 1965 to 1985 was typical of most relatively large programs, both then and now (Mackay, 2005; Bradshaw, 2009). The target duration of the breeding scheme was 12 years: year 1 – crosses (200–300); year 2 – visual assessment of seedlings (100 000) in a glasshouse; year 3 – visual assessment of

Table B37.1 James Hutton Institute (formerly SCRI) strategy for breeding finished cultivars.

Year	Strategy
0	**Decide objectives and evaluate potential parents**
	Midparent values used to predict mean performance of crosses for quantitative traits + other genetic information
	GLASSHOUSE
1	Choose parents and make 200 crosses
2	Seedling progeny tests on 200 progenies × 2 replicates × 25 seedlings (late blight, potato cyst nematodes, visual assessment of tubers)
	Select best 40 progenies (after first cycle will also have midparent values for fry color and other traits from year 5 of previous cycle)
	SEED SITE
3	Tuber progeny tests on 40 progenies × 2 replicates as 2,000 spaced plants (visual assessment of tubers and fry color). Select 500 spaced plants at harvest (four tubers of each plant)
	Sow more seed of 10 best progenies in the glasshouse to provide a further 10 × 250 = 2,500 (four tubers of each) clones for year 4
	Select clones for use as parents in next cycle of crosses at random from those (500) advancing to year 4
4	3,000 unreplicated four-plant plots (including parents of next cycle of crosses)
	Assessment for yield and quality and special disease tests

	Seed site (number of plants)	Clones (number)	Ware site (number of plots and plants per plot)
5	6	1,000	2 × 5; include parents used in crosses
6	20	360	2 × 10
7	100	120	Two harvests or sites of 2 × 10
8	300	40	Ware trials at a number of sites
9	700	20	Ware trials at a number of sites
10	2,000	2	Official trials
11	2,000	1	Official trials
	Multiplication and commercialization from virus-free stock		

single spaced plants (50 000) at seed site; year 4 – visual assessment of unreplicated small plots (4000) at seed site and limited post-harvest assessment of quality and disease resistance; years 5–7 – ware (yield) trials (1000, 500, and 200 clones) at breeding station, seed production at seed site and disease and quality testing; years 8–10 – multisite trials (60, 10, and 5 clones) in Britain and overseas and larger-scale seed production at seed site; years 11 and 12 – statutory National List (NL) trials (one or more clones), registration for Plant Breeders' Rights and multiplication from disease-free stock; year 13 – new cultivar(s) added to the National List, 12 years after crossing. Further information on all of these stages has been reviewed elsewhere (Bradshaw, 2007).

Research in the 1980s found that intense early generation visual selection for most quantitative traits was ineffective, particularly between seedlings in a glasshouse and spaced plants at a seed site. The solution to this problem developed and implemented at SCRI from 1985 was the use of progeny tests to discard whole progenies (= full-sib families) before starting conventional within-progeny selection at the unreplicated small-plot stage. Seedling progeny tests were developed for disease and pest resistance, and tuber progeny tests for quality traits. More true seed of the best progenies would be sown to increase the number of clones on which to practice selection in seeking new cultivars. In programs targeted to particular end users, duration was reduced by using progeny tests to discard whole progenies, by starting replicated trials earlier at more than one site and by using micropropagation to multiply promising clones for more extensive testing (Mackay, 2005). Once promising clones had been identified after both the first and second year of ware trials, they were used as parents in the next round of crossing to keep the momentum of the program going. This avoids delaying progress while waiting to obtain more information on potential parents over further clonal generations. In effect, combined between and within full-sib family selection is operated on a five or six year cycle, but it could be done on a three year

cycle with limited within-family selection. The latter is desirable when one wishes to combine genes from more than two parents as quickly as possible at the start of a new program. Finally, such a recurrent selection program can accommodate new breeding objectives and germplasm whilst continuing to maintain progress (Bradshaw *et al.*, 2003, 2009). Table B37.1 shows how these principles are currently implemented in commercially funded breeding.

Genetic knowledge and molecular marker assisted selection

As knowledge increases about the number and chromosomal locations of genes affecting economically important traits, breeders should be able to design better breeding programs. They will be able to select parents that complement one another genotypically as well as phenotypically. In the offspring, they will be able to determine the seedling population size required for certainty of finding the genotype with the desired combination of genes (alleles) and hence traits. If this population size is too large to handle in practice, then the required number of cycles of crossing and selection can be determined. A big impact on the efficiency and rate of progress would be the identification of superior clones genotypically as seedlings in the glasshouse and the use of modern methods of rapid multiplication to progress them to commercialization. This will require molecular marker assisted selection or preferably direct recognition of the desired allele at a genetic locus (Bradshaw and Bonierbale, 2010). The discovery and tracking of such alleles should be easier now that the potato genome has been sequenced (http://www.potatogenome.net).

