population of hybrid plants contains the mix of alleles and the qualities required by the breeder.

Clonal propagation

It is not necessary for plants that are propagated vegetatively (see Chapter 10) to be homozygous since there is no gamete formation and hence no re-assortment of alleles that might generate new genetic variation within the variety. Thus plants selected for particular characteristics, and propagated vegetatively, will produce progeny plants that are true to type, even if they are highly heterozygous.

Breeding clonally propagated plants consists largely of making new hybrids, selecting for improved types in subsequent generations and then fixing the best-performing types by propagating them vegetatively.

F1 hybrid breeding

It is possible to produce a uniform population of plants from seed even though the plants themselves are heterozygous. This is so-called F1 hybrid breeding and is based on Mendel's original observation that hybridisation of two different inbred lines results in a uniform F1 generation. The disadvantage of F1 breeding is that the F1 plants do not breed true, so that each *F1 seed* generation has to be recreated by hybridising the two parent lines. This means that the grower cannot retain seed year to year and that the seed is more expensive to produce than seed from inbred or open-pollinated breeding systems. Despite this double expense to the grower, F1 breeding is employed because, in many species, heterozygous plants are more vigorous and robust than homozygous types. For example, F1 hybrid ornamentals may produce significantly larger flowers than normal, while F1 hybrid vegetables may crop more heavily. This phenomenon is called *hybrid vigour* or heterosis. Its genetic basis is complex and still debated. In practice, heterosis means that if a comparison is made of the performance of the offspring from pairwise hybridisations among a group of parental lines that are typically, but not always, inbred, then certain parent combinations will produce offspring with higher levels of vigour (heterosis) than others. The specific level of heterosis between particular pairs of parents is called specific combining ability (SCA). By creating hybrids between parents with high SCA, breeders are able to produce F1 seed that results in plants with better performance than either of the parent lines or the best inbred lines of the crop.

A major problem in F1 hybrid breeding is the need to ensure that the seed harvested from the parent plants is indeed hybrid seed and not the product of self-pollinations. Several techniques are therefore employed to prevent self-pollination and force hybrid-seed production. In tomatoes the flowers of the maternal parent are hand-emasculated. In onions a *cytoplasmic male sterility* (*CMS*) system (discussed below) is used to ensure that the female parent does not produce pollen, while a *self-incompatibility* (*SI*) system is used in some brassica vegetable breeding. At various times chemical emasculation using selective gametocides has been tested, but the effective use of a chemical spray to disrupt pollen development in maternal parents has proved difficult in practice.

As its name suggests, CMS prevents plants from making viable pollen. Consequently, CMS plants will only set seed if the stigma receives pollen from another, male-fertile, plant. The CMS character is determined by DNA in the mitochondria organelles present only in the cytoplasm. This type of male sterility is relatively common, and has been identified in sweet pepper (*Capsicum* spp.), sunflower (*Helianthus annuus*), carrot (*Daucus carota*), petunia (*Petunia* spp.) and tomato (*Lycopersicon esculentum*). Genetic male sterility is determined by nuclear genes, and is found in fennel (*Foeniculum vulgare*), lettuce (*Lactuca sativa*) and broad beans (*Vicia faba*).

Self-incompatibility (SI) is a genetically determined system to prevent or deter self-fertilisation. There are some subtle differences in how different SI systems work but essential to all of them is the principle that only certain combinations of SI alleles in the male and female gametes, or parent plants, permit successful fertilisation. A crude analogy is of a lock-and-key system, where only some lock-and-key combinations permit fertilisation. Pollen is unable to develop properly on an 'incompatible' stigma and so fails to fertilise an egg cell. The genetics of the system usually means that an individual's own pollen and stigmas are incompatible, precluding self-pollination.

In either case, the cultivation of a mixture of the two parents, usually as separate rows or blocks, will