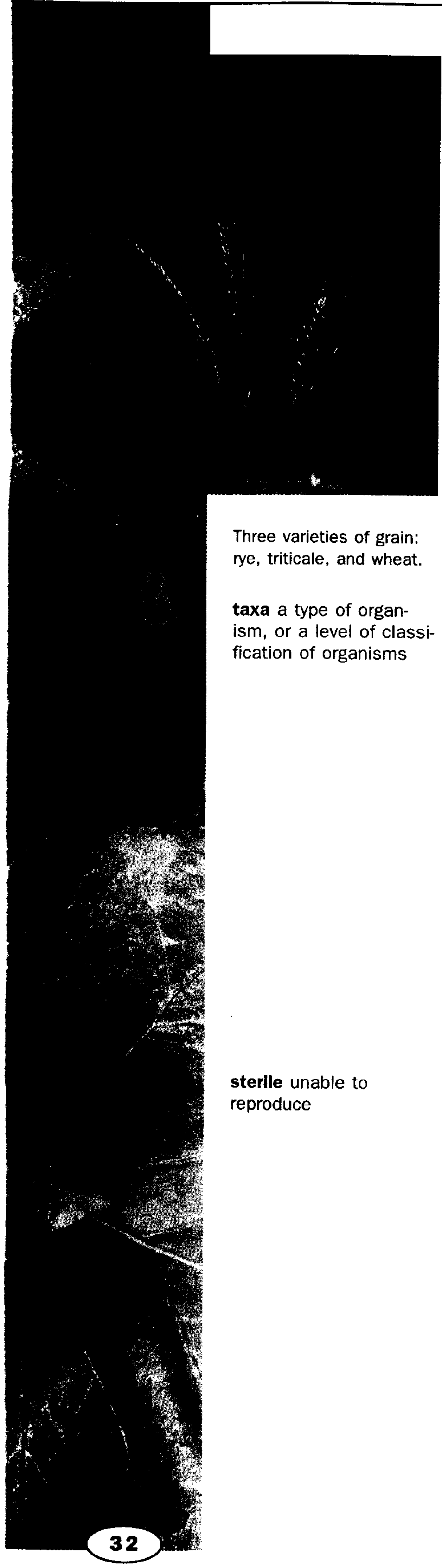
Hybrids and Hybridization



Three varieties of grain: rye, triticale, and wheat.

Hybridization is generally defined as the interbreeding of individuals from two populations or groups of populations that are distinguishable on the basis of one or more heritable characters. By extension, a hybrid is an individual resulting from such interbreeding. Hybrid zone refers to a region in which hybridization is occurring. Artificial hybridization refers to instances in which these crosses occur under controlled conditions, often under the direction of plant or animal breeders. In contrast, natural hybridization involves matings that occur in a natural setting.

Factors Limiting Natural Hybridization

A variety of factors serve as reproductive barriers among plant **taxa**. These barriers, which can be subdivided into those acting prior to fertilization (prezygotic) or following fertilization (postzygotic), restrict natural hybridization and help maintain species boundaries.

taxa a type of organism, or a level of classification of organisms

Prezygotic Barriers. The potential for natural hybridization is largely determined by the proximity of potential mates in both space and time. The likelihood of hybridization is therefore governed, to a large extent, by differences in the ecology (spatial isolation) and/or phenology (temporal isolation) of the individuals of interest. Even if ecological and temporal differentiation are absent, pollen transfer may be limited by differences in floral morphology (form). Differences in traits such as floral color, fragrance, and nectar chemistry can influence pollinator behavior and may discourage the transfer of pollen among different species (ethological isolation). Alternatively, the structure of the flower may preclude or limit pollination of one taxon by the pollinator(s) of others (mechanical isolation). Finally, even if pollen transfer is successful, the pollen may not germinate on a foreign stigma; if it does, the pollen tubes may fail to effect fertilization due to slow growth or arrest prior to reaching the ovule (cross-incompatibility).