Widening the genetic base for future potato breeding

In future, for many traits, greater use can be expected of the world collection of 3527 potato cultivars native to Latin America which is maintained by the International Potato Centre (CIP) in Peru (Huaman *et al.*, 1997). In addition, further improvements in resistance to abiotic and biotic stresses should come from a greater use of wild species, given the wide range of habitats in which they have evolved. The Inter-genebank Potato Database (IPD) contains 7112 different accessions of 188 taxa (species, subspecies, varieties and forms) out of the 247 tuber-bearing wild potato taxa recognized by Hawkes (Huaman *et al.*, 2000) and data are available for more than 33 000 evaluations covering 55 traits. The species form a polyploid series from diploid ($2n = 2x = 24$) to hexaploid ($2n = 6x = 72$). By manipulation of ploidy, with due regard to Endosperm Balance Number, virtually any potato species can be utilized for the introgression of desirable genes into *S. tuberosum* (Ortiz, 2001; Jansky, 2006). In the past, it took up to five backcross generations and 30 years to transfer a major dominant resistance gene from a wild species into a successful cultivar but today molecular marker assisted introgression offers the possibility of faster progress. As potatoes are heterozygous outbreeders, use of the same recurrent parent during introgression would result in a self of the recurrent parent, and hence inbreeding depression. This can be avoided by using different Tuberosum parents for each backcross but would result in an entirely new cultivar, which may or may not be the desired outcome. The only way to introduce a gene into a known cultivar is by the transgenic route. Hence, the molecular cloning of natural resistance genes and their transfer by *Agrobacterium*-mediated transformation into well-adapted but susceptible cultivars is being pursued in a number of laboratories worldwide. Given the timescale of conventional breeding, the genetic improvement of popular potato cultivars such as Russet Burbank by transformation is an attractive proposition, despite public concerns about GM (genetically modified) crops in some countries. Transformation also offers the possibility of improvements through gene silencing and through the introduction of novel traits into potato, such as those mentioned by Bradshaw and Bonierbale (2010).

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protected by scales. When potatoes sprout, the sprouts are lateral branches with several buds. A section across a tuber reveals a pithy central core with branches leading to each of the eyes.

37.8 Cultivars

Four cultivars account for about 75% of the potato acreage in the United States – Russet Burbank, Katahdin, Kennebeck, and Red Pontiac. These major varieties represent the most major shapes of potato – the long cylindrical and russet skin of the Russet Burbank, the red and short rounded shape of Truimph.

Many new modern cultivars have been developed for various markets – baking, frying, cooking, canning, creaming, dehydrating, and chipping. These cultivars have certain specific characteristics that make them suitable for their specific uses. The round smooth-skinned white eastern cultivars are used for chipping (potato chips) and cooking (boiling), while the mutated western types are used for baking and frozen products (mainly French fries). The russet potato varieties have higher dry matter content than the eastern types. Dry matter is measured by the specific gravity of the tuber. High dry matter (1.085 specific gravity or higher) is desired for baking and processing. For frying, boiling, or mashing, the tuber should have a specific gravity of 1.080 or higher and at least 19.8% solids plus 14% starch.

37.9 Reproductive biology

37.9.1 Floral biology

Potato has a terminal inflorescence consisting of 1–30 (but usually 7–15) flowers, depending on the cultivar. The five petals give an open flower a star shape. A flower also has a stigma that protrudes above a cluster of five large, bright-yellow anthers. The corolla color varies from white to a complex range of blue, red, and purple. Flowers open, starting with those nearest the base of the inflorescence and proceeding upwards at the rate of about 2–3 each day. At the peak bloom, there are usually 5–10 open flowers. Flowers stay open for only 2–4 days; the receptivity of the stigma and duration of pollen production is about two days.

37.9.2 Pollination

Potato is predominantly self-pollinated. The peak time of pollination is early morning. Pollen may be

collected ahead of the time of use and kept in a cool dry place (e.g., in a desiccator for longevity). Pollination is most successful when temperatures are not high. Some breeders collect the desirable flowers to be used a day ahead and laid out to dry. The pollen is then shaken out over a sieve. The pollen is collected in tubes for use.

37.10 Common breeding methods

Potato has a wide array of wild germplasm that easily crosses with cultivated types. Hybridization is the principal procedure for gene transfer. Selection is conducted in the F_1 because the parents are also widely used in modern potato improvement. Protoplast fusion techniques may be used to fuse monoploid (1x) to form dihaploids (2x). A cross of $4x \times 2x$ using a particular accession of *S. phureja* as male is a technique for generating haploids at a high frequency. Hybridization can be used to increase the frequency of tetraallelic loci and, thereby, increase the intra- and interlocus interactions for increased vigor. The techniques of unilateral sexual polyploidization ($4x \times 2x$) or bilateral sexual polyploidization ($2x \times 2x$) may be used in potato breeding. They are practical procedures because many diploid potatoes hybridize among themselves or with tetraploid species.

Genetic engineering procedures have been used to achieve the development of *Bt*-resistance to Colorado potato beetle and viral coat protein-based resistance to several viral disease (e.g., the potato leaf roll virus – PLRV). The cloning and use of the *AGPase* gene has enabled cultivars with high solids to be developed.

37.11 Establishing a breeding nursery

37.11.1 Field nursery

Breeders commonly cross potatoes in the greenhouse because pollination in the field does not yield good seed. Instead, some breeders produce the pollen source in the field and cut stems containing large inflorescences for use in the greenhouse. Parents for pollen sources should be free from virus infection and should be properly managed, protecting against insect pests, and fertilizing and irrigating the plants for healthy flowers to be produced.

37.11.2 Greenhouse nursery

Potato is a long-day plant. Hence, at least 16 hours of sunlight (or 20 klux of artificial light) are needed to successfully grow potato to flowering and maturity. The greenhouse temperature should be maintained at about 19 °C. Potato may be planted with seed potato or stem cuttings. Plants may be raised in a ground bed or in pots placed on raised benches. Crossing is often done in the winter. The vegetative growth is controlled by pruning and staking the plants to make the flowers more accessible.

37.12 Artificial pollination for hybridization

37.12.1 Materials and equipment

A mechanical vibrator may be used to aid pollen collection to pollinate a large number of plants. Pollen that is shed is collected in test tubes. A blunt scalpel may be used to scrape pollen from the anthers for direct deposit on the anthers.

37.12.2 Emasculation

Mature unopened buds are selected for emasculation. At this stage, the petals appear ready to open. Emasculation may be done in the afternoon for pollination the next morning. Greenhouse grown plants usually fail to set fruit, unless hand-pollinated. Consequently, in the absence of air current (e.g., from ventilators, open doors) that may agitate the flowers to cause pollen shed, emasculation is not necessary. However, it should be noted that there is always a possibility of some selfing occurring under such circumstances.

