Genetic principles and the use of native seeds—just the FAQs, please, just the FAQs

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ABSTRACT

To make intelligent choices in the marketplace, native seed customers should have a working understanding of genetic principles and terminology as they apply to self-pollinated, cross-pollinated, and apomictic plant materials. Customers should understand the genetic implications of a species' breeding system, the various approaches used to decide what should be planted where, the risk of inbreeding or outbreeding depression, the meaning of commonly misunderstood terms such as "ecotype" and "cultivar," and the role of hybridization and artificial selection in plant materials development. Plant material selection involves consideration of geographic (such as ecoregion, precipitation, winter hardiness, soil type), genetic (molecular markers), and adaptation (field testing) data.

KEY WORDS

genetics, adaptation, polyploidy, inbreeding depression, outbreeding depression, cross-pollination, self-pollination, apomixis, ecoregion, ecotype, seed transfer zones, cultivar, hybridization, selection

NOMENCLATURE

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Many native plant customers lack basic information about seeds and genetics because it has not been part of their formal educational training. I find that many critical concepts are readily understood once the consumer develops a working knowledge of pertinent vocabulary. Thus, I intend to provide an explanation of the "Greek" that tends to bewilder growers and users of native plants. This set of frequently asked questions (FAQs) and common frustrations arises from my experience in dealing with people who are knowledgeable about plants in general but lack a background in the seed trade and genetics. Terms in boldface are defined in the glossary found at the end of this article.

1. Genetics, ugh! They didn't require that class, so I didn't take it. Just give me the basics. What do I really need to know?

The **genotype** for a trait is determined by the cumulative effects of **alleles** (each coding for a particular variant state, for example, brown eye or blue eye) at a single **locus** (physical position on the chromosome) or loci (plural of locus) that influence the trait. The term **gene** has an ambiguous meaning—it may refer to either a particular allele or a particular locus. In a **diploid** plant, each locus has 2 alleles inherited from either parent, which may be the same (**homozygous**) or different (**heterozygous**). Unlike animal species, plants are often **polyploid**. A tetraploid, for example, has 4 alleles per locus, all of which contribute to the genotype. A particular locus may or may not exhibit **dominance**; if present, the dominant allele will preclude expression of the **recessive** allele, or alleles (in a polyploid), although this effect may only be partial depending on the particular locus and its alleles.

The **genotype** is the genetic make-up, but it may refer to any of several levels, for example, a locus, trait, organism, or **population**. Like "gene" and "genotype," "**genome**" also has an ambiguous meaning. It may refer to the general genetic make-up of a **taxon** (subspecies, species, genus, and so on) or to a specific diploid set of chromosomes in a polyploid species.

The **phenotype**, the measured expression of the trait of an individual or population, is determined by a plant's genotype for that trait plus other contributing factors, for example, the environmental conditions in which the plant is growing, the interaction between genotype and environment, and the measurement (experimental) error. Only genetic effects, not phenotypic effects induced by the environment, are **heritable**, and only those are transmitted from parent to progeny. **Dominance**, as well as many of the interactions between alleles at different loci, collectively known as **epistasis**, are not heritable in diploid organisms because these *combinations* of alleles are not passed on from parent to progeny in the egg or sperm. In diploids, only *individual* alleles are inherited because eggs and sperm of diploid organisms are **haploid**, meaning that they have only 1 of the 2 sets of chromosomes of the parents and therefore have only one of the parent's 2 alleles present at each locus.

2. What's the significance of polyploidy?

Polyploidy is present when the plant's chromosome number is a multiple (normally an even multiple) greater than 2 of the **base chromosome number** (x) of its taxonomic group, for example, the species and its relatives. It is common in certain plant families, for example, the grasses. **Ploidy** refers to the particular state, whether it is diploid ($2x$), tetraploid ($4x$), hexaploid ($6x$), octoploid ($8x$), and so on. For example, western wheatgrass (*Pascopyrum smithii* [Rydb.] A. Löve [Poaceae]) is an octoploid ($2n = 8x = 56$).