Postzygotic Barriers. Assuming that fertilization occurs, the resulting hybrid progeny (offspring) may fail to survive to reproductive maturity due to developmental aberrations (hybrid inviability). If the hybrids do survive, their flowers may be unattractive to pollinators, thereby restricting further hybridization (floral isolation). Alternatively, the hybrids may be attractive to pollinators but partially or completely **sterile** (hybrid sterility). Finally, even if first generation hybrids are viable and fertile, later-generation hybrids may exhibit decreased levels of viability and/or fertility (hybrid breakdown).

sterile unable to reproduce

History of Investigations

The scientific study of hybridization dates back to Carolus Linnaeus (1707–1778). In 1757, as part of an investigation as to whether or not plants reproduce sexually, Linnaeus produced hybrids between two species of goats-beard (*Tragopogon porrifolius* and *T. pratensis*). Although this work served primarily as proof of the sexual nature of reproduction in flowering plants, Linnaeus argued that "it is impossible to doubt that there are new species produced by hybridization generation." Shortly thereafter, Joseph Gottlieb Kölreuter (1733–1806) revealed two important flaws in Linnaeus's conclusions. Kölreuter first showed that hybrids from interspecific crosses are often sterile "botanical mules," a result that led him to conclude that hybrids are difficult to produce and unlikely to occur in nature without human intervention or habitat disturbance. He went on to demonstrate that, although early generation hybrids are often **morphologically** intermediate to their parents, later generation hybrids tend to revert back to the parental forms. This finding apparently refuted Linnaeus's earlier suggestion that hybrids were constant or true-breeding and represented new species.

morphologically related to shape or form

In the latter part of the eighteenth century through the nineteenth century, hybridization techniques were widely applied to plant and animal breeding, a focus that continues today. The utility of hybridization for breeding programs lies in the fact that first-generation hybrids often exceed their parents in vegetative vigor or robustness. This phenomenon, known as hybrid vigor or heterosis, has been used to maximize yields in crop plants. Early botanists were also interested in the validity of hybrid sterility as a species criterion. This work was accompanied by increasingly frequent reports of natural hybrids between wild plant species. There was, however, little discussion of an evolutionary role for hybridization during this period, although sporadic reports of true-breeding hybrids continued to surface.

In the mid-nineteenth century, Gregor Johann Mendel (1822–1884) used hybridization to solve the problem of heredity. By analyzing the hybrid progeny of crosses between distinct varieties of garden pea (*Pisum sativum*), Mendel was able to demonstrate that genetic information is passed from one generation to the next in discrete units, and that these units (later known as genes) exist in pairs (later known as **alleles**). This work, which went largely undiscovered until 1900, provided a framework for the development of modern genetics.

allele(s) one form of a gene

Importance of Hybridization

In the early twentieth century, three key discoveries laid the foundation for modern evolutionary studies of hybridization. The first discovery was by Øjwind Winge (1886–1964), who showed that new, true-breeding hybrid species could be derived by the duplication of a hybrid's chromosome complement (i.e., allopolyploidy). A second important discovery resulted from the work of Arne Müntzing (1903–1984), G. Ledyard Stebbins (1906–2000), and Verne Grant (1917–) on the possible origin of a new species via hybridization without a change in chromosome number (i.e., homoploid hybrid **speciation**). A third key advance resulted from studies of natural hybrid populations by Edgar Anderson (1897–1969) and coworkers. Anderson suggested that interspecific hybrids might be favored by natural selection and thus contribute to the formation of **intraspecific taxa** such as varieties or subspecies.

speciation creation of new species

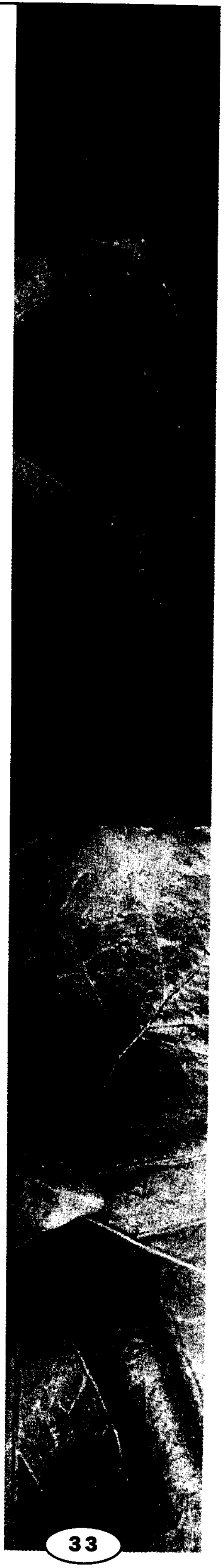
intraspecific taxa levels of classification below the species level

Allopolyploid Hybrid Speciation. Polyploidy refers to the situation in which an organism carries more than two full chromosomal complements. When the chromosome complements come from different species, these individuals are referred to as allopolyploids. **Allopolyploidy** is without a doubt the most frequent solution to the problems of hybrid sterility and segregation. In its simplest form, **genome** duplication in hybrids leads to the formation of fertile allopolyploids. This most commonly occurs via the fusion of unreduced (**diploid**) gametes.