37.12.3 Pollination

The best time to pollinate is in the morning, soon after the flowers are fully open. This is the time when pollen is most abundant. Flowers with plump, bright-yellow anthers capped with a brownish tips give the best quality pollen. Because flowers in inflorescence do not all open at once, pollinating three days per week will allow most of the suitable flowers to be pollinated. It is best to pollinate flowers in the same inflorescence with the same pollen source, to reduce contamination. A blunt scalpel may be used to deposit pollen on the stigma, or the stigma may be dipped

into the tube containing pollen. To authenticate hybridity, anthocyanin pigment markers may be incorporated into the breeding program.

37.13 Natural pollination

Potato has a significant amount of self-pollination. Crossing blocks may be used if one of the parents to be crossed is self-incompatible. This will make all fruits produced on the plant to be hybrids.

37.14 Seed development

Successful crosses develop into small fruits. It is recommended that each set of fruits is inserted in a paper bag about four weeks after pollination, to prevent loosing fruits (and seed) to fruit drop. Softened fruits are picked for seed extraction. The seeds are squeezed into a beaker of water and then strained through a cheese cloth. The seeds of tetraploid species have seed dormancy ranging from about six months to about two years.

37.15 Breeding objectives

Some of the major breeding objectives in potato breeding are discussed next. The order of presentation is arbitrary.

37.15.1 Tuber yield

Increased tuber yield is the primary objective of potato breeding. Tuber yield and shape are influenced by photoperiod. Responsive to photoperiod is quantitatively inherited.

37.15.2 Adaptation

- **Heat tolerance.** Temperature variation is critical in potato production. While germination and growth are favored by warm temperatures, tuberization is favored by cool temperatures. Tuberization is inhibited at temperatures above 29 °C. Heat tolerance desirable for tuberization when unseasonable weather occurs during the production season.
- **Frost resistance.** This trait is desirable for areas where fall potatoes are grown.
- **Drought resistance.** This trait is necessary for production under rainfed conditions.
- **Disease resistance.** Some of the key diseases of economic importance to potato production include:
  - **Late blight.** Caused by *Phytophthora infestans*, this fungal disease is the most economically costly in potato production, causing both foliar and tuber decay. Breeding for resistance is complicated by the fact that foliage resistance and tuber resistance may differ in the same plant. Resistance conditioned by major genes (designated R_1, R_2, R_3, etc.) has been discovered.
  - **Charcoal rot.** Caused by *Macrophomina phaseoli*, this disease occurs when temperatures are high. It is a common storage disease.
  - **Viral disease.** Several viral diseases occur in potato fields, the most economic important one being the virus X. Plant response to this virus is varied including resistance to infection, hypersensitivity, and immunity. Viral coat protein-based resistance to PLRV has been developed.
- **Root-knot nematode.** The root knot nematode (*Meloidogyne incognita*), along with other nematodes, cause economic damage to potato tubers.

37.15.3 Insect resistance

- Aphids – Pubescent cultivars have resistance to aphids.
- Colorado potato beetle (*Leptinotarsa decemlineata*) can cause over 50% loss of a potato crop by feeding on the leaves. *Bt* resistance to this insect has been developed.

37.15.4 Potato tuber quality improvement

Potatoes are sold for the fresh market (for baking, cooking) or processed (chip, frozen, starch, alcohol). The quality standards differ according to the product or end use. Long-term storage is a major aspect of marketing potatoes for chip processing. The reducing sugar content of the tuber should be low to avoid the browning of chips (caramelization) during preparation. Many cultivars have a low temperature sweetening potential, making them unsuitable for processing to chips. Cultivars are being developed that will not accumulate reducing sugars at colder storage. High solids are also desired in potato breeding. Cultivars with high solids have been developed by genetic engineering procedures, using the *AGPase* gene.

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http://www.umaine.edu/paa/Breeding/B&Gsec31802.htm – Web site of the Potato Association of America (accessed March, 24 2012).

Outcomes assessment

Part A

Please answer the following questions true or false.

1 Potato originates in India.
2 Potato is cool season crop.
3 Cultivated potatoes are tetraploids.
4 High reducing sugars are desired for chipping potato.

Part B

Please answer the following questions.

1 Exposure of potato tubers to light promotes the formation of a toxic alkaloid called .....
2 Potato bears fruits called .....
3 Give three major diseases and insect pests of potato.

Part C

Please write a brief essay on each of the following topics.

1 Discuss the artificial pollination of potato.
2 Discuss the importance of temperature adaptation in potato production.
3 Discuss the common potato breeding methods.

38

Breeding cotton

Taxonomy

Family	Malvaceae
Genus	*Gossypium* L
Species	*Gossypium hirsutum* L.

38.1 Economic importance

Cotton is the most important natural fiber in the world for textile manufacture, accounting for about 50% of all fibers used in the textile industry. It is more important than the various synthetic fibers, even though its use is gradually reducing. It is grown all over the world in about 80 countries. The United States is the second largest producer of cotton after China, producing 16.52 million bales on 14.6 million acres in 1999. Most of the cotton is produced in the Cotton Belt. Most of the production currently occurs west of the Mississippi River, thanks to the spread of the devastating boll weevil attack in the eastern states of the United States. The leading production states in 2000 were Texas, Mississippi, Arkansas, and California, in this order of decreasing importance. Other important cotton producing states are Alabama, Arizona, Tennessee, Georgia, Louisiana, South Carolina, North Carolina, Missouri, Oklahoma, and Minnesota.

On the world scene, 88.7 million bales of cotton were harvested from 32.2 million hectares in 2000. The leading producing countries in the world are China (Mainland), the United States, India, Pakistan, Uzbekistan, and Turkey. China and the United States produce nearly 50% of the total world production. Other major producers are Mexico, Brazil, Egypt, Greece, and Columbia.