Two types of polyploidy occur (Stebbins 1947). The first is allopolyploidy (or **alloploidy**), where the resultant species originates through hybridization between 2 distinct progenitor species. An example is western wheatgrass, which arose as a hybrid between 2 tetraploid species, beardless wildrye (*Leymus triticoides* [Buckley] Pilger [Poaceae]) and thickspike wheatgrass (*Elymus lanceolatus* [Scribn. & J.G. Sm.] Gould) (Dewey 1975). The tetraploid hybrid between the 2 species is sterile, but if both gametes are doubled before hybridization or the hybrid doubles afterward, the octoploid hybrid is fertile.

The second type of polyploidy is autopolyploidy (or **autoploidy**), which results when a chromosome-doubling mutation occurs in a plant or in both gametes of the same species that unite. For example, most bluebunch wheatgrass (*Pseudoroegneria spicata* [Pursh] A. Löve [Poaceae]) populations are diploid ($2n = 14$) but some are autotetraploid ($2n = 28$), having spontaneously doubled their chromosome number. Because the diploid and autotetraploid races are so closely related, they are considered to be a single species, but a high degree of sterility occurs when the diploids and tetraploids hybridize to form triploids. Thus, for restoration purposes one would generally not wish to introduce a ploidy level to a site where another of the same species is already present.

Traditionally, autoploids have been considered to be rare, to be generally maladaptive, and to feature a single evolutionary origin and resultant genetic uniformity (Soltis and Soltis 1993). Thus, they have often been considered to be evolutionary "dead-ends." Recent work has shown, however, that autoploids, while not as frequent as alloploids, are much more common than previously believed and much more likely to have had multiple origins than a single origin. Autoploids have a great deal more genetic variation among progeny than in diploids, so rather than evolutionary "dead-ends," they may actually hold an evolutionary advantage. For example, tetraploid bluebunch wheatgrass material ($2n = 28$) is found predominately in the northwestern portion of this species' distribution, that is, Washington and British Columbia (unpublished data). Basin wildrye (*Leymus cinereus* [Scribn. & Merr.] A. Löve [Poaceae]) populations are exclusively tetraploid ($2n = 28$) throughout most of its range but are exclusively autooctoploid ($2n = 56$) in the northwestern portion of its range, that is, British Columbia, Washington, and parts of California, Oregon, and Idaho (unpublished data).

3. How do cross-pollinated and self-pollinated species differ botanically ?

The manner in which plants reproduce, that is, their **breeding system**, is relatively constant across populations of the species. Examples of breeding systems are cross-pollination (allogamy), self-pollination (autogamy), both of which are sexual, and apomixis (see FAQ 4), an asexual form of reproduction by seed. When **selfing** occurs in **cross-pollinating** species, serious **inbreeding depression** is usually evident. Elaborate **self-incompatibility mechanisms** may be in place to prevent selfing. In contrast, **self-pollinating** species lack these mechanisms and, while they may exhibit some inbreeding depression, it is not severe enough to result in maladaptation. While most sexually reproducing plant species are primarily self-pollinating or cross-pollinating, some otherwise cross-pollinating species are quite capable of selfing (Fryxell 1957) because of a lack of self-incompatibility mechanisms and the absence of severe inbreeding depression. Likewise, some self-compatible species that mostly self-pollinate can frequently cross-pollinate, particularly if they produce large amounts of pollen.

Many biological features influence breeding system (Briggs and Knowles 1967). The ultimate mechanism to ensure cross-pollination is **dioecy**, the state of having male and female flowers on different plants. In other species, for example, maize (*Zea mays* L.), **imperfect** flowers located separately on the same plant, that is, tassels (male) and silks (female), encourage cross-pollination. **Cleistogamous** flowers pollinate while still closed, effecting self-pollination, while **chasmogamous** flowers pollinate when open, permitting cross-pollination. Some plant species, for example, *Lespedeza* Michx. spp. (Fabaceae), feature both types of flowers on the same plant and produce both self- and cross-pollinated seeds (McKee and Hyland 1941). While breeding system is generally consistent across populations of a species, genetic variation may exist for the *degree* of self-incompatibility in predominately cross-pollinating species or for the *degree* of outcrossing in predominately self-pollinating species.

