Organic Seed Alliance

Advancing the ethical development and stewardship of the genetic resources of agricultural seed

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Introduction to On-farm Organic Plant Breeding

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I. Introduction

Why plant breeding is important

The history of the domestication of our crop plants is also the history of plant breeding. Through many generations of laborious human selection, wild plants became usable as agricultural crops.

Our hunter-gatherer ancestors had to have an intimate relationship with plants to notice the genetic variation that existed and continually arose in order to make meaningful progress in the domestication process. This is one of the fundamental precepts of plant breeding and gives these early innovators full status as plant breeders.

Coupled with early human selection was a strong element of *natural selection*. All of the ancestors to our modern crop species were grown without supplemental nutrition, fertility, or pest protectants, and were constantly exposed to the challenges of the environment. The best of the farmer-breeders sped this process along by selecting from the most desirable plants for their food and fiber value, using these as the parental stocks for subsequent generations. This balance between human and natural selection persisted until the beginning of the industrial agricultural era of the 20th century.

All agricultural crops have continuously changed with the selection pressures applied from both farmers and the environments in which they were cultivated. When farmers and the environment changed, the crop changed. Many of our crops continue to change and adapt to new challenges.

The number of environments that crops are bred in, and the number of breeders, have both shrunk over the past 100 years. This is because farmers in most agricultural regions of the globe do little or no plant breeding anymore, and the number of regionalized seed companies doing breeding has also drastically shrunk in the past 40 to 60 years.

With the advent of the industrial agricultural model there has been a narrowing of the set of traits that are considered critical to the production of most modern crops. The industrial model has also led to a gradual specialization shift in where and how many of the most economically important crops are grown. In the pre-industrial agricultural era, almost all crops were spread across many environmental and geographic niches to satisfy the diversity of agricultural settlements. This meant that they were constantly adapting to a diversity of climatic conditions and the ever-changing needs of the human agricultural societies that were using these crops. The farmers in each region were the breeders. Some farmers were undoubtedly better breeders than others. There has always been some specialization in many aspects of agricultural societies, but in this pre-industrial era, every agricultural community certainly had the seed needed by that community. Seed of each of these community varieties were genetically unique from a similar variety of the same crop in the next community. This patchwork of unique varieties is then multiplied thousands of times across the unique environments of agricultural communities around the globe.

Crop genetic diversity in the pre-industrial era was also much greater than what currently exists in modern agriculture because the diversity within each community variety was far richer. Farmers did not demand the kind of trait uniformity that is now the norm in our modern crops. This ***allelic**** diversity was part of every crop population and was reflected by many unique ***genotypes*** (and ***phenotypes***) in each field.

There was a great blossoming of seed companies in North America and Europe in the second half of the 19th century. With the advent of seed as a commercial commodity, and the emergence of seed companies, there was an incentive to produce seed of crop varieties that were much more uniform and predictable. These early seed companies were regional in nature. They relied on a central store in a metropolitan center and supplemented with mail orders for much of their business.

The industrialization of agriculture in the 20th century led to a much higher degree of specialization. Specific regions with more "ideal climates" for a certain crop type and prime agricultural land became centers of large-scale production for certain crops. In addition, plant breeding programs started

*Definitions for technical words that are italicized and bolded can be found in the glossary catering to industrialized systems, from mechanical planting, cultivation, and harvesting, to the needs of the packers, shippers, and retailers handling the crop post-harvest.

The philosophy of organic plant breeding

As organic plant breeders, we have an opportunity to shape organic agriculture in fundamental ways. By making new varieties available to organic farmers, we are able to give these farmers new options.

Building a healthy, sustainable agriculture future requires farmer-centric seed systems at the regional level, where farmers and the communities they serve consciously choose which crop genetics they use, how they are maintained, and how these genetics are controlled.

Done well, organic plant breeding can help ensure that farmers control the seed they use. Breeding work can give farmers free access to genetic resources and the freedom to grow what they please, while supplying them with the knowledge and skills to both grow seed and improve a crop's characteristics to best meet their needs.

Over the past several decades, plant breeding has become increasingly formalized and centralized. Breeding work that was once done mainly in farmers' fields is now done almost exclusively by large seed companies and on state-run agricultural experiment stations. Most breeders working for large seed companies, as well as most public breeders, focus their attention primarily on the largest markets for seed, which are typically large, conventional farming systems located in prime agricultural regions. This focus on the needs of large-scale, conventional agriculture leaves organic farmers without varieties that are adapted to the needs of their systems. Research has found that the lack of organically adapted varieties leaves organic farmers at a disadvantage, resulting in, among other things, lower yields than if they had varieties adapted to their systems. Organic, on-farm breeding work is devoted to serving the needs of these organic farmers.

Our farming ancestors never stopped breeding

All good farmers who survived and flourished were, by necessity, plant breeders. They used observational skills to determine and select the best adapted plants every year. This meant selecting the highest yielding, best tasting, and most disease-resistant plants. All of the heirloom crop varieties we know and enjoy today were developed over a long, rich period of our history, telling the tale of our plant breeding ancestors who were making selections and saving seed from the healthiest and most vigorous plants year after year. These farmers were constantly striving to improve varieties to better suit their needs, engaging in a constant dance of improvement and co-evolution with their food.

These ancestors were never fully satisfied with the crops they had. They wanted to improve their farmer-bred varieties (sometimes called ***landraces***), since it could mean the difference between life and death for their families and communities. Modern organic farmers who are choosing to produce and select crop varieties to flourish in their regional agro-ecosystems are rubbing shoulders with the best farmer-breeders of the past who domesticated and continually improved our crop genetic resources.

There will always be a need to adapt new varieties to current challenges, such as climate change. Classical plant breeding allows us to select, adapt, and continually co-evolve with our food crops. This form of plant breeding is not to be viewed as "messing" with nature, and it is certainly not genetic engineering. The principles of evolution show us that there is always variation in biological populations, environmental conditions always change, and no biological entity ever stays the same in response to its environment. In other words, no organism is ever static in nature. Selection pressure and change over time are inevitable. We advocate for an evolutionary breeding model that allows the varieties we use to be part of the sustainable agricultural systems we are pioneering.

Returning farmers to their role as seed stewards

Our work at Organic Seed Alliance (OSA) is intended to empower farmers to again be part of the seed system that most farmers have been divorced from for almost 100 years. Over the last century, we have not only lost valuable genetic diversity through modern agricultural practices, we have also lost much of the farmer knowledge needed to steward the genetic resources that are most important to them and their communities. We believe there is just as much important work to be done in training farmers to breed, maintain, and grow high-quality seed crops adapted to the needs of low-input, agro-ecosystems as there is for preserving the genetic resources of the past. The best way for valuable genetic resources to become part of modern agriculture is to get them into the hands of farmers. As skilled stewards, these farmers will continue to adopt and further adapt the genetics to their needs. It is therefore critical that farmers first have access to these genetic resources.

Our breeding work is done on agro-ecological farms by applying sound classical plant breeding methodology. We emphasize building genetic resilience and diversity into every crop population. Our plant breeding work strives to establish a diversified and ecologically-based agriculture, to foster the management of crops genetics at the regional level, and to strengthen a region's economy. OSA promotes the stewardship of seed in a manner that encourages the adaptation of plant genetics to the ecological and market needs of farmers and the communities they feed. This includes helping farmers perform on-farm plant breeding in the same manner as our most innovative ancestors. To not encourage such improvements would be a disservice to farmers, eaters, the planet, and future generations.

II. Plant Breeding Basics

This section covers the basics of how to create and improve varieties for your organic farm. First we describe the basic steps of plant breeding. Then we describe some basic genetic principles and how they apply to plant breeding.

In its essence, plant breeding can be boiled down to the following:

Select plants with superior genes from a genetically variable population of plants.

How you do this will depend on your goals, the crops you are working on, and the time and resources you want to invest.

Selection in theory and practice

Selection in plant breeding refers to the process of choosing which plants produce the next generation of a population.

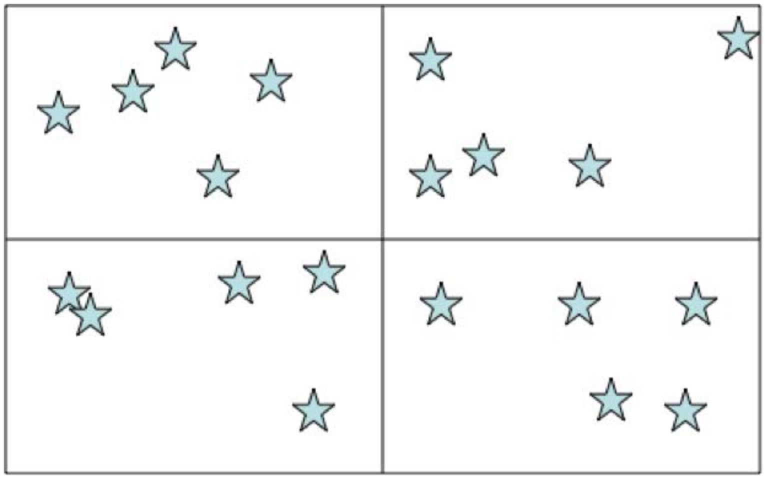
There are two major types of selection appropriate for on-farm breeding: mass selection and family selection. There are benefits and drawbacks to each type of selection. Whether you use one or the other, or a combination of both, will depend on the crop you are improving as well as your timeframe, resources, and ultimate goals.