38.2 Origin and history

The exact origin of cotton is not conclusive. However, two general centers of origin appear to have been identified – Indo-China and tropical Africa in the Old World (Mohenjo Daro, Indus Valley of Asia in 2500 BC), and South and Central America in the New World (Huaca Prieta, Peru in 8000 BC). Cotton was cultivated in India and Pakistan, and in Mexico and Peru about 5000 years ago. Cotton was grown in the Mediterranean countries in the fourteenth century and shipped from there to mills in the Netherlands in Western Europe for spinning and weaving. Wool manufacturers resisted its introduction into Europe until the law banning the manufacturing of cotton was repealed in 1736. Similarly, the English resisted the introduction of cotton mills into the United States until Samuel Slater, who previously had worked in a cotton mill in England, built one in 1790. Three types of cotton are grown in the United States – Sea Island, American–Egyptian, and Upland. These types probably originated in the Americas, the first two are believed to have come from South America. Upland cotton may have descended from Mexican cotton or from crosses of Mexican and South American species.

Principles of Plant Genetics and Breeding, Second Edition. George Acquaah.

World production of cotton occurs between latitudes 45 °N and 30 °S, where the average temperature in summer is at least 25 °C. Cotton requires a frost-free production (175–225 days), availability of moisture and abundant sunshine for good plant growth, development, and ripening

38.3 Germplasm resources

Germplasm collections are held in banks in the United States and other parts of the world. In the United States, obsolete cultivars of *Gossypium hirsutum* is maintained at the US Cotton Physiology and Genetics Laboratory, Stoneville, Mississippi, whereas the US Cotton Research Laboratory, Phoenix, Arizona, maintains accessions of *G. barbadense*. Texas A&M University, College Station, maintains a collection of diploid cottons and race stocks of *G. hirsutum*, whereas the National Seed Storage Facility, Fort Collins, Colorado, maintains seeds of various cotton types.

38.4 Cytogenetics

Seven genomes of *Gossypium* species, designated *A, B, C, D, E, F*, and *G*, have been identified according to chromosomal size and affinity at meiosis. The basic chromosome number of *Gossypium* is 13. Most (45) of the 60 known species are diploids ($2n = 2x = 26$). Cotton may be divided into two major groups:

(i) **Old world cotton** ($2n = 26$). The diploids in this group have *A, B, E*, or *F* genomes. The cultivated types have the AA genome and comprise *Gossypium herbaceum*, which has five races that originated in Africa and Asia, and *G. arboreum*, which has six races of tree cotton and is found in India.

(ii) **New world cotton** ($2n = 52$). These are tetraploids with the genome *AADD* (13 pairs of each of large and small chromosomes). The dominant species are *Gossypium barbadense* (Sea Island and Egyptian cotton) and G. *hirsutum* (upland cotton).

Sixty two translocations that identify chromosomes 1 through 25 of the 26 chromosomes of the diploid cotton are known. They have been used to locate genes on chromosomes and the production of anueploids, among other uses.

38.5 Genetics

A genetic linkage map of *G. barbadense* and *G. hirsutum* is available. Homoeologous gene pairs related to several homoeologous chromosomes have been discovered. For example, there is homoeology between the loci for anthocyanin pigmentation (R_1R_2) and cluster fruiting habit (cl_1cl_2) of linkage groups II and III. Isogenic lines of a number of allotetraploid mutants (e.g., glandlessness, plant hairiness, okraleaf) have been developed.

Anthocyanin pigmentation is controlled by a multiple allelic series, while monopodial and sympodial branching habits are influenced by several major genes and minor genes. Flower color is controlled by two duplicate genes, $\Upsilon_1\Upsilon_2$. Υ_1 conditions yellow petals in all allotetraploids (except *G. darwinii*) in which Υ_2 conditions petal color. Yellow petal color in *G. barbadense* is controlled by Υ_1. *G. hirsutum* has mostly cream petals ($\Upsilon_1\Upsilon_1y_2y_2$). However, both yellow and cream petals occur in wild forms. Eleven male sterility loci have been identified, 10 of which are located on *G. hirsutum* and one on *G. barbadense*.

Because of high cross-pollination in cotton, a cultivar can have a high level of heterozygosity that is uncharacteristic of self-pollinated cultivars. Further, the genetic constitution of a cultivar can change from year to year. Both genetic and CMS have been identified in tetraploid cotton. The Ms_4 dominant gene confers complete sterility on plants.

38.6 Cultivars

The varieties of cotton in cultivation are derived from four species that produce seed fibers (lint) that is of economic value.

38.6.1 G. hirsutum

About 87% of all cultivated cotton is derived from this species. They are grown in America, Africa, Asia, and Australia. About 99% of all US cotton is this type, which is also classified as upland cotton. The varieties in this type produce fiber of variable length and fineness. The plant can attain a height of two meters.

38.6.2 G. barbadense

This type accounts for 8% of the world's cotton production and is grown in America, Africa, and Asia.

The plant can reach a height of 2.5 meters and has yellow flowers and small bolls. It is also classified as Egyptian cotton and has long, fine, and strong fibers. They are used for manufacturing sewing threads. These are also called "Pima" cotton. New Pima cultivars are identified by a number (e.g., Pima S-1 and Pima S-6).

38.6.3 G. aboreum

This species constitutes about 5% of the total production and is grown mainly in East Africa and Southeast Asia. The plant can attain a height of two meters and has red flowers. The varieties from this species are also classified as Asiatic cotton.

38.6.4 G. herbaceum

This species is also classified as Asiatic cotton. The fibers produced are short (less than 1 inch) and poor quality. This type of cotton fiber is used for manufacturing surgical supplies.

Another classification of cotton based on fibers, from longest to shortest, is Sea Island > Egyptian > American Upland long staple >, American Upland short staple >, and Asiatic.