Some species have temporal, spatial, or chemical mechanisms to encourage cross-pollination. The condition when a plant sheds pollen before its stigmas are receptive is termed **protandry**, and the reverse condition is termed **protogyny**. **Heteromorphic incompatibility** occurs in **perfect** flowers when stamens and styles are of different lengths, a mechanism to ensure cross-pollination by insects (Darwin 1892). In species with **gametophytic self-incompatibility**, for example, many *Trifolium* L. (Fabaceae) species, a haploid (n) pollen grain will only fertilize a plant with which it does not share incompatibility **alleles** (Briggs and Knowles 1967). In contrast, in species exhibiting **sporophytic self-incompatibility** the pollen is nonfunctional when the self-incompatibility alleles of the male parent plant ($2n$), rather than the gamete, are the same as in the female. To ensure pollen dispersal, wind-pollinated species typically produce more pollen and may have larger anthers than self-pollinated species (Jensen and others 1990).

4. How do cross-pollinated and self-pollinated species differ genetically ?

Loci in an individual of a cross-pollinated species may be **heterozygous** (the 2 alleles inherited from the 2 parents are different) or **homozygous** (the alleles are identical), whereas loci in an individual of a self-pollinated species are mostly homozygous. A preponderance of homozygous loci is found in self-pollinated species because the 2 gametes forming the zygote typically come from the same inbred parent. However, increased heterozygosity occurs following occasional hybridization (**crossing**) of 2 parents. Dominance, the ability of an allele to supersede the other, is considerably more significant in cross-pollinated species than in self-pollinated species, even when heterozygosity is present (Robinson and others 1949; Robinson and others 1954).

In a cross-pollinated species each individual is typically genetically different from every other individual in the **population**, meaning that the population is **heterogeneous**. A population of a self-pollinated species typically has a much higher degree of **homogeneity**. If the parent plant is highly **inbred**, a common situation in a self-pollinating population, its progeny will be genetically very similar to one another.

Species that are widespread, long-lived, and cross-pollinated package a greater percentage of their total genetic variation within populations and a lesser percentage between populations (Hamrick and others 1991). Therefore, variation among populations is said to be **continuous**. But in species that are endemic, ephemeral, and self-pollinated, most genetic variation is packaged between populations, and variation among populations is **discontinuous**. Hamrick and others (1991) reported that, on average, self-pollinated species had 5X greater genetic diversity among populations than cross-pollinated species because of much greater gene flow among populations for the latter group. Stebbins (1950) stated that a species' pattern of genetic variation depends on whether interchange of genes between individuals or populations is more-or-less free, resulting in a continuous pattern, or whether interchange of genes is restricted by isolating mechanisms, resulting in a discontinuous pattern.

Reproduction as described above is sexual, but some species, commonly **allopolyploids**, are also capable of asexual reproduction by seed, known as **apomixis.** Mother plants can "carbon-copy" their **genotype** in their seeds, so in such cases all **dominance** and **epistasis** effects are **heritable**, unlike with sexual reproduction. Apomixis may be either **facultative**, meaning that it is not exclusive, that is, sexual reproduction as well as apomixis occurs in the same plant, or **obligate**. Different plant genotypes may produce relatively different proportions of sexual versus apomictic progeny. Species that are facultative apomicts are more often cross-pollinated than self-pollinated (Fryxell 1957).

5. How do I know what to plant where?

Provenance testing entails data collection on many **accessions** (seed sources) at many sites over several years, especially for long-lived species. While such data have been considered the "gold standard" to match material to site, it is difficult to include a truly comprehensive set of native-site accessions in such a test because the magnitude of such an experiment quickly becomes unmanageable. Furthermore, only a few locations of these tests can typically be supported. Because large experiments like this are difficult to conduct, their data tend to be spotty, so other procedures have been developed to fill in the gaps.

Seed transfer zones have long been used as an extrapolation tool for coniferous timber species (Randall 1996; Randall and Berrang 2002; Johnson and others 2004). These are geographical zones of probability within which seed sources may be presumably transferred without loss of productivity and between which transfer is discouraged (Rehfeldt 1991). Plant traits, for example, growth, phenology, and cold hardiness, are measured on native-site populations in a common environment and correlated with environmental data from those sites. Traits correlated with environmental parameters are presumed to be influenced by natural selection. Geographic distribution of these traits is used to construct the zones. These extrapolations are specific to individual species. Attempts to develop generic extrapolations that ignore species differences are less satisfactory.