allopolyploidy a polyploid organism formed by hybridization between two different species or varieties (*allo* = other)

genome the genetic material of an organism

diploid having two sets of chromosomes, versus having one (haploid)



tetraploid having four sets of chromosomes; a form of polyploidy

progenitor parent or ancestor

Allopolyploidy has several consequences that are relevant to hybrid speciation. First, it may lead to instantaneous reproductive isolation between the new allopolyploid species and its diploid parents. Crosses between **tetraploid** and diploid individuals, for example, will produce triploid offspring that are partly or completely sterile due to the presence of unpaired chromosomes in meiosis. Second, genome duplication can generate biochemical, physiological, and developmental changes, giving polyploids ecological tolerances that are quite different from those of their diploid **progenitors**. Altered ecological preferences increase the likelihood of successful establishment of an allopolyploid because it need not compete directly with its diploid parents. Third, genome duplication provides a means for stabilizing the hybrid vigor often associated with first-generation hybrids. This also contributes to the evolutionary potential of a newly arisen allopolyploid species. Finally, genome duplication promotes a series of genetic and chromosomal changes that increases the differences between the polyploid species and its diploid progenitors. These include the loss of deoxyribonucleic acid (DNA), the silencing or divergence of duplicated genes, and the increase in frequency of alleles that perform best in a polyploid genetic background.

genotype the genetic makeup of an organism

Homoploid Hybrid Speciation. The evolutionary conditions required for homoploid hybrid speciation are much more stringent than for allopolyploidy. Unlike allopolyploids, homoploid hybrids are not instantaneously reproductively isolated from their parents (because the chromosome number remains the same), and new hybrid **genotypes** are likely to be lost though matings with their parents. Thus, models for homoploid hybrid speciation must explain how a new hybrid genotype can become reproductively isolated from its progenitor species.

The most widely accepted model of homoploid hybrid speciation is the recombinational model of Stebbins and Grant. In this model, the genes or chromosomal rearrangements responsible for hybrid sterility are assumed to assort in later generation hybrids to form lineages characterized by a new combination of sterility factors. The new hybrid lineages would be fertile and stable yet partially reproductively isolated from their parents by a sterility barrier. Although early authors focused on evolution of sterility barriers, naturally occurring hybrid species appear to have become isolated from their parental species by both ecological divergence and sterility barriers. Thus, models of this process now incorporate both ecological and genetic isolation. Modern contributions to the study of this process include rigorous experimental and theoretical tests of the model, as well as the gradual accumulation of well-documented case studies from nature.

interspecific hybridization hybridization between two species

Introgressive Hybridization. As discussed above, the development of reproductive isolation represents a major challenge for the origin of homoploid hybrid species. Thus, it is perhaps not surprising that intraspecific taxa such as varieties, ecotypes, or subspecies more commonly arise via **interspecific hybridization** than do fully isolated hybrid species. The process by which intraspecific taxa arise via hybridization is straightforward. In natural hybrid zones, interspecific hybridization is often followed by backcrossing to one or both parental species. This process is referred to as introgression, and it produces hybrid offspring that largely resemble one of the parental species, but also possess certain traits from the other parental species. If the hybrid gene combinations become fixed, the resulting hybrid products are referred to as stabilized introgressants. As with allo- and homoploid hybrid species, most stabilized introgressants are ecologically divergent with respect to their parental species. Thus, ecological divergence appears critical to successful establishment; otherwise, new introgressants are likely to be eliminated by competition and/or gene flow with parental populations. Although molecular markers have been used since the 1970s to document introgressive races and subspecies in many groups of plants and animals, the overall contribution of introgression to adaptive evolution remains poorly understood. SEE ALSO BREEDING; BURBANK, LUTHER; CULTIVAR; EVOLUTION OF PLANTS; PHYLOGENY; POLYPLOIDY; SPECIATION; SPECIES; TAXONOMY.

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Hydroponics

Hydroponics is the practice of growing plants without soil. Plants may be suspended in water or grown in a variety of solid, **inert** media, including vermiculite (a mineral), sand, and rock wool (fiberglass insulation). In these cases, water that permeates the medium provides the nutrients, while the medium provides support for root structures. Hydroponics allows precise control of nutrient levels and oxygenation of the roots. Many plants grow faster in hydroponic media than in soil, in part because less root growth is needed to find nutrients. However, the precise conditions for each plant differ, and the entire set up must be in a greenhouse, with considerable investment required for lights, tubing, pumps, and other equipment.

inert incapable of reaction

Sprouts growing in a hydroponic hot house in Japan.