38.7 American Upland cotton

Four types of *G. hirsutum* (called American Upland cotton) are grown in the United States.

(i) **Eastern Upland.** This type has medium-sized open boll, and medium length staple. It is resistant to fusarium wilt.
(ii) **Delta highland.** This type is grown mainly in the Mississippi Delta, Texas, and Arizona. It has small to medium open boll and medium staple.
(iii) **Plains or storm-proof.** This type of cotton is so-called because the bolls are closed or only partially open at maturity, and hence the fiber resists being blown away by the wind. The bolls are large with short staple and medium fiber length. It is grown in Oklahoma and Texas.
(iv) **Acala.** Grown widely in California, this type of cotton has medium to large bolls, medium to long staple, strong fiber, and long fruiting period.

The Pima cottons are also grown in the United States in places like Arizona, New Mexico, Texas, and California, and make up only about 1% of the total US cotton acreage.

38.8 General botany

Cotton (*Gossypium* spp.) belongs to the family Malvaceae, the Mallow family. There are about 40 species in this genus, but only four species are grown for their economic importance as fiber plants. It is considered an annual plant but it grows as a perennial in tropical areas where the average temperature for the coldest months stays above 18 °C. The plant has a central stem that attains a height of 2–5 feet. It has a deep taproot system. The leaves are arranged spirally around the stem. They are petioled and lobed (3–7 lobes). The stem and leaves are pubescent.

The flowers have five separate petals with the stamens fused into a column surrounding the style. Three large leaf-like bracts occur at the base of the flower. The ovary develops into a capsule or boll (the fruit). The fruit bud (young fruit) is called a **square**. When dry, the capsule splits open along the four or five lines. Bolls average about 1.5–2 inches long. Only about 45% of the bolls produced are retained and develop to maturity. The plant is predominantly self-pollinated. When pollinated by foreign pollen, the phenomenon of **xenia** causes a reduction in fiber length.

An open, mature cotton boll reveals the economic product, a fluffy mass of fibers surrounding the seeds. Each fiber is a single-cell hair that grows from the epidermis of the seed coat. The long hair is called **lint** and the short hair, **fuzz.** Most wild species of cotton do not have lint.

38.9 Reproductive biology

38.9.1 Floral biology

Generally, cotton has perfect flowers. It takes 21–25 days for the square to reach anthesis. While in the bud form, a flower is enclosed by three bractioles (occasionally, four) forming the epicalyx. The base of the flower is occupied by a five-lobed calyx. The cotton flower is large, the petal length reaching 9 cm in some cultivars. In most species, the corolla opens widely, but *G. barbadense* and *G. raimondii* have tubular flowers. The corolla is commonly white (in *G. hirsutum* and *G. arboretum*), while it is yellow (and

Industry highlights

Cotton breeding

Don L. Keim

Delta and Pine Land Company, One Cotton Row, PO Box 157, Scott, MS 38772, USA

Modern upland cotton, *Gossypium hirsutum*, is an allotetraploid which though primarily self-pollinated is readily cross-pollinated by insects. Cotton varieties are developed primarily by pure line breeding techniques. But many varieties have traditionally been mixtures of closely related genotypes as a result of cross-pollination, cotton morphology and breeding procedures. Uniquely, the primary economic value is not the seed itself, but in the fiber produced as an extension of the seed coat cells.

Historically, a major factor contributing to the high cost of cotton production has been in the area of insect management. Insects most affecting US production have been the bollworm/budworm complex, *Heliothis virescens* and *Helicoverpa zea*, and the boll weevil, *Anthomonas grandis*. Recent adoption of new practices has dramatically reduced control costs associated with these two pests. The government-sponsored Boll Weevil Eradication Program has practically eliminated boll weevil as a pest in the major areas of the US Cotton Belt. Additionally, in 1996 farmers began adopting the use of transgenic cotton which contained a gene that confers resistance to the bollworm/budworm complex. This gene was developed by Monsanto and was given the trade name Bollgard® in cotton.

Cotton breeding procedures uniquely are affected by two key factors. Firstly, the fiber must be removed from the seed (ginning). Secondly, the remaining short fibers (seed fuzz) must also be removed with acid (delinting) so that the seed is "flowable" and can be planted with modern equipment. These processes, ginning and delinting, are costly in resources (time, effort, money). Additionally, cotton breeding is expensive due to the need for much hand harvesting (hand picking), the limited number of seed per boll, and the need for hand selfing.

These factors, along with the need for expensive fiber quality evaluations, make the resource cost per unit of genetic gain much higher for cotton when compared to several other crops (Figure B38.1). Given fixed resources, the genetic gain will generally be less with cotton.

Until recently, cotton could have been considered to be relatively "unbred" when compared to the state-of-the-art in crops like corn, soybeans and wheat. In the past, resource limits had forced cotton breeders to have fewer populations with small populations sizes and to advance limited numbers of relatively unselected strains.

The recent widespread adoption and use of transgenic varieties has greatly increased the value of the seed. Seed companies reaping this value have been able to place more resources in the hands of breeders. The recent gains in lint yield and fiber quality have been a direct result of these increased resources, as well as from efficiencies gained from the modernization of breeding procedures.

Breeding program

A major effort in my program has been to maximize the gain enabled by the added resources made available. Several technique and procedural changes have been adopted to increase the efficiency of the utilized resources. This has resulted in an increased number of populations, larger population sizes, heavy selection pressure, and the early identification of superior strains.

Such changes have included: extensive utilization of winter nurseries (time savings); modified single seed descent procedures (cost and labor savings); single boll to $F_{3:4}$ progeny row advancement (cost, labor, and time savings); $F_{4:5}$ progeny row yield testing (higher selection pressure); and yield trial technique changes (higher selection pressure). Additionally, changes in harvest mechanization and data collection have enabled better utilization of resources in the advanced stages, where developments costs are much higher. The breeding procedure utilized in my program is outlined in Table B38.1.