Although less preferable than provenance testing, in its absence indirect geographic approaches utilizing biotic and abiotic variables may suggest where materials are most likely to be adapted. Examples include the USDA Natural Resources Conservation Services (NRCS) Major Land Resource Area maps (USDA SCS 1981) and **ecoregion** (Bailey 1976, 2001; Omernik 1987, 1995; US EPA 2002) maps showing regions of relative homogeneity in ecological systems (Figures 1 and 2).

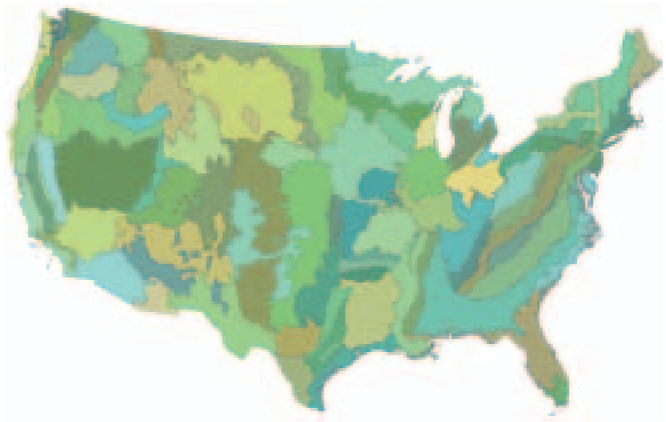

Figure 1. Omernik Level III Ecoregions of the conterminous US (US EPA 2002).

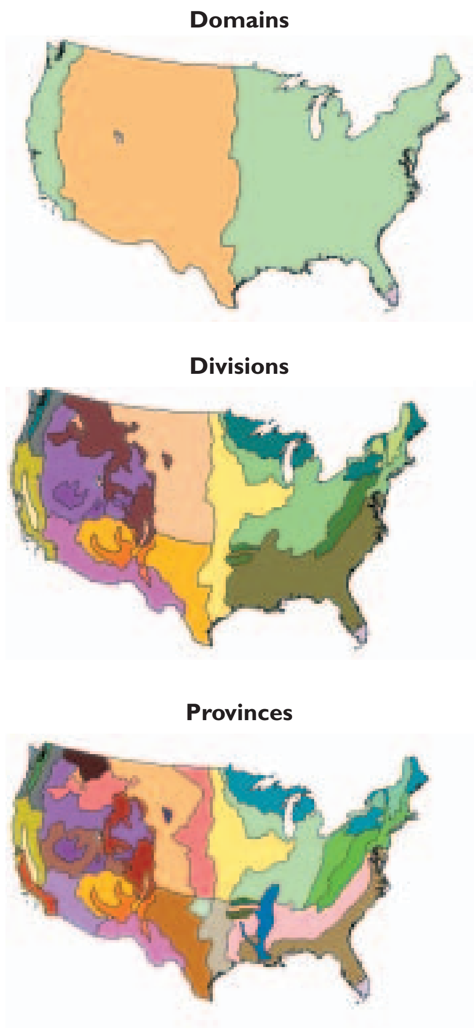

Figure 2. Bailey's ecosystem domains, divisions, and provinces in the conterminous US (Bailey 2001).

In contrast to these subjective expert-opinion maps, Hargrove and others (2000) have developed non-subjective maps based strictly on quantitative soil and climatological data. Focal point seed zones (Parker 1992) are similar to seed transfer zones, but they provide more specific range of adaptation guidelines about specific seed sources. The focal point seed zone identifies the geographical region within which the material collected from a specific site is likely to be adapted based on the climatic similarity of the collection site to other sites. Geographic Information System (GIS) tools are now being developed to map seed transfer zones and focal point seed zones.