With ***mass selection***, you make selections based on how individual plants within a population perform. Mass selection is the most straightforward breeding method. As such, it requires minimum time, labor, and record keeping. Because of the simplicity, it can make working with large populations more practical during the breeding process. However, it does have a few drawbacks when compared to family selection. First, because your selections are based solely on the plant's ***phenotype*** (its outward appearance), you are more likely to choose a plant based on environmental influence rather than on superior genetics. For example, the soil where that plant is growing may be more fertile in comparison to a neighboring spot in the field. The second drawback with using mass selection is the potential that undesirable ***recessive*** genes may be carried by the plants you select in a hidden ***heterozygous*** state.

Gridded selection is one technique that can be used when doing mass selection to help account for the influence of field variation on plant phenotypes. When using gridded selection, imagine the field that is planted with your breeding population divided into a grid of smaller sections. For example, the field could be divided into quarters. When selecting, attempt to select an equal number of plants from each section. Even if, for example, the plants in the northwest corner of the field look inferior in general to the other quarters, select the best plants from that section.

In contrast to mass selection, with family selection you are looking at the overall performance of a group of related plants (a family) and using the

Gridded Selection



Key: Each star represents a selected plant

Figure 1. Gridded selection is one technique that can be used when doing mass selection to help account for the influence of field variation on plant phenotypes.

family's overall performance to make selections. In family selection, you plant a series of rows of plants, where each row comes from seed saved from a single selected plant from the previous generation. The advantages of family selection are two-fold. First, because you are making selections based on a whole row of plants that are closely related (siblings or "sibs"), or more than one row for each family if you are using replication (see more about this concept below in the theory section), it becomes less likely that you might select plants based on the influences of very localized environmental effects. Second, because you are able to see many closely related plants next to each other, you are more likely to spot some plants exhibiting deleterious recessive traits that may be carried in a given family.

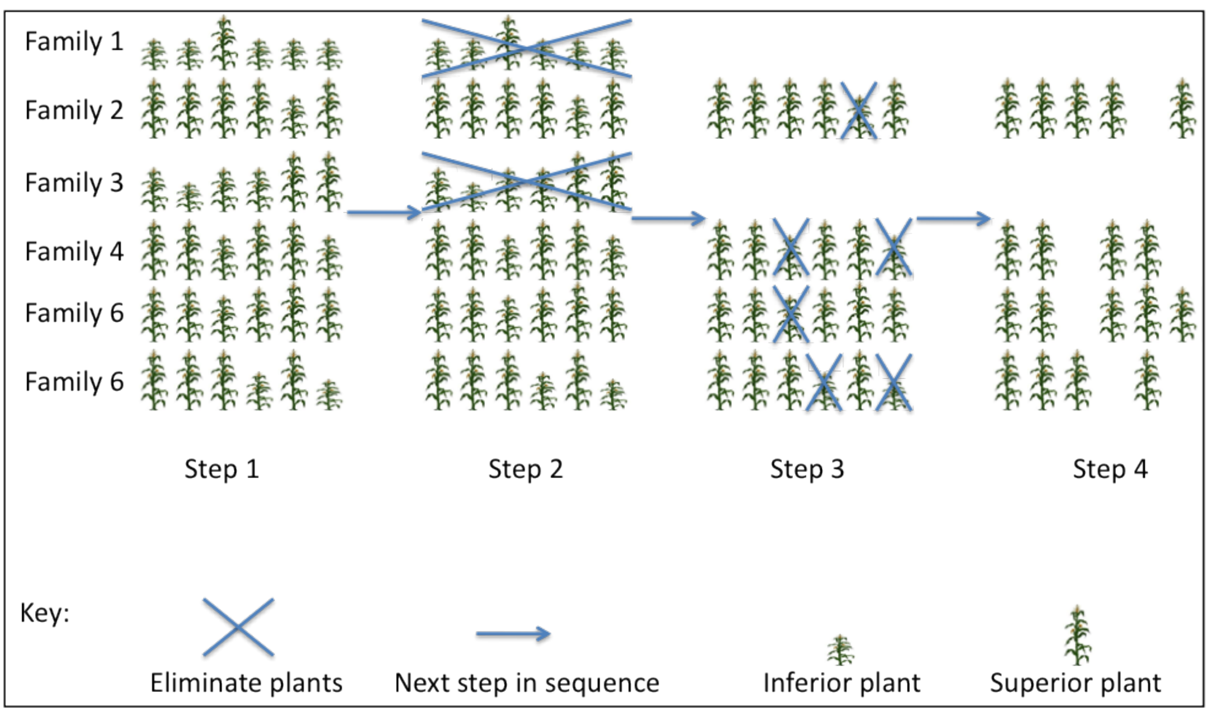


Figure 2. This diagram exhibits the steps to execute family selection in three successive steps.

Figure 2 exhibits the steps to execute family selection in three successive steps. In step 1, each of the rows is a family in a corn breeding program, with the same row represented left to right sequentially across the three selection steps. Step 1 involves evaluating each family as a whole based on the performance of the entire row. Step 2 is to eliminate any families that do not have a high proportion of superior plants. Although there are no hard and fast rules in plant breeding, when deciding which families to select, at OSA we eliminate a family unless it has at least 60 to 70% acceptable plants. Once you have determined which families to keep, step 3 is to eliminate the poorest 30 to 40% of the plants within these families. Step 4 shows the final field arrangement, with only the selected plants in the selected families remaining.

The families that are used in family selection can come in various forms. Three of the most common forms are half-sib families, full-sib families, and S1 families. Half-sib (HS) families are families where all of the plants share a common mother but may have different fathers. You would produce a half-sib family by saving seed from a plant that has been allowed to openly pollinate with many other plants. All of the seed you save from that plant shares a mother, but each seed was potentially created by fertilization with pollen from different fathers. Plants in a full-sib (FS) family share both a mother and father. You would produce a full-sib family by conducting a controlled pollination between two plants. Plants in an S1 family all come from a self-pollination. In other words, they all share the same single parent, which acted as both mother and father. All three of these families have their uses. In general, as you go from families with less relatedness to families with more relatedness (HS to FS to S1), the families become more uniform. This uniformity allows you to better predict how *their* offspring will perform. In addition, with S1 families in particular, you are better able to see the traits controlled by recessive genes in that family. However, FS and S1 families often take more time and effect to produce, and they create a greater risk for inbreeding in cross-pollinating species.

Selection can, and should, be done at many points throughout the season. Selection for traits such as germination, vigor, plant stature, leaf shape, color, and weed competitiveness can occur early in the season. By planting at a high initial density, some of these traits can be selected for during the thinning process. Many vegetable crops, such as carrots, lettuce, cabbage, onions, and kale produce a harvestable crop before pollination. On the other hand, the harvestable crop of some crop types, such as corn, winter squash, tomatoes, and melons, can only be evaluated after pollination occurs. It is desirable to do as much selection as possible before pollination occurs to increase the rate of progress of your breeding work. Any selection done after pollination is less effective than selection done before pollination. This is because in the latter scenario the pollen from inferior plants is allowed to fertilize the superior plants, thus passing their genes onto the next generation.

The final concept to understand in selection is the ***selection intensity***. In essence, the selection intensity is based on the fraction of plants, or families, you select from the starting population. For example, you would be practicing a greater intensity of selection if you selected only 50 plants out of 500 to save seed from than if you selected 300 plants out of 500. As you increase the selection intensity, you will make more progress in your breeding. However, especially in cross-pollinated crops, you need to avoid ending with too small of a population, which can increase the risk of inbreeding depression or losing valuable genetic diversity that you may need in the future. A general guide on the minimum number of plants to keep in your population can be found in OSA's *Seed Saving Guide for Gardeners and Farmers*. Because it is important to avoid going below these minimum population size recommendations, the best way to increase your breeding efficiency – through increasing the selection intensity – is to start with more plants.

There are two broad terms that convey the intensity of selection. The term ***positive selection*** is used when a substantial fraction of the plants in a population are being removed. ***Negative selection***, also known as ***roguing***, refers to the removal of only a small fraction of the population, usually 10 to 20% or less, during a season. Many times, such as when maintaining a variety, negative selection may be all that is needed. Even if you are unsure of which plants are best in your population, you will probably be able to spot and remove the poorest performing plants and the plants that are obvious off-types. This concept is best expressed in the old plant breeding axiom: "I don't always know what I like, but I always know what I don't like!"

How to select

How do you actually practice selection in the field? There are a number of methods for choosing which plants will produce the next generation of the breeding population. A few of these methods are described below.

Eliminate inferior plants or entire families as you identify them. This method can be easily used when selecting for traits during thinning, as mentioned above, or when practicing negative selection. This method has the advantage of being very simple and direct: cut down, hoe out, or pull up any plants that do not meet your selection criteria. The method has a few limitations, however. First, if your breeding population has relatively few good plants and requires a high selection intensity, it can be more time-consuming to identify the inferior plants instead of identifying the few superior plants. Second, if you are looking for multiple traits at once, and you don't expect to find plants that perfectly exhibit these traits, you may need a more robust way of selecting plants based on their overall performance across multiple traits.