A key aspect addressed, is the degree of outcrossing due to pollinator activity. At Scott, the main breeding station, very little outcrossing occurs. In those nurseries the plants are treated as self-pollinated. In Costa Rica, a high degree of outcrossing occurs; therefore, selfing is required in the F_3 generation. A single selfed boll is harvested from each plant.

For each population, two opportunities are given for intensive selection, in the $F_{3:4}$ single boll-derived rows and in the $F_{4:5}$ plant-derived progeny rows. In the $F_{3:4}$, intensive visual selection is practiced, along with post-harvest selection based on lint percentage (a component of lint yield) and fiber quality. The $F_{4:5}$ progeny are planted in single rows which are replicated twice. Visual pre-selection at harvest is followed by harvest for lint yield, lint percentage and fiber quality. Values for each row are compared against the average values of four surrounding check rows. Selected lines are advanced to replicated tests and breeder increase.

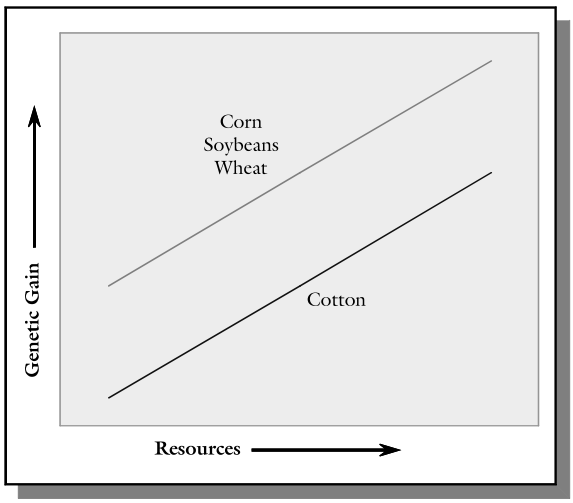

Figure B38.1 A comparison of resource cost per unit genetic gain between cotton and selected field crops. Figure courtesy of Don L. Keim.

The testing advancement schedule includes breeder tests within region for two years and an advanced testing program which involves uniform testing across all regions. Experimental lines advanced to the fourth year of testing (Stage 4) are, additionally, entered into independently conducted trials managed by the Technical Services Department.

Transgene introgression program

At the beginning the second year of testing, conventional lines are crossed to transgene donor parents to begin backcross introgression. Typically, three backcrosses are made prior to deriving lines homozygous for the desired transgene(s). Once $F_{2:3}$ rows are grown in transgene isolation, the breeder of the recurrent parent becomes responsible for selection, evaluation and advancement of lines. In many instances, lines showing close similarity are combined to form a bulk for testing and increase.

In all phases, of transgenic development the plants or seeds are evaluated for transgene presence, purity and zygosity. All seed lots through to commercialization are evaluated for transgene purity.

Key transgenic introgression lines or bulks are entered directly into the Advanced Testing Program as prior performance history exists for the conventional recurrent parents. Lines must go through gene equivalency evaluation prior to release approval by the technology provider. This is done to assure the transgene is effective in the specific genotype.

Table B38.1 Cotton breeding program.

Year	Location	Generation	Procedure/nursery	Harvest	Selection
1	Scott, MS	F_0	Crosses made		None
1	Costa Rica winter	F_1	Single row	Bulk	None
2	Scott, MS	F_2	Bulk population, F_2 yield trial	Modified bulk (single lock from 300+ plants)	Light visual, some populations discarded
2	Costa Rica	F_3	Bulk population	Single selfed boll from 200 plants	Light visual
3	Scott, MS	$F_{3:4}$	Progeny rows (7 ft)	Two plants per selected row	Heavy visual, fiber quality
4	Scott, MS	$F_{4:5}$	Progeny rows (27 ft) two replicates	Bulk row	Heavy visual, lint yield, fiber quality
5	Scott and Winterville, MS	$F_{4:6}$	Replicated tests	Bulk harvest, breeder increase	Lint yield, fiber quality, yield consistency
6	Three midsouth locations	$F_{4:7}$	Replicated tests, begin transgenic integration	Bulk harvest, breeder increase	Lint yield, fiber quality, yield consistency
7	Advanced Testing Program	$F_{4:8}$	Replicated tests	Bulk harvest, breeder increase	Lint yield, fiber quality, yield consistency

Program successes

One of the dilemmas faced in cotton improvement is the negative association of lint yield and fiber quality. In the early 1990s, as new higher yielding varieties were released, the fiber fineness (higher micronaire) and length tended to decrease. As fiber quality is determined and reported on each bale, growers suffered penalties in the marketplace. Early on, the higher yield overcame the lower price, thus increasing the growers' income. In recent years the penalties for less than desirable fiber have become more severe, negating many advantages of higher yielding varieties. Thus, a major goal of my program has been to develop higher yielding varieties with improved fiber traits.

One result has been the release of DP 491, a conventional, high yielding variety with the outstanding fiber quality traits of lower micronaire, very long fiber and high strength (Table B38.2). DP 491 was developed from a cross of DP 5415 × DP 2156. Apparently, transgressive segregation was captured in DP 491 for micronaire, length and strength. The fiber characteristics of the DP 5415 parent are average with a tendency to have high micronaire. The other parent, DP 2156, is a stripper type variety with very poor fiber characteristics.

DP 491 was converted to a "stacked gene" variety (containing the Bollgard® and Roundup Ready® transgenes) by backcrossing. The resulting recent release, DP 488 BG/RR, has shown to have similar advantages in lint yield and fiber quality over DP 458 BG/RR, the DP 5415 backcross derived, stacked gene variety (Table B38.3).