6. It's an ecotype, right ?

An **ecotype** was originally defined to be "an ecological sub-unit to cover the product arising as a result of the genotypical response of an ecospecies to a particular habitat" (Turesson 1922). Since then, workers such as Gregor (1946) and Langlet (1959) have found many examples of species with **continuous** genetic variation across geographical space as opposed to the **discontinuous** pattern suggested by Turesson's (1922) data. Stebbins (1950) thought Turesson's sampling was inadequate, so that populations measured at discrete intervals give the false impression that genetic variation is discontinuous. Erroneously, in my opinion, this has led some (Quinn 1978; Barbour and others 1999) to believe that because populations are genetically different, ecotypes are synonymous with populations—hence the term "ecotype" has no meaning.

Most scientists will concede that genetic variation of **self-pollinating** species tends to be more **discontinuous** than that of **cross-pollinating** species where gene flow is greater (Quinn 1978). Differential selection pressure, driven by the presence of a heterogeneous environment and sharp environmental boundaries, also contributes to a discontinuous pattern (Quinn 1978). **Selection pressure** operates against the homogenizing effects of **gene flow**. The presence of geographical features that limit gene flow, for example, mountain ranges, may also contribute to a discontinuous pattern.

Stebbins (1950) clarified that, while ecotypic variation can always be found, some species are more conspicuously ecotypic than others, that is, they have more discontinuous genetic variation. For example, a high degree of ecotypic variation has been found in the self-pollinating native grass *Elymus elymoides* (Raf.) ssp. *brevifolius* (J.G. Sm.) Barkworth (Poaceae), both at the whole-plant and DNA levels (Jones and others 2003; Larson and others 2003). Therefore, if you ask the question "is it an ecotype," be sure that you and the respondent are using the term in the same fashion. A less ambiguous question might be "on a scale of one to ten, is the genetic variation of this species more continuous or discontinuous?" One must have a comprehensive understanding of the particular species to be able to offer a legitimate answer to this question.

7. Isn't the genetic base of cultivars too narrow or Isn't the genetic base of cultivars too broad ?

Some have the impression that **cultivars** (synonymous with **varieties**) are necessarily narrow in **genetic base**. Uniformity is a desirable characteristic of **self-pollinating** crops and **cross-pollinating** crops with hybrid seed production systems, for example, wheat (*Triticum aestivum* L.) and maize. Most row-crop cultivars are genetically narrow, but cultivars need not be narrow by definition. When it is desirable, a cultivar may be designed to be broad, and for regulatory purposes it needs only to correspond to the degree of variability stated in the **release** document. The term **ecovar** has been coined and trademarked to describe an "ecological variety" of a native plant, meaning that it has an intentionally broad genetic base (Wark and others 1995).

Conversely, some fear that cultivars may have too broad a genetic base. It is true that many cultivars of cross-pollinated species designed for wide adaptation, such as the forage grasses and legumes, often have a broad genetic base. But again, this is not a requisite feature of a cultivar. Furthermore, cultivars may be either "**genetically manipulated**" or "**natural**" (genetically unaltered wildland populations). Most of the native plant cultivars released by USDA NRCS Plant Materials Centers, for example, are "natural" (Davis and others 2002). These were chosen for release after favorable comparison with many other natural **accessions** of the same species.

In short, the term "cultivar" should not be anathema. But the consumer may wish to know the breadth of an individual cultivar's genetic base, its genetic history, and its geographical origin.

8. Shouldn't I be concerned about outbreeding depression ?

Outbreeding depression is used to describe the loss of vigor or adaptation that sometimes results from hybridization among distantly related **populations** or individuals (Templeton 1986; Montalvo and Ellstrand 2001; Hufford and Mazer 2003). Its significance is hotly debated, but it is a reason commonly given to avoid plant material with a broad **genetic base** or the introduction of material to a site that is not genetically identical to material originating from the site. It should be helpful to understand that outbreeding depression and **heterosis**, that is, hybrid vigor, are located along the same homozygosity–heterozygosity continuum (Hufford and Mazer 2003), with inbreeding depression representing the pole opposite outbreeding depression and heterosis being intermediate.