Select superior plants or families as you see them. This method is the converse of the one just described. Typically you walk your breeding field on a number of occasions throughout the season, evaluating for one or more traits at appropriate times. To select a plant or family, place a flag or stake next to the plant or family. You can use different colored flags during evaluations for different traits, or you can make notes on a stake or in a notebook to describe why you are selecting certain plants or families. This method is useful when finding a small percentage of superior plants or families out of a larger population. This method can also cut down on extensive record keeping when the choices of which plants or families to select are obvious.

Select superior plants of families based on data. This method involves recording measurements or scores for each plant or family for the traits of interest. The data is then used to make selections. This method is the most time and labor intensive of the three and only becomes practical when dealing with smaller numbers of plants or families (less than a few hundred). However, there are a number of reasons to use this method. First, this method is useful for identifying a small number of families that performed best based on a range of traits that are measured over the season. For example, say you want to pick out the best kale families based on early vigor, leaf color, resistance to early aphid pressure, and length of harvest season. In this case, you may need to make your selection at the end of the season, but you will need detailed information about each family's performance throughout the whole season. Second, this method helps in cases where the traits are not immediately visible but you need some measurements to evaluate. These measurements might include weighing yields or measuring plant heights. Third, this method works well when you have planted your families in multiple replications and want to find the average performance of a family across all replications.

When recording data to guide selections, a trait can either be measured or scored. To measure a trait, tools such as scales or yardsticks are used to get a value. To score a trait, you assign a value to a plant or family based on a rating system. For example, you might score leaf size on a scale from 1 to 9, where 1 represents a tiny leaf and 9 represents a large one. When scoring traits, begin by walking the entire field to assess the range of expression within the population for the trait of interest. The plants or families with the worst or least desirable expression of the trait will be the 1 on your scale and the plants or families with the most desirable expression will be your 9. Then proceed to score all plants or families based on that range, attempting to use the whole range of scores from 1 to 9. More information on how to conduct these evaluations can be found in OSA's *On-farm Variety Trials: A Guide for Organic Vegetable, Herb, and Flower Producers*. Both this guide and data sheets for evaluating and selecting plants are available for free download at www.seedalliance.org.

A crop's mating system and how it affects plant breeding

The way a plant mates can be described as falling along a spectrum between *strongly self-pollinating* and *strongly cross-pollinating.* Where a crop falls on this spectrum has several implications for which breeding method will be most effective. This idea will be discussed in detail below.

Self-pollinated crops

In plants, self-pollination occurs when the sperm of an individual plant fertilizes an ovule of the same plant. Essentially, the plant mates with itself. The plant's inbred offspring receive all of their genes from this one and only parent. Thus, the offspring are very genetically similar to this parent. All predominately self-pollinating plants have perfect or bisexual flowers, where both the male and female sexual structures are borne in each flower. Self-pollinating plants also have flowers that exclude cross-pollination as described below.

There are two important advantages of self-pollination. First, in plants that have evolved to become extremely well adapted to their environment, self-pollination offers a way to ensure that a plant's offspring will be just as well adapted as its parents. In other words, self-pollination is a way of replicating success. Second, self-pollination helps to ensure reproductive success under a variety of environmental circumstances, as it does not require the presence of wind, insects, or animals to transfer pollen from one plant to another.

The plants that we call *strongly self-pollinating* rely almost completely on self-fertilization to reproduce. The perfect flowers of these plants have evolved ways of excluding pollen from other flowers to prevent cross-pollination. For example, the flowers of most modern tomato varieties have anthers that form a cone around the pistil, effectively sealing off the flower's stigma from any pollen other than its own. In peas, the petals of the flower are typically closed when the stigma first becomes receptive to pollen, giving pollen from its own anthers exclusive access to the stigma. When the pea flower opens, it is nearly always already fertilized. Other examples of strongly self-pollinating plants include common beans, wheat, and oats.

However, even a strongly self-pollinating plant will occasionally cross with another plant of the same species. For example, bees can eat through or tear open flowers and deposit pollen from a different plant of that species. A number of plant breeders and seed growers have also noted that with the increase of insect activity that usually occurs in organically managed systems, there is often an increase in the percentage of crosses that occur in strongly self-pollinating plant species. Also, under certain climatic conditions, the flowers of some self-pollinating plants will open earlier than normal and the stigma will be receptive to receiving pollen from another plant before it has a chance to self-fertilize. And of course humans can perform controlled crosses between self-pollinating plants by intentionally transferring pollen from one plant to another.

Cross-pollinated crops

On the other end of the biological spectrum are cross-pollinated plants. Cross-pollination occurs when the sperm of one plant fertilizes an egg of a different plant of the same species. In other words, a plant mates with another plant of the same species. When two plants cross-pollinate, they produce offspring that are genetically different from either parent. In general, all plants have the potential to cross-pollinate, because every plant can be fertilized by another plant of the same species.

The central advantage of cross-pollination is that it facilitates a plant species' ability to adapt to changing environments. Plant species that constantly mix their genes into new combinations increase the likelihood that at least a few individuals within the species will have the right combination of genes to withstand new environmental challenges.

Breeding self-pollinated crops vs. breeding cross-pollinated crops

The mating system of the crop affects breeding strategies in some fundamental ways. Self-pollinated crops need less isolation distance from each other and other compatible species than cross-pollinated crops to avoid unintended cross-pollination. The need for less isolation makes it easier to manage several simultaneous breeding projects of the same species in a limited space, and will allow you to grow your breeding project near a commercial crop without threat of cross-contamination. It is generally harder to make crosses between self-pollinated plants than cross-pollinated ones. In order to overcome a self-pollinated plant's tendency to only self-pollinate, some hand labor is often required, such as removing the male parts of one plant (known as emasculation) and collecting and bringing in pollen from another plant. For on-farm breeding projects, cross-pollinated crops can be handled with simple techniques like strain crossing, explained below.

The challenge of cross-pollination in self-pollinated crops has an important additional effect. Populations of cross-pollinated crops can easily cross-pollinate and recombine their genes. On the other hand, after an initial cross is made in a self-pollinated crop, each subsequent generation of self-pollination rapidly fixes groups of genes. See below for an illustration of this phenomenon.

Doing breeding work with self-pollinated crops allows you to easily create uniform varieties from crosses. Once these varieties are developed, they are much easier to maintain compared to cross-pollinated varieties.

Finally, self-pollinated crops suffer less from inbreeding depression. This allows you to work with fewer plants in a self-pollinated breeding program compared to a cross-pollinated breeding program and still produce a vigorous variety.

As figure 3 shows, if we follow the generations of plants after a cross is made in either a self-pollinated species or in a cross-pollinated species, fundamental differences arise in the structure of the populations. In a cross-pollinated species, the plants in each generation are able to ***intermate***. Intermating creates a unified ***gene pool*** and allows new combinations between plants to be made each year. In contrast, unless humans intervene to make additional crosses, self-pollinated plants will self-pollinate in each generation after the initial cross. Self-pollinating in each generation leads to each plant deriving separate families or ***lines***. In each generation, the plants in each family will become more uniform within the family, while stronger differences will arise between families. The genotypes of each family become fixed, and new genetic combinations between families only occur through hand-pollination or through rare natural cross-pollination. The consequence for breeders is that, when dealing with self-pollinated crops, a sufficient number of lines must be created and maintained to find a line that has all of the traits of interest from both parents. In contrast, the gene pool of cross-pollinated crops can be gradually improved by eliminating the worst plants or families, and allowing the best to cross-pollinate to create new combinations that may contain the desired traits from both parents.

Inbreeding depression is a loss of vigor due to self-pollination or the crossing of genetically similar plants. Essentially, inbreeding depression is the reverse of ***heterosis*** (hybrid vigor). Inbreeding depression results from the accumulation of ***ho-***

Comparison of Attributes of Self- and Cross-pollinated Crops

	Self-pollinated crops	**Cross-pollinated crops**
Isolation	Less	More
Crossing	Harder	Easier
Self-pollinating	Easier	Harder
Inbreeding depression	Less	More