Another recent release from this program was DP 432 RR, a high yielding early Roundup Ready® variety. DP 432 RR has shown in tests distinct yield and fiber quality advantages over the popular ST 4793 RR, a backcross derivative of ST 474 (Table B38.4). DP 432 RR was developed from a straight cross of ST 474 × DP 5415 RR, rather than from the more typical backcross introgression of transgenes.

The examples presented demonstrate that the yield–quality barrier is not insurmountable. In fact, numerous experimental lines, developed by Delta and Pine Land Company breeders, exist which demonstrate the ability to combine high yield and high fiber quality.

The future

The future holds great promise for genetic improvement of cotton. In addition to continued lint yield and fiber quality improvement through intensive conventional breeding, opportunities exist with new transgenes, marker assisted selection, and in broadening the useful diversity in the germplasm base.

Table B38.2 Comparison between new release DP 491 and DP 5415.

Head to Head Comparisons - Beltwide

Variety	Value $/A	Lint Yield lb/A	Lint Percent	Micronaire	Length 2.5% span	Strength g/Tex
DP 491	725	1096	40.4	4.3	1.17	31.1
DP 5415	621	948	37.7	4.6	1.12	29.5
No. tests	96	105	105	101	100	96
% wins	86%	87%				
Significance[1]	***	***	***	***	***	***

[1] paired t-test across tests

Table B38.3 Comparison between new release DP 488 BG/RR and DP 458 B/RR.

Head to Head Comparisons - Beltwide

Variety	Value $/A	Lint Yield lb/A	Lint Percent	Micronaire	Length 2.5% span	Strength g/Tex
DP 488 BG/RR	808	1201	37.6	4.3	1.16	31.4
DP 458 B/RR	732	1094	36.3	4.4	1.11	30.7
No. tests	87	90	90	87	87	87
% wins	76%	76%				
Significance	***	***	***	***	***	***

Table B38.4 Comparison between new release DP 432 RR and ST 4793 RR.

Head to Head Comparisons - Beltwide						
Variety	**Value $/A**	**Lint Yield lb/A**	**Lint Percent**	**Micronaire**	**Length 2.5% span**	**Strength g/Tex**
DP 432 RR	805	1208	38.1	4.4	1.13	31.2
ST 4793 RR	766	1164	38.8	4.6	1.10	30.5
No. tests	121	123	123	121	121	121
% wins	74%	65%				
Significance	***	***	***	***	***	***

Several new transgenes are being evaluated in upland cotton. Monsanto has developed a second Bt gene to be used in combination with the initial Bt gene (Bollgard II®) in order to increase effectiveness against Lepidopteron pests and to prevent or greatly delay the advent of insect resistance. Initial varieties were released in 2003.

Roundup Ready® Flex is a new glyphosate resistance gene developed by Monsanto which is designed to give a longer window of application than the original Roundup Ready® trait in cotton. Regulatory approval has been granted, and initial releases were made in 2006.

Concomitant with the great success of Bollgard® and Roundup Ready® in the marketplace (almost 80% of 2004 US cotton acreage was planted to transgenic varieties), other technology providers are entering the market with other transgenes conferring herbicide or insect resistance. Liberty Link® cotton, which contains resistance to glufosinate herbicide, was approved and became commercially available in 2004. Dow has developed Widestrike® technology (lepidopteron pest resistance) in cotton and received regulatory approval for 2005 plantings. Syngenta has developed the VIP technology in cotton providing resistance to lepidopteron pests and is seeking regulatory approval.

Marker assisted selection offers the potential to enhance screening for traits that are not easily evaluated. One example may be root-knot nematode resistance screening. Screening for this pest involves expensive and time consuming greenhouse procedures. A marker or set of markers closely linked with the resistance gene(s) would greatly aid the breeder in identifying root-knot nematode resistant genotypes. Initial work in identifying markers associated with similarly useful traits is a major focus of the Delta and Pine Land Company molecular breeding program. Once established, marker assisted selection for specific traits will be integrated into the commercial breeding programs.

My crossing program has extensively involved the use of diverse upland varieties from all over the world. A key criteria for selecting parental lines is that they be high yielding in the regions for which they were developed. These lines were crossed with germplasm adapted primarily to the US mid-south. In several instances, three-way crosses were made utilizing an additional mid-south adapted parent.

However, upland cotton germplasm derives from a very narrow base relative to other crops. Marker studies have indicated little polymorphism (5–17%). A strong need exists to reach beyond this pool into the diverse sources, such as upland race stocks and related species. Short-day sensitivity is a major barrier to the utilization of race stocks of upland cotton (modern upland varieties are day-length insensitive). Barriers brought about by chromosomal and genomic incompatibilities has limited the broad use of related species crosses. Identification of desired traits and associated markers will enable the rapid and focused utilization of exotic germplasm.

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various shades of yellow) in *G. barbadense* and *G. herbaceum*.

Each flower has an anther column that may bear about 100 anthers in *G. hirsutum*. The tip of the stigma is exserted above the column. The pistil is compound and has 3–5 carpels. The ovary develops into a three- to five-loculed capsule (boll) containing 7–9 seeds that are covered with lint.

38.9.2 Pollination

Cotton is predominantly self-pollinated but up to about 30% and sometimes even higher cross-pollination occurs. Once in bloom, the flower is usually receptive to pollination for no more than eight hours. Pollination is predominantly by insects.

38.10 Common breeding methods

Like other self-pollinated species cotton improvement follows three general approaches – introduction, selection, and hybridization. The most common breeding procedure used in cotton breeding is hybridization. It is used for generating recombinants, followed commonly by pedigree selection to identify superior genotypes. The goal of breeding cultivars in cotton is to achieve sufficient uniformity for major traits (e.g., plant type, fiber properties, disease resistance) while retaining some heterozygosity for vigor. Pure line selection is rarely if ever practiced in cotton breeding because of the floral biology. Some breeders use recurrent selection to concentrate genes of quantitatively inherited traits. Introgressive hybridization to incorporate many economically important traits has been achieved in cotton. This includes genes for disease resistance, insect resistance, and fiber quality.