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I'll use 3 examples to explain this continuum for a **cross-pollinated** species. If a plant crosses with itself (**selfs**) or a close relative, the offspring are generally maladapted because of **inbreeding depression** resulting from excessive **homozygous** loci. This is generally only a problem in a **self-incompatible** species where selfing is not the natural condition. But if the **genetic distance** between 2 parents, that is, the average disparity between their alleles, is great enough, the offspring may be especially vigorous because of **heterosis** (Moll and others 1962). Genetic distance is not necessarily highly correlated with the geographic distance between the parents. It does, however, tend to increase with geographic distance (Larson and others 2001; Massa and others 2001; Larson and others 2003), though not necessarily on a linear scale and not necessarily to the same extent in all directions.

However, if genetic distance between parents of a hybrid becomes too great, for example, if they are widely separated genetically (perhaps even different subspecies or species), the genetic incompatibility between them may overshadow any positive effects of heterosis (Moll and others 1965). Incidence and magnitude of the resultant **outbreeding depression** is much less than for inbreeding depression (Moritz 1999). In regards to introduction of novel genetic material into a population, the potential negative effects of outbreeding depression may be offset by positive effects of reduced inbreeding depression, enhanced ability to respond to a novel or rapidly changing environment, and restoration of connectivity among components of a **metapopulation** that have been fragmented by man, termed "genetic ghettos" (Frankel 1974; Moritz 1999).

There are 2 generally accepted but clearly unrelated mechanisms of **outbreeding depression** (Templeton 1997). The **coadaptation mechanism** (described above), also known as **hybrid breakdown**, results in impaired ability to reproduce due to the disruption of favorable interaction of **alleles** at multiple **loci** (**epistasis**). It should be suspected when difficulties arise following hybridization among species, subspecies, or chromosome races. Templeton (1986, 1997) argues that natural selection may overcome these negative impacts and that evolutionary processes should be preserved rather than simply genotypes. Outbreeding depression may also be caused by the **local adaptation mechanism**, also referred to as **dilution** (Hufford and Mazer 2003) in which hybridized material is unadapted to the local environment. The implication is that adaptation is not only local, but very local (Waser and Price 1985, 1989), a conclusion that has not been reconciled with the seed dispersal literature. Note that dilution conceivably could occur within a species, subspecies, or chromosome race. Wide hybridization is not required. While the propensity of this problem cannot be predicted, its likelihood may be minimized by using material from a nearby origin or a similar environment.

My point is that nature may have erected barriers to **hybridization**, but this does not justify a disregard of hybridization. It merely alerts the practitioner that the beneficial effects of hybridization have their limits. Deleterious effects beyond these limits are more conspicuous in some situations than others. Hybridization may have positive and negative impacts. Our goal should be to harness the positive impacts and avoid the negative ones, rather than to avoid hybridization altogether (Burton and Burton 2002).

9. I don't want anything that's been bred, do I ?

In many circumstances a plant breeding approach to native plant material development is inappropriate. Species with a long generation time, for example most trees and shrubs and some forbs, do not lend themselves to plant breeding like many grasses. In other cases, preservation of genetic identity is paramount. The principles of conservation genetics dictate that genetic identity should be maintained when lands are being managed for conservation of plant populations and accompanying evolutionary forces (Meffe and Carroll 1997), an approach known as ***in situ* germplasm conservation** (Frankel and others 1995; Becker and others 1998). In these cases, only local material should be used to ameliorate disturbances.

In general, artificial selection is of less significance in **self-pollinating** than in a **cross-pollinating** native species. This is because most genetic variation in self-pollinating species is found between populations rather than within populations as is typical for cross-pollinating species (see FAQ 4). Having said this, there are many situations for which a plant breeding approach is not only acceptable but preferred, especially for cross-pollinating species. While some assume that local, that is, unselected, material is the best adapted to the local site, this is not necessarily the case. Artificial selection by a plant breeder can often increase resistance to common stresses, for example, drought, cold, salinity, insects, and diseases, rendering plants healthier than they would be otherwise. This is because artificially imposed stresses can be applied to a much greater degree than to which they typically occur naturally. Sites have usually been designated for restoration precisely because they have been badly disturbed (Jones 2003). Enhanced stress tolerance is generally desirable in these situations.