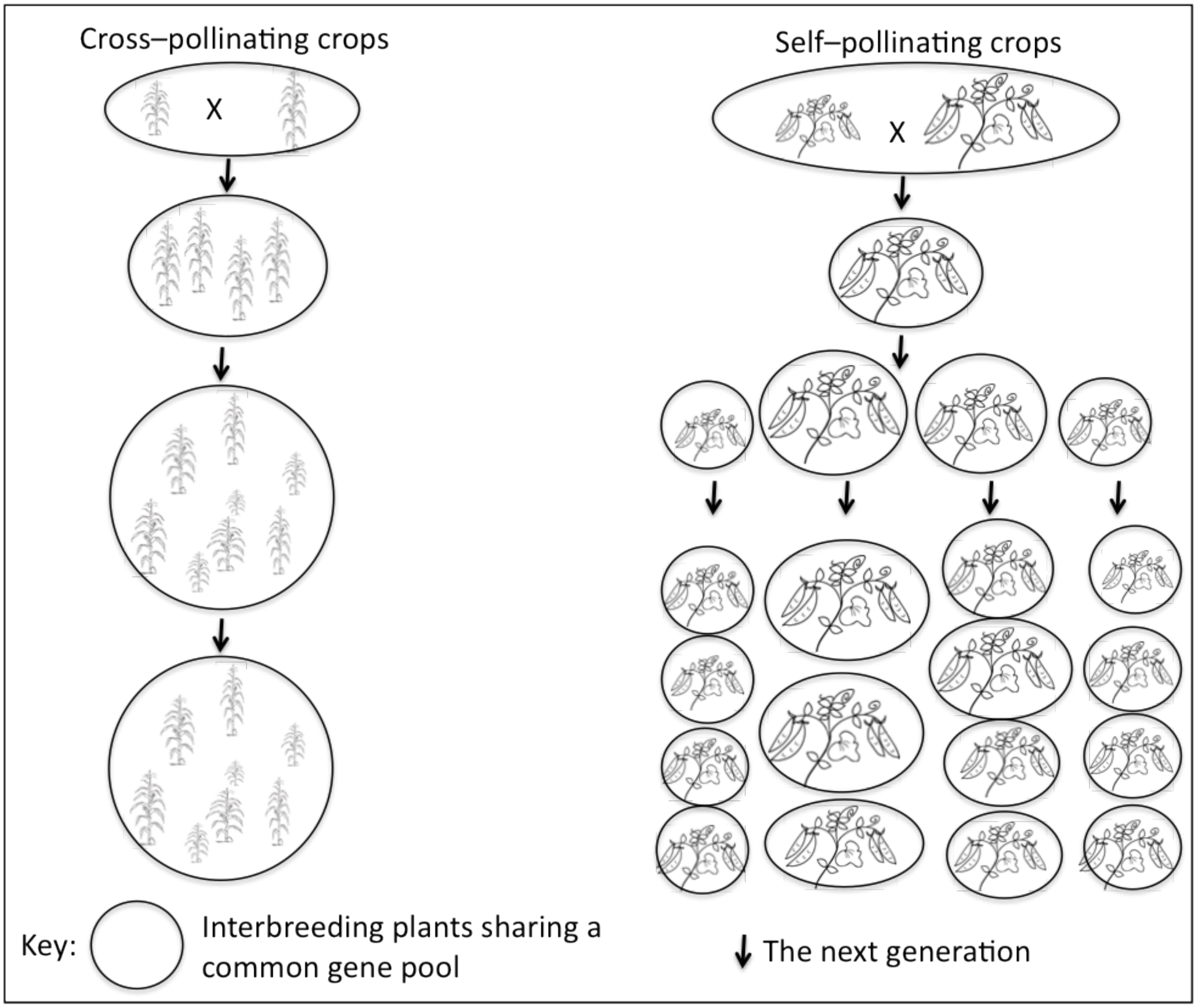


Figure 3. This diagram show how populations of self-pollinated and cross-pollinated crops differ in their genetic structures.

mozygous pairs of rare and detrimental ***recessive alleles***. To simplify the idea, figure 4 serves as an example where there is a rare mutant recessive allele, a, in a population. If a plant has two copies of this allele (*aa*), the plant cannot effectively produce chlorophyll. The plant appears very light green and grows poorly. As long as a plant has one copy of the functioning allele, *A*, it will be able to produce chlorophyll. In other words, plants with the genotype *AA* or *Aa* are healthy. A small fraction of the population carries this allele as a ***heterozygote*** (*Aa*). When these *Aa* plants cross-pollinate (on the right-side of figure 4), almost all of the pollen they receive will carry the dominant *A* allele, and their offspring will be healthy, even if half of the offspring are carrying the deleterious recessive a allele. However, if these heterozygous *Aa* plants self-pollinate, or if they pollinate with close relatives, the situation changes. As you can see on the left in figure 4, when one of these plants self-pollinates, 25% of their offspring will be homozygous aa and will show the detrimental effects from having two copies of this allele. Most cross-pollinating plants carry many deleterious recessive alleles. These plants rely on cross-pollination among large populations to avoid inbreeding. With self-pollinating plants, on the other hand, selection has acted over many generations to weed out the plants with deleterious alleles.

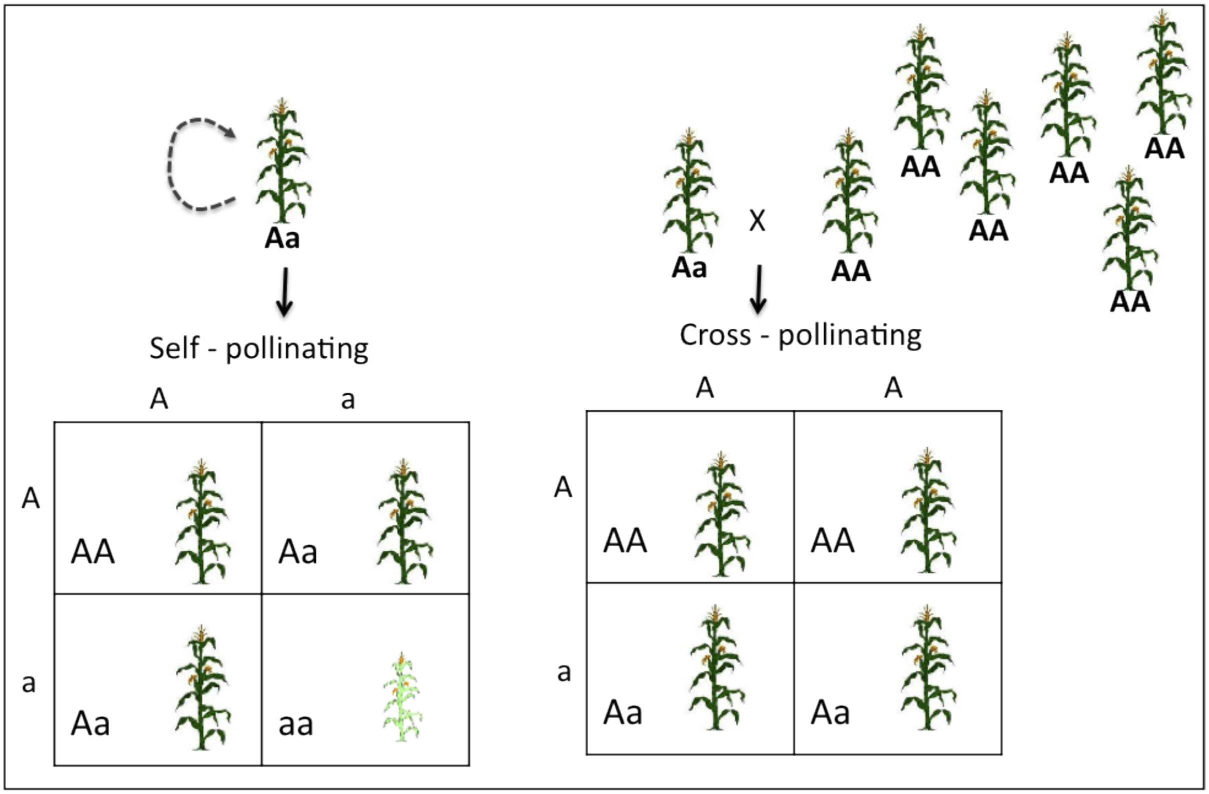


Figure 4. Inbreeding depression results from the accumulation of homozygous pairs of rare and detrimental recessive alleles. This diagram serves as an example where there is a rare mutant recessive allele, *a*, in a population.

III. Developing a Plant Breeding Plan

Thinking about your target environment

In a perfect world, plant breeders could develop varieties that thrived in any situation and anywhere on the planet. In fact, most large seed companies strive to produce varieties that can be grown across wide geographic regions in many agricultural situations. This concept is known as ***broad adaptation***. However, varieties that are broadly adapted may not be the best variety for any given area, and they may require high levels of inputs to recreate the growing environment under which they were bred. Creating broadly adapted varieties may also require extensive testing that most smaller breeding programs do not have the resources to undertake. In contrast to breeding broadly adapted varieties, ***specifically adapted*** varieties are bred to excel in specific environments. These varieties are not expected to do well everywhere, just in the target environment. The concept of the relative performance of a variety changing based on the environment it is growing in is called the ***genotype by environment interaction*** (GxE).

One of the first steps in planning a breeding project is to identify the target environment. The environment can be as broad or narrow as you choose, keeping in mind that additional resources will be required as the breadth of the project increases. Developing a broadly adapted variety will require more time and resources than developing a variety specifically adapted to your local conditions and challenges.