Hybrid cotton seed is produced by hand emasculation and pollination, or hand pollination with male sterility, in places where labor is inexpensive, such in India. Where labor is expensive, the A-B-R male sterility system is used to produce hybrid seed.

38.11 Establishing a breeding nursery

Spacing in rows may be 3–8 inches in 40-inch rows. A final stand of 2–3 plants per foot of row is optimum. Cotton responds to moderate amounts of balanced fertilization. Cotton breeders commonly use the greenhouse for crossing and selfing. The advantage of this practice is the control the breeder has over the environment to ensure proper flowering and fruiting, especially, in photoperiod sensitive cottons.

38.12 Artificial crossing

38.12.1 Materials and equipment

Some of the materials and equipment used by breeders are fine-tipped tweezers, soda straw, and wired paper tags.

38.12.2 Emasculation

Flowers are emasculated at the whitebud stage. Usually, emasculation is done in the afternoon before anthesis. The flower is large enough to allow emasculation using bare fingers to be possible (but requires skill). Commonly, tweezers are used to strip off the anthers. Cultivars of the *G. barbadense* species do not tolerate loss of petals during emasculation. A drop of gibberelic acid solution (100 ppm) may be applied at the base of the anther to increase the chance of fruit set. A section of soda straw may be used to protect the stigma prior to pollination.

38.12.3 Pollination

The day before use, the flower to be used as the pollen source should be protected from contamination from the visitation of insects by sealing the corolla by tying it with copper wire or securing it with a paper clip (or some other techniques). It is advisable to inspect the flower for intrusion by insects before using the flower. The stigma is fully receptive on the morning of anthesis. Pollen is deposited directly on the stigma using the anthers. Pollen remains viable in the field for only a few hours after anthesis. Some breeders use a soda straw to scoop up the pollen and slip it over the stigma.

To authenticate hybridity, various markers may be incorporated into the breeding program. For example, the dominant R_1 allele in *G. hirsutum* conditions

a wine-red plant color. Pollinated flowers are tagged with a wired tag.

38.13 Natural pollination

As previously indicated, cotton is capable of cross-pollination to a great extent. Genetic male sterility is used to aid mass crossing in the field. The crossing block may have to be isolated for this purpose.

38.14 Seed development

Date to maturity varies among species and cultivars. Small crossing blocks are harvested by hand and delinted using a micro-gin. The fuzz is removed by chemical treatment with sulfuric acid and then dried at 43 °C before storage.

38.15 Breeding objectives

Some of the major breeding objectives in cotton are:

- **Lint fiber yield.** The primary components of fiber yield are number of bolls per plant, size of bolls, and percentage lint, of which the number of bolls per plant is most important. Plant breeders select plants that are prolific. Bolls with five locks yield higher than those with four locks. Boll number and size are negatively correlated, making it difficult to improve both traits simultaneously. Recurrent selection may be used to break this undesirable association.
- **Agromorphological traits.** Harvesting is mechanized in cotton production in the United States. Traits that facilitate mechanized harvesting include lodging resistance, bolls set high on the plant, bolls borne singly and natural leaf shedding at maturity. Early maturing and rapid fruiting are also desirable traits.
- **Adapation.** Cotton is produced in dry regions of the world. Consequently, drought resistance is an important breeding objective for this crop.
- **Disease resistance.** Some of the major diseases of cotton are:
  - **Seedling diseases.** Some of the major diseases of cotton are caused by *Fusarium* spp., *Pythium* spp., and *Rhizoctonia solani*. These soil-borne fungi cause diseases to seedlings in wet soil, including damping-off and seed rot. The consequence of this disease is reduced crop stand.
  - **Nematodes.** The root-knot nematode, *Meloidogyne incognita* is a destructive pest in some growing regions. Resistance to the disease is quantitatively inherited.
  - **Verticillium wilt.** This disease occurs widely in the United States. Some genotypes with resistance occur in the *G. barbadense* species.
  - **Bacterial blight.** Also called angular leaf spot, bacterial blight (*Xanthomonas malvaceaum*) is widespread throughout all cotton production regions. Resistance to the disease is conditioned by two or more major genes with minor or modifier genes.
- **Insect resistance.** The major insect economic insect pests of cotton are the boll weevil and bollworm.
  - **Boll weevil.** Caused by *Anthonomus grandis*, this insect pest causes cotton squares to drop. Early maturing cultivars tend to escape the pest.
  - **Cotton bollworms.** Various lepidopteran insects belong to this group of devastating insects pest of cotton. These include the cotton bollworm (*Helicoverpa zea*), tobacco budworm (*Heliothis virescens*), and pink bollworm (*Pectinophora gossypiella*). Genetic engineering procedures have been used to address the attack by these pests through the development of *Bt* cultivars.
- **Fiber quality.** The quality traits of importance in the cotton industry include fiber length, fiber strength, and fiber fineness. Breeding objectives include improving fiber length and uniformity for improved spinning performance and utility of cotton. The fiber strength determines yarn strength, while fiber fineness affects the texture of feel of the fiber. Fiber strength is important for the current technology of open-end (rotor) spinning, which demands stronger fibers.
- **Seed quality.** In addition to lint, cotton is also grown for its seed oil. A major goal in breeding seed quality in cotton is to reduce the pigmentation that discolors the seed oil. The use of glandless cotton cultivars (glands produce gossypol, a terpenoid compound responsible for the discoloration of the seed oil) helps to improve seed oil quality. However, glandless cultivars are more susceptible to insect attack.