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GLOSSARY

Accession
An individual source of seeds (of many in a collection) harvested in the wild or produced under cultivation.

Allele
One of two corresponding copies of a gene in a *diploid* organism that may be identical or different.

Alloploidy
The *polyploid* condition in which the two or more evolutionary progenitors are distinct taxa.

Apomixis
A mechanism of asexual reproduction by seeds such that progeny are genetically identical to the parent.

Autoploidy
The *polyploid* condition that has arisen via chromosome doubling from a single progenitor.

Base chromosome number
The minimum number of chromosome pairs for any species within a taxonomic group, for example, a genus or family, symbolized by x. The number may be calculated as the chromosome number divided by the *ploidy* level; for example, for hexaploid bread wheat $x = 42/6 = 7$.

Breeding system
The manner of sexual reproduction, either *self-pollinating* or *cross-pollinating*, or some combination thereof (also known as mating system).

Chasmogamous
Floral fertilization occurring when flowers are open, facilitating *cross-pollination* by wind or animals.

Cleistogamous
Floral fertilization occurring when flowers are closed, ensuring *self-pollination*.

Coadaptation mechanism
One of two mechanisms to explain outbreeding depression; when genes for adaptation to a local site negatively interact with genes introduced from off-site following hybridization via epistasis to reduce reproductive ability (see *hybrid breakdown*).

Continuous variation
The state when genetic variation changes very gradually from *population* to *population* rather than sharply between clusters of populations (see *discontinuous variation*); typically occurs in *cross-pollinating* species with adequate *gene flow* among *populations*.

Crossing (or cross-pollinating)
The practice of a plant being pollinated by another individual of the same species rather than by itself; this may be encouraged by *self-incompatibility* mechanisms.

Cultivar
A plant material intended for seed production under cultivation that has been approved for *release* to the public through a formal process.

Dilution
One of two mechanisms to explain outbreeding depression; reduced adaptation to a site occurring when site-adapted material is hybridized with off-site material.

Dioecy
The state of a species whose flowers bearing anthers (pollen) and pistils (eggs) occur on separate plants.

Diploid
A species or individual whose chromosome number is double the *base chromosome number*; not a *polyploid*.

Discontinuous variation
The state when evolutionarily divergent *populations* are genetically discrete because there is minimal *gene flow* among them.

Dominance
1. The state of an *allele* that partially or completely "covers" the complementary *allele*. 2. The interaction of the 2 *alleles* at a single *locus*.

Ecoregion
A geographical region that is relatively *homogeneous* for characteristics of ecological consequence; may be determined at any of several levels.

Ecotype
A group of genetically similar *populations* that are adapted to a particular environment.

Ecovar
A trademarked name that describes plant materials that have been improved for seed production traits but without the reduced genetic variation that may be associated with *selection*.

Epistasis
When a trait is determined by the interaction of *alleles* at multiple *loci* rather than determined by a single *locus*.

Facultative apomixis
The state when asexual reproduction by seeds occurs sometimes, but not always; otherwise sexual reproduction occurs.

Gametophytic self-incompatibility
The state when *self-incompatibility* is genetically controlled by the *genotype* of the pollen grain itself rather than its parent plant, as in *sporophytic self-incompatibility*.

Gene
1. An *allele*. 2. A *locus*.

Gene flow
The movement of genes between *populations* due to pollen or seed dispersal.

Genetic base
The relative magnitude of genetic variation within a plant material ranging from narrow to broad; for example, an F1 single-cross corn hybrid has a narrow genetic base.

Genetic distance
A DNA-based measure of the difference between 2 populations or individuals ranging from zero to one.

Genetically manipulated
Modified from *"natural"* by *selection*, *hybridization*, or chromosome or DNA manipulation.

Genome
The sum genetic material of an organism, species, or diploid chromosome set.

Genotype
The genetic effect of a *locus* or trait in an individual or population without consideration of confounding environmental influences.

Haploid
The chromosome number of the egg or sperm; half of the somatic (whole-plant) chromosome number; for example, for hexaploid bread wheat ($2n = 42$), the haploid number is $n = 21$.

Heritable
Able to be inherited by an offspring from the parent; measured on a percentage basis from zero to 100.