When detailing the target environment where you want your variety to excel, there are several important factors to consider. Some of these are:

- Geographic region (day length and frost-free period)
- Temperature regime (highs, lows, fluctuations, and cumulative heat units)
- Rainfall (amount and timing)

- Soil type
- Disease pressures
- Weed pressures

You should also consider cultural factors in your target environment, such as:

- Cropping system (direct seeding vs. transplanting)
- Irrigation system (overhead, drip, or flood/furrow)
- Fertilization (type and frequency)
- Cultivation techniques (frequency of plowing, mechanical vs. hand techniques)

Finally, consider the market and social factors that are integral to your target environment, including expectations for:

- Color
- Storage properties
- Flavor
- Culinary uses
- Quality of product
- Transportation ability

Determining traits

Knowing what you want is critical to *getting* what you want. The most successful breeding projects have clearly defined traits that are being selected for or against. Prior to starting the breeding effort, it is important to take the broadly defined goals for the variety and dig down to define exactly what you will be looking for in the field. It may be very easy to come up with a list of the traits through brainstorming. Another way to understand which traits are important is by discussing the best currently available varieties. What are the traits that make certain varieties so great? What are they lacking? A useful concept is that of an ***ideotype***. An ideotype is essentially an idealized crop variety that is perfectly suited to a particular set of production and market criteria. What would this ideal variety look like? How would it perform? What traits would it need to have to be successful? What are the traits that are important to the farmer and marketplace?

Some examples of traits that you may want to select for include:

- Plant height
- Plant stature
- Days to maturity
- Harvestable yield
- Color
- Flavor
- Texture
- Storage life
- Seedling vigor
- Pest Resistance
- Disease Resistance

Prioritizing traits

Once you have compiled a list of traits, the next step is to prioritize them. In general, a breeding project should not attempt to actively select for more than five or six traits at any given time. There may be more than five traits that are important, but it's not feasible to work on everything all at once. Also consider that some traits may be easily fixed, or "locked in," by choosing parents that share these traits. In this case, effective selection may be achieved simply by throwing out a couple of off-type plants here and there.

To prioritize the traits and limit the list to five, two questions to consider are:

- Is the trait easily measurable?
- How heritable is the trait?

How can the traits be measured?
Plant breeding is an exercise in balancing what we want with the resources we have to do the work. Most plant breeding projects have limited resources, so it makes sense to avoid breeding for traits that require excessive labor. It might be wonderful to develop a lettuce variety that supports a diverse flora of microorganisms around its roots, but unless your program has the resources to determine the identity of a wide variety of species of soil microbes inhabiting hundreds of lettuce lines, you will need to work with traits that are easier to measure and select. In the process of prioritizing selection criteria, consider when and how the trait(s) will be measured. This plan doesn't need to be fleshed out, but it should be sufficiently detailed so that you have an idea of how much work will be required. Will you be able to visually rate the trait on a 1 to 9 scale? Will you be able to quickly measure the trait with a yardstick or a scale? How many times throughout the season will the trait need to be measured?

How easily can the traits be inherited?
The second item to consider when determining which traits to prioritize in your breeding project is the ***heritability*** of the traits. Simply stated, heritability expresses the likelihood that a trait you see in a plant this year will show up in the plant's offspring. Put another way, heritability expresses what fraction of the appearance of a trait comes from the plant's genetics as opposed to the environment. Although each crop and situation is different, traits that are highly heritable often include such qualities as color, shape, and spines versus spinelessness. The more highly heritable a trait is, the easier it is to select and see rapid progress from one generation to the next. Traits with low heritability typically include yield and various forms of stress tolerance (i.e., drought, salinity, and heat tolerance). These traits require more breeding expertise, as well as a more finely tuned experimental field model to tease out subtle differences in these traits to make improvements across cycles of selection. We recommend that you choose only a couple of traits with low heritability to select for in your breeding project, especially at the beginning. Many traits, such as flavor, plant height, and disease resistance, may be either highly heritable or less heritable, depending on the population. Getting advice from a formally trained breeder who has experience with your crop of interest can help you define which traits are more or less heritable.

Choosing parents

Germplasm is a general term that refers to the collection of genetic resources for a plant species. Varieties, landraces, collections, breeding lines, and unimproved material are all types of germplasm. Essentially germplasm is any form of living tissue (e.g., seeds, cuttings, roots, and tubers) from which plants can be grown. Germplasm is the parental material used to begin your breeding work. Sourcing quality germplasm determines how easily and rapidly you will be able to develop your desired variety.

There are two main factors to consider when choosing germplasm:

- Quality: the germplasm should include elements of the ideotype you are striving to produce
- Variability: the germplasm should have variation for the trait(s) you want to improve

Consider varieties that:

- Perform well in your target environment
- Are considered to be commercial standards
- Contain unique traits that you want to incorporate into your project

Many valuable varieties for breeding work can be found in the catalogs of domestic and international seed companies. However, be aware of legal protections on some varieties that restrict their use for breeding or limit what you can do with them in other ways. These protections include plant patents, utility patents, plant variety protection certificates, and licenses. You can find more information about these protections on eOrganic's intellectual property protection page at http://www.extension.org/pages/18449. Always investigate your germplasm sources to ensure there are no legal restrictions on breeding.

Besides seed companies, you can also source germplasm from:

- Farmers
- Seed exchanges
- Germplasm Resource Information Network: http://www.ars-grin.gov/

Unless you are already familiar with the germplasm you want to use in your project, it is wise to conduct variety trials to evaluate the available sources of germplasm. More information on how to conduct variety trials can be found in OSA's *On-farm Variety Trials: A Guide for Organic Vegetable, Herb, and Flower Producers*.

Here are four categories of germplasm that are useful to evaluate and consider for use in organic plant breeding:

1) *Heirloom* varieties: This category includes family or community-based heirlooms as well as non-hybrid commercial crop varieties that were in existence before World War II. Heirlooms are ***open-pollinated*** (OP) varieties that were selected, adapted, and maintained over generations within families or agricultural communities. They were often uniquely adapted to the challenges of the soil, climate, and endemic diseases of particular regions. In many cases, the commercial varieties released during this period by regional seed companies were improved or refined heirloom varieties already important to that particular region. These commercial OP varieties were either developed by one of the many regional seed companies that flourished during the early 20th century or by plant breeders at one of the land grant universities. These varieties were then made widely available to farmers and gardeners across the region.

2) Early modern varieties: This is a term for crop varieties developed by both regional seed companies and land grant universities from the end of World War II until about 1980. Most of these varieties are not F1 hybrids but open-pollinated varieties in cross-pollinated crops and "pure line" varieties in self-pollinated crops. Early modern varieties were bred for the conditions of specific regions. The breeding of vegetables and other minor crops wasn't usually done under optimum fertility or heavy sprays. Many of these varieties that are still used today have proven their worth as "workhorse varieties," and a number of farmer-breeders have chosen varieties out of this category to serve as germplasm for their breeding projects .

3) F1 hybrid varieties: Hybrid varieties were first extensively developed in corn during the 1920s and began to represent a large part of the variety offerings of many cross-pollinated crops after World War II. Hybrids became popular for a number of reasons. They are an effective way to create genetically uniform, vigorous varieties. In addition, they represent a form of biological intellectual property protection for the seed companies that develop them because the offspring of hybrids do not grow true-to-type (due to their highly heterozygous nature). Because many breeding efforts since World War II have focused on developing hybrid varieties, a lot of the most elite crop varieties currently are hybrids. Hybrids are often genetically diverse and can represent good germplasm for many breeding projects.

4) Modern open-pollinated varieties (non-hybrids): Various seed companies are breeding good open-pollinated varieties (generally small- to medium-sized regional companies) as are some public breeders at land grant universities. The best modern open-pollinated varieties provide excellent germplasm for breeding programs.

Before beginning a breeding project, it is a good idea to screen crop varieties from a wide swath of germplasm sources, including some from each of the four categories above. This process will help you identify the highest quality germplasm currently available. The potential for increasing your success and decreasing your frustration is greatest when you begin a project with the best possible germplasm.

Creating a breeding timeline

Figure 5 on the following page is a summary of a general breeding timeline. After the summary, we will go through the steps in more detail.

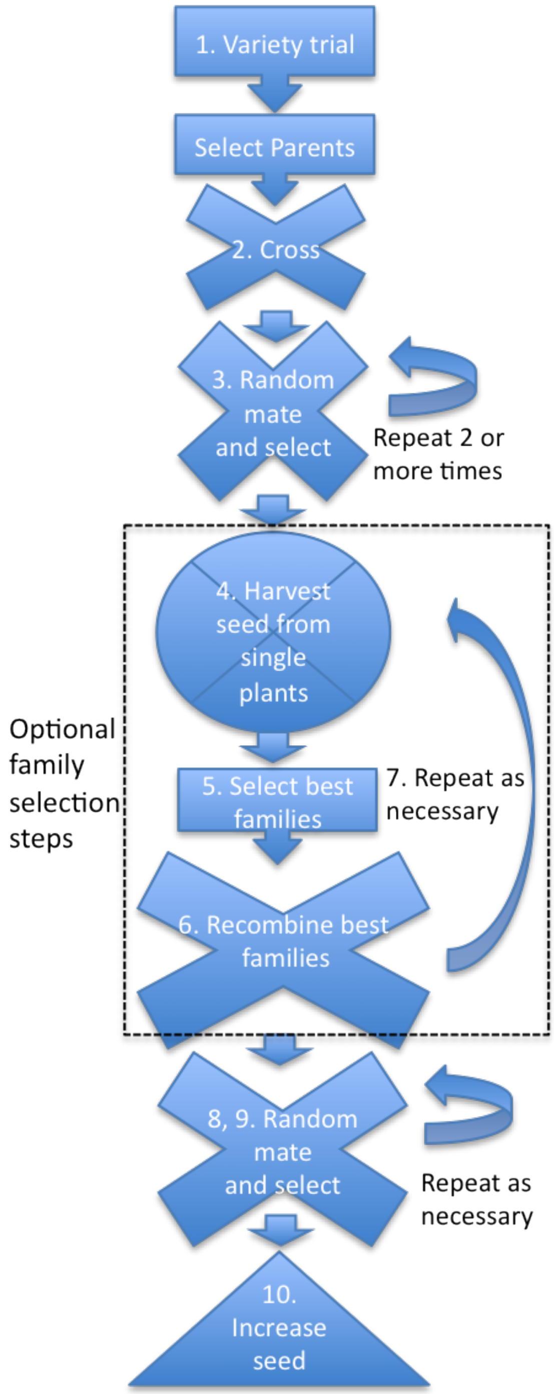


Figure 5. This diagram shows a summary of a general breeding timeline.