Heterogeneous
The state when different individuals of a *population* are genetically dissimilar.

Heteromorphic incompatibility
The mechanism of separation of the sexes in a *perfect* flower, discouraging *selfing* and encouraging outcrossing.

Heterosis
Enhanced performance exhibited when divergent individuals or populations are hybridized; equivalent to hybrid vigor.

Heterozygous
The state of having 2 different *alleles* at an individual *locus* in an individual plant.

Homogeneous (homogeneity)
When individuals of a *population* are genetically identical or similar to one another.

Homozygous
The state of having 2 identical *alleles* at an individual *locus* in an individual plant.

Hybrid breakdown
The state of malperformance by advanced generations of a hybrid among distantly related individuals or taxa despite seemingly good performance of the first generation of the hybrid; an example of *outbreeding depression*.

Hybridization
Crossing between 2 individuals of the same or different species.

Imperfect
The state of a flower that has only 1 sex present.

In situ germplasm conservation
Conservation of genetic material in the wild through designation of genetic reserves to allow continuation of evolutionary processes, as opposed to *ex situ* conservation in a seed bank.

Inbred
Having enhanced *homozygosity* due to *selfing* or mating among relatives.

Inbreeding depression
That state of malperformance resulting from *selfing* or the *mating* of close relatives.

Local adaptation mechanism
One of two mechanisms to explain *outbreeding depression*; when genes for adaptation to a local site are diluted by genes introduced from off-site following *hybridization*.

Locus (plural loci)
The position on 2 corresponding chromosomes that corresponds to a particular pair of *alleles*.

Metapopulation
A "greater" *population* that consists of individual populations connected by *gene flow* and are thus related.

Natural
For seed regulatory purposes, not *genetically manipulated* by *hybridization* or *selection* from material collected in the wild.

Obligate apomixis
The state when asexual reproduction by seeds always occurs in a plant or species, that is, sexual reproduction never occurs.

Outbreeding depression
The state of reduced performance when distantly related individuals or taxa are hybridized.

Perfect
The state of a flower that has both sexes present.

Phenotype
The measured trait of an individual or *population* as determined by the *genotype*, environmental influences, and their interaction.

Ploidy
The chromosome level of a plant expressed as a whole number times the *base chromosome number*, for example, diploid, triploid, tetraploid, hexaploid.

Polyploid
The state of having multiple chromosome sets (*genomes*) in a *taxon*; that is, not diploid, but triploid, tetraploid, and so on (see *autoploidy*, *alloploidy*).

Population
A group of related individuals genetically connected by *gene flow*.

Protandry
That state when anthers (male) shed pollen before the pistils (female) of the same plant are receptive, a mechanism that encourages *cross-pollination* and discourages *self-pollination*.

Protogyny
That state when pistils (female) are no longer receptive by the time the anthers (male) of the same plant shed pollen, a mechanism that encourages *cross-pollination* and discourages *self-pollination*.

Provenance testing
Comparison of plant materials of the same species at multiple sites to determine adaptation.

Recessive
The state of an *allele* that is partially or completely "covered" by the complementary *allele*.

Release
1. A plant material made available to the public. 2. To invoke the formal approval process that occurs before an organization makes seeds available to the public.

Seed transfer zone
Regions on a map within which plant materials may be moved with minimal risk of maladaptation; typically drawn for individual species.

Selection pressure
Evolutionary or anthropogenic forces that exert preference for a *genotype* over another.

Self-incompatibility mechanisms
Physiological mechanisms that discourage fertilization by disrupting pollen grain (male) germination and/or pollen tube development on the pistil (female) of the same plant.

Selfing (or self-pollinating)
The practice of a plant pollinating itself to produce seeds.

Self
1. The act of *self-pollinating*. 2. Progeny resulting from *self-pollination*.

Sporophytic self-incompatibility
The state when *self-incompatibility* is genetically controlled by the *genotype* of the parent plant rather than the pollen grain as in *gametophytic self-incompatibility*.

Taxon
A taxonomic group of related plants, for example, a family, genus, species, or subspecies.

Variety
1. A taxonomic subdivision of a subspecies. 2. *Cultivar*.