Step 1. Conduct variety trials to identify the best potential parental germplasm.

Step 2. If necessary, make crosses between parents. If adequate variation exists in a favorable existing variety, then no crosses are necessary.

Step 3. If you are working with a cross-pollinating crop and you made crosses, allow the offspring to randomly mate for at least two or three generations while removing obvious undesirable plants. In the case of self-pollinated crops, allow the plants to naturally self-pollinate for at least two or three generations after the cross, removing only truly dysfunctional plants.

At this point, you can conduct a breeding program purely based on mass selection by proceeding to step 8. To conduct family selection, first go through steps 4 through 7.

Step 4. Grow a large population and save seed separately from individual plants. The seed from individual plants become families.

Step 5. The following generation, grow families out in rows. Plant each row from seed harvested from an individual plant. Evaluate and select the best performing families and plants.

Step 6. Harvest seed from the selected plants within the selected families. Depending on what you see and your goals, either keep seed from individual plants separate or combine within families.

Step 7. Repeat the process of growing and selecting family rows until you are satisfied with the performance of all families.

Step 8. Once the selected families are all acceptable, combine the seed of these families into a bulk population.

Step 9. Grow the bulked population again and remove the least desirable plants. Repeat as necessary.

Step 10. Once the population is uniformly acceptable, increase seed for release.

Here are further details on each step:

Step 1. Conduct variety trials to identify the best potential parental germplasm.

Before committing to a long-term breeding project, carefully evaluate potential parental germplasm. This evaluation typically takes the form of a variety trial. A variety trial is a systematic way to evaluate a set of varieties using good trial design. The purpose of a trial design is to help minimize the environmental variation to ensure that the differences observed represent genetic differences between plants. More information on how to conduct variety trials can be found in OSA's *On-farm Variety Trials: A Guide for Organic Vegetable, Herb, and Flower Producers*.

Step 2. If necessary, make crosses between parents. If adequate variation is present in a favorable existing variety, then no crosses are necessary.

To improve your population, some degree of variation for important traits is necessary. See Section **IV. Theories of field-based organic breeding** below for more information about how variation works. To have a variable population, you need to either start with germplasm that is variable for the traits you intend to improve, or you need to create variation by crossing two or more varieties together. These crosses can be made in a number of ways, depending on your goals and resources.

Types of Crosses

Controlled pollinations: Plant breeding might evoke an image of breeders making controlled crosses, perhaps with tweezers, magnifying glasses, and small paintbrushes. The general strategy will depend on whether the species you work with has ***perfect*** flowers or not. Perfect flowers have both male stamen and female pistils on the same flower. If the plant has perfect flowers, you will generally need to *emasculate* the female parent by removing the male stamen and then transfer pollen from the male parent. If the plant has only unisexual flowers – flowers that contain either all male or all female parts – there is no need to emasculate. You just transfer pollen from a male flower to a female flower. After pollinating, some sort of cover is often used to exclude other pollen from contaminating the cross.

Open pollinations: These crosses are also know as ***strain crosses*** or blind crosses, and are done by allowing one plant or a set of plants to cross with another plant or set of plants without making an attempt to ensure that pollen is only transferred between certain plants. This is accomplished by bringing all of the plants together and allowing them to freely cross-pollinate. Outside pollen is excluded either by isolation distance or by caging the plants inside a structure that prevents insects and pollen from entering.

Hybrids: These varieties can be used as premade crosses, saving a step in the breeding process. Keep in mind, however, that most hybrids are made by crossing two narrowly selected inbred parents and therefore a population formed from a single hybrid will have comparatively little genetic diversity relative to one created from a strain or blind cross between open-pollinated varieties.

Step 3. If you are working with a cross-pollinating crop and you made crosses, allow the offspring to randomly mate for at least two or three generations while removing obvious undesirable plants. In the case of self-pollinated crops, allow the plants to naturally self-pollinate for at least two or three generations after the cross while removing undesirable plants.

Prior to selection, grow your new breeding population for a few generations, allowing the plants to flower and freely cross-pollinate. During this time, you may practice negative ***mass selection*** to rogue out the worst performing plants.

It is tempting to begin intensive selection in the generation after your crosses are made, as plant breeding can be such a long process. However, we recommend that you do not skip this step. In cross-pollinated crops, allowing a few generations of random mating breaks up the ***linkage*** between genes. Simply stated, linkage refers to how genes in a plant will tend to travel together. For example, if you cross a tall plant with dark leaves with a short plant with light leaves, you're more likely to get either a tall dark plant or a short light plant than you are to get a tall, light plant or short, dark plant. Random mating for a couple generations allows the genes to shuffle and makes it more likely that you will see new combinations of genes in the population.

For self-pollinated crops, it is also valuable to wait for at least two or three generations before making any significant selections. The reason for this is different than for cross-pollinated crops. As described in the previous discussion of differences in genetic structures between cross- and self-pollinated crops, random mating and the breaking of linkages does not occur in self-pollinated crops. Instead, each plant derived from the offspring of a cross has the potential to become a separate, independent family line with unique combinations of fixed pairs of genes. As each of these lines continues to self-pollinate over the course of a few generations, each line will become more uniform and the differences between lines will become more obvious. It will be easier to make distinctions between families if sufficient time has passed to allow the families to essentially become fixed and distinct from one another.

Additionally, the more generations you spend improving the population by this gradual process (mass selection), the better the genetics of the population will be, and the more likely you will be successful in the later phases of breeding.

These generations will also give you a chance to get to know the population, to see what kinds of variation exist in it, and to evaluate what its strengths and flaws are. Use these years to refine your goals, traits of interest, and evaluation techniques. Remember, when practicing selection, make sure the field location represents the location you want to select for and is relatively uniform throughout.

Step 4. Grow a large population and save seed separately from individual plants. The seed from individual plants become families.

During this generation you will be selecting your best plants to serve as parents for families. Evaluate your plants multiple times throughout the season, considering the goals and traits you have prioritized. Since there may be some variation in the soil quality, weed pressures, and other factors in your field, select the best plants from all parts of the field equally. If all of the plants in one corner of your field look worse off than the rest, still try to pick some of the best looking plants in that patch – those are plants that can survive under some environmental stress or potentially sub-optimal conditions.

If your crop is cross-pollinating and is a crop where you have an opportunity to evaluate and select the best plants before pollination occurs, you will make faster progress by removing all inferior plants from the field before pollination occurs. In this way, any cross-pollination that occurs will only be between the selected plants.

When you harvest seed from selected plants, put seed from each plant into a separate bag. The seed in each bag represents a family. Label each family with a unique number. Along with the number on each label, you may want to make notes about why you selected that plant. These plants will represent families for the next generation's round of selection. In the case of cross-pollinated crops, try to save seed from at least 20 to 50 individual plants. In the case of self-pollinating crops, save seed from at least 30 to 100 plants.

Step 5. The following generation, grow family plots by planting each separate plot with seed harvested from an individual plant. Evaluate and select the best performing families.

This generation you will be looking at the progeny of your selected plants as families. In breeding terms, this is the process of ***family selection***. This means you will plant seed from each plant that you selected in separate plots or rows, just as if you were conducting a trial, following the best practices of trial design as outlined in OSA's *On-farm Variety Trials: A Guide for Organic Vegetable, Herb, and Flower Producers*.

Examine each plot as a whole. How does this family of related plants look? On average, which families look best given your goals and traits? Select the best families based on their overall quality, and eliminate the other families, preferably before they have a chance to cross-pollinate with the selected families. Look for families where at least 60 to 80% of the plants are acceptable.

Next, select the best plants within the best families. Aim to eliminate 30 to 40% of the plants within a family, keeping in mind the minimum population size you want to maintain to keep the population healthy (see box, "Why maintain large population sizes?").

Step 6. Harvest seed from the best plants within the best families.

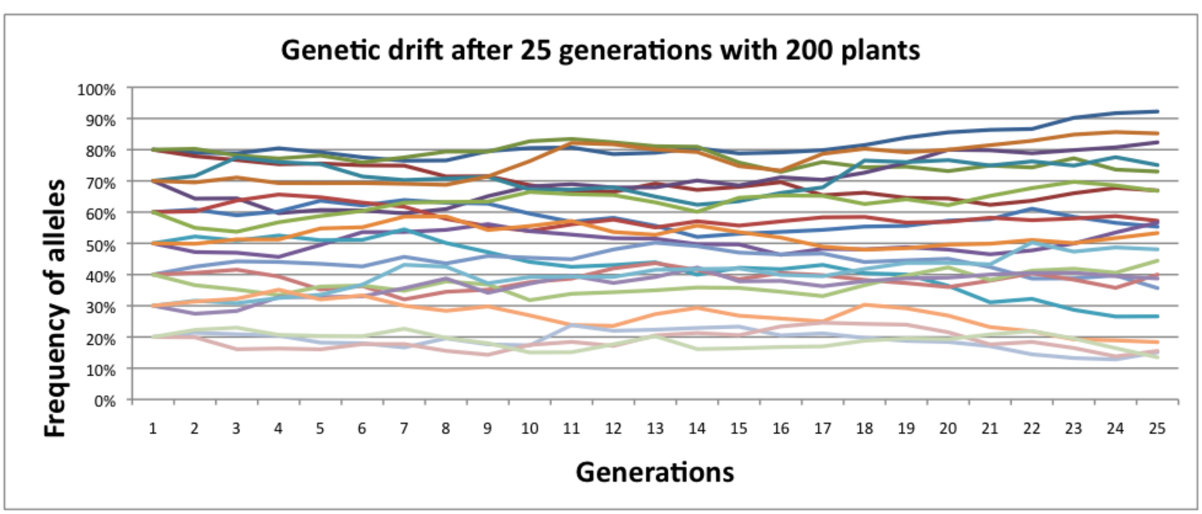
At this point, save the seed from each family. In other words, combine the seed from all of the selected plants within each family so that you end up with a separate bag for each family.

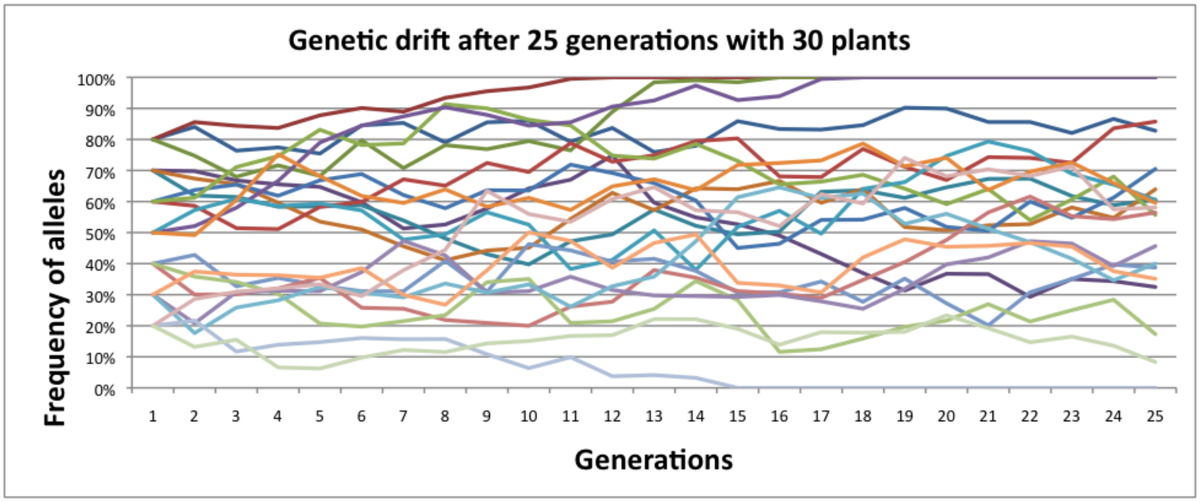
Why maintain large population sizes?

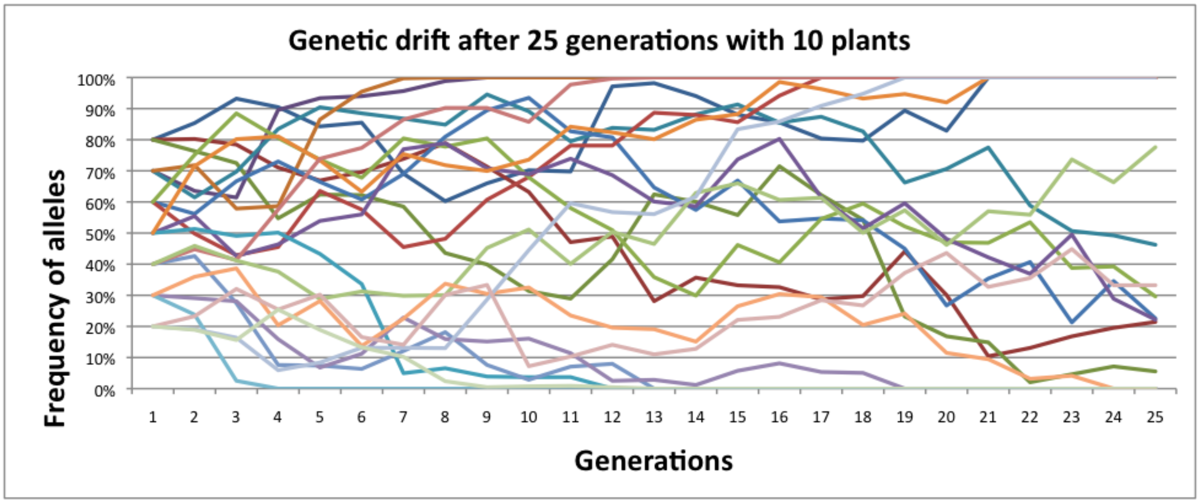
What is the advantage of maintaining large numbers of plants in your breeding populations? After all, if you have a few excellent looking plants in the field, why save seed from any plants that don't look as nice? There are two main reasons to maintain large populations.

In the case of cross-pollinating crops, large populations help avoid inbreeding depression. Inbreeding depression is a loss of vigor due to the crossing of genetically similar plants. Plants suffering from inbreeding depression germinate poorly, yield poorly, and succumb more quickly to environmental stress. In general, plants that are strongly cross-pollinating are most susceptible to inbreeding depression, while those that are strongly self-pollinating are least susceptible.

The second reason to maintain large population sizes is to avoid losing important genes through ***genetic drift***. Genetic drift is the random change in the frequency of genes in the population as it reproduces. Even in the absence of selection, the population that grows from one generation to the next may have a slightly different percentage of genes just by chance. If, by chance, none of the plants in a given generation carry a certain gene, it will be lost to the population. This is much more likely to happen in small populations than in large ones. The three charts below show a simulation of the change in gene frequency after 25 generations for some hypothetical genes that are found in between 20 to 80% of the plants in a population to start with. When the population size is kept at 200 plants, all of the genes are still present in the population at the end of 25 generations. With only 30 plants, one-fifth of the genes are fixed or lost within 25 generations. When seed is saved from only 10 plants every generation, the majority of genes are fixed or lost within 25 generations.







Step 7. Repeat the process of growing and selecting family plots until you are satisfied with the performance of all selected families.

The following generation, continue to plant the selected families in separate plots and evaluate them again throughout the season. If, during the second round of evaluations, some of the families no longer seem acceptable, discard those families. Also eliminate all inferior plants within the selected families that you decide to carry on to the next generation.

Step 8. Once the selected families are all acceptable, combine the seed of these families together into a bulk population.

For these past few generations, you have been maintaining the population as a set of separate families. Once all of the remaining families meet your goals, you can combine them together to reform the population.

Step 9. Grow the population again and remove the least desirable plants. Repeat as necessary.

Once the families have been reformed into a single population, you can maintain this population in subsequent generations through mass selection (i.e., selecting the best individual plants to reproduce each generation). If at any point you believe the variety needs to be more intensively selected, you can complete another cycle of family selection by saving seed separately from individual plants and planting them in individual plots the following generation, as previously described.

Step 10. Once the population is uniformly acceptable, increase seed for release.

As you increase the seed, continue to rogue out any undesirable plants as they arise.

IV. Theories of Field-based Organic Plant Breeding

Looking at broccoli seed and kale seed, you may not be able to tell them apart. They are both small, brownish-grey seeds, essentially indistinguishable from one another. But plant the seed in the ground, and as they germinate and grow into mature plants, the differences become greater. The kale seed produces kale plants with broad, curly green leaves, while the broccoli seed produces broccoli plants with large, tight flower heads. What exactly is contained in that seed that causes broccoli seed to grow into broccoli and kale seed to grow into kale? Genes, made up of DNA, "program" the way plants (and all living things) grow, the way they look, and the way they taste, among many other characteristics. Genes are how a plant's programming passes down from one generation to the next. As plant breeders, our job is to pick the plants with the best genes and make sure those genes get passed down.

This section will introduce you to the basics of genetics by explaining how genes are passed from one generation to the next and how those genes determine the appearance and performance of plants.

How genes travel from parents to offspring

Just as it is in humans, DNA is bundled together into packages called ***chromosomes*** in plants. Plants also have multiple chromosomes, each of which contains many genes. Most crop species are diploid, meaning they have two sets of chromosomes: one set from their mother and one from their father. For example, tomatoes, in general, have 12 pairs of chromosomes, with two #1 chromosomes, two #2 chromosomes, etc., for a total of 24 chromosomes. However, some plants are polyploidy, meaning they have more than two sets of chromosomes. For example, common wheat is a hexaploid, meaning it has six sets of chromosomes. Although polyploidy is found in a number of important crop plants, for the sake of simplicity, we will focus only on diploid species for the following explanations and examples.

To reproduce, plants produce sperm and eggs. Sperm and eggs have only one set of chromosomes rather than two. Again, looking at tomatoes, while the rest of the plant has 24 chromosomes, the sperm and eggs only have 12. When each sperm or egg is created, it receives, at random, either a chromosome from the plant's mother or a chromosome from the plant's father. This makes each sperm and egg unique. Later, when the sperm is carried on the pollen and fertilizes an egg, a unique new plant will be created. Because of this, plants created from the same cross between two plants can all look different. The exception to this is if the parent plants are highly genetically uniform, which can occur either through inbreeding a cross-pollinated species or the use of pureline self-pollinating varieties. In this case the offspring from the cross will all look nearly identical.

How genes determine the appearance and performance of plants

As we learn more about the complexity of life, we see more deviations and exceptions to how we originally understood genes to function. Nevertheless, although the following descriptions are simplified versions of highly complex systems, they are still relevant and useful for plant breeding work.

Genes are instructions for our cells, written in the language of the nucleic acids that make up DNA. Cells "read" these instructions and make proteins. Typically, one gene makes one protein. Each chromosome contains hundreds or thousands of genes – most of the instructions necessary to create a plant.

As mentioned, half of those genes will come from the mother (maternal) and half from the father (paternal). For any given trait that is controlled by one gene, such as growth habit in tomatoes, a plant will have a maternal gene and a paternal gene. What if the maternal and paternal genes differ? For example, what if the gene received from the mother produces proteins that make a shorter, determinant plant, while the gene from the father makes a larger, indeterminate plant? For many traits there are genes that result in properly functioning proteins and genes that result in defective, non-functioning proteins. Also, for many traits, one properly functioning gene is enough to create sufficient protein to meet the plant's needs. In these cases, if a plant has just one copy of a gene that encodes for functioning proteins, it will look and function the same as if it had two of those genes. Only when there are no copies of that gene present to encode for the functioning protein do we see a difference in appearance. To illustrate, let us look at determinant versus indeterminate growth habit in tomatoes. Figure 6 illustrates tomatoes that have: (1) two functional copies of the "self-pruning" gene (*Sp*), (2) one copy of *Sp* and one non-functional "self-pruning" gene (*sp*), and (3) two non-functional "self-pruning" genes.

Notice that tomatoes 1 and 2 look the same. That is because only one copy of *Sp* was required to produce the proteins that allowed the tomato to grow continuously. Only when both copies were non-functional, as in tomato 3, does the tomato end up short and determinate. In this case, we would call *sp* a ***recessive*** gene and *Sp* a ***dominant*** gene. In the case of dominant and recessive genes, the fundamental concept to understand is that recessive genes are only visible in the ***phenotype*** of a plant (what a plant looks like) when two copies of the gene are present, whereas a single copy of a dominant gene will result in the dominant phenotype.

How genes travel together during reproduction

Ultimately, when we engage in plant breeding we are participating in the sexual reproduction of plants. In this sexual process, some of the parental cells undergo meiosis, splitting their chromosome pairs into ***gametes***: either sperm or eggs. These gametes then combine with a complementary gamete and form a ***zygote***, which is the beginning of a new plant. One of the ways in which this process profoundly affects plant breeding is through the phenomenon of linkage.

Linkage refers to the fact that some genes reside on the same chromosome and are thus physically linked together. In breeding, we often represent linked genes with two lines, each line connecting one of the linked pairs of genes:

$$\frac{\text{A} \quad \text{b}}{\text{a} \quad \text{B}}$$

In this example *A* and *b* are linked together on one half of a chromosome pair, while *a* and *B* are linked on the other half. Linkage causes some outcomes that we would not anticipate if the genes were

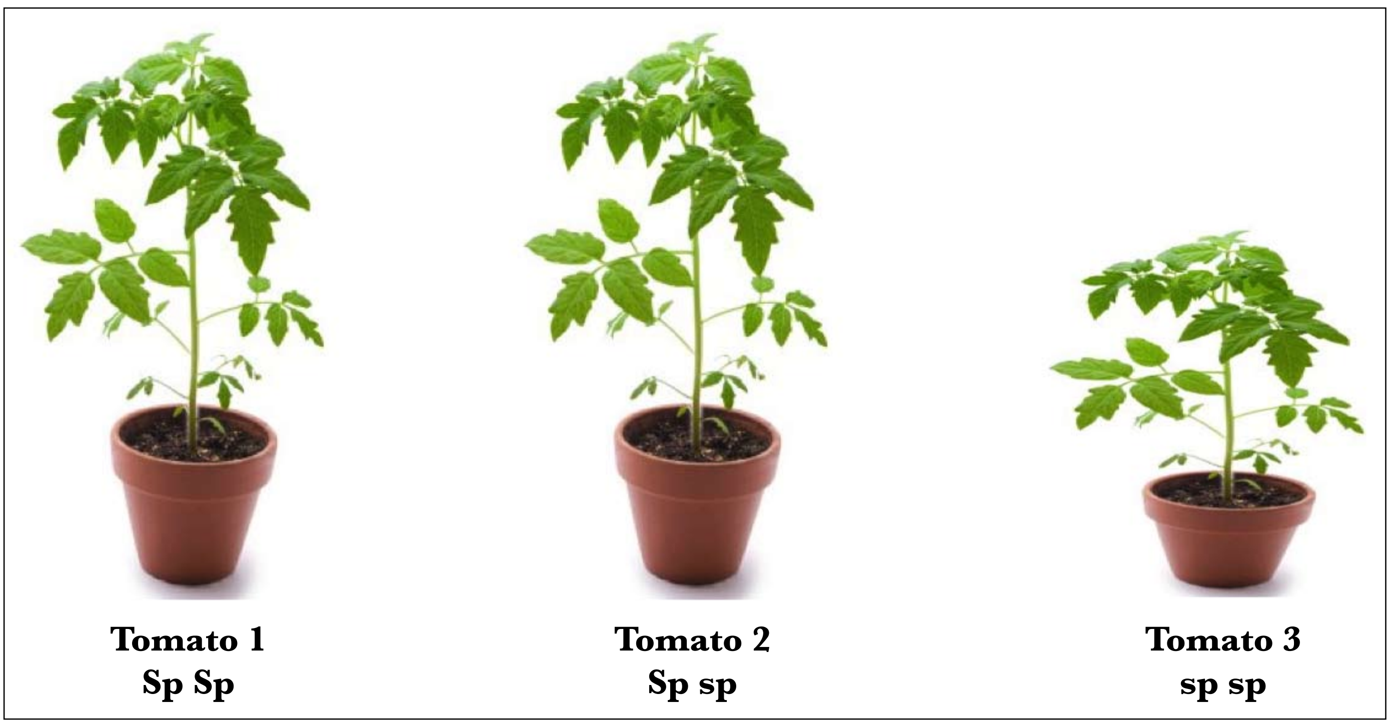


Figure 6. This figure illustrates determinant versus indeterminate growth habit in tomatoes.

not linked. For example, if we self-pollinated the above plant, we would get the following offspring: *AAbb*, *aaBB*, and *AaBb*. We would not see any *AABB* or *aaBB*, because *Ab* and *aB* are linked pairs that travel together through the process of meiosis. This is what happens during reproduction:

$\frac{A \quad b}{a \quad B} \longrightarrow$ Gametes: $\underline{A \quad b}$ $\underline{a \quad B} \longrightarrow$

Zygotes: $\frac{A \quad b}{A \quad b}$ $\frac{A \quad b}{a \quad B}$ $\frac{a \quad B}{a \quad B}$

But what if the most desirable genotype is *AABB*? Unfortunately, linkage prevents this genotype from occurring. When linkage causes an abundance or lack of genotypes that is disproportionate to what we would expect based on the genes that are in the population, we call it ***linkage disequilibrium***. Fortunately, nature has a way to reduce the effects of linkage by ***crossing over*** chromosomes.

During meiosis, pairs of chromosomes connect together. When they come apart again, parts of one chromosome can end up swapped with parts of the other chromosome that it paired with. This swapping of chromosome pieces breaks up linked genes. Depending on how close two genes are to each other, the linkages between them may break up more or less quickly and easily. Tightly linked genes, or those that are very close together, are more difficult to break apart than those that are loosely linked or farther apart from each other. It is possible for genes to be so tightly linked that breaking them apart is virtually impossible. Here is an illustration of how crossing over acts to break apart linked genes:

$\frac{A \qquad b}{a \qquad B}$ $\qquad$ $\frac{A \qquad b}{a \quad \times \quad B}$ $\qquad$ $\frac{A \qquad B}{a \qquad b}$

Why are linkage and linkage disequilibrium important for us as breeders? There are many reasons, but two of the most important are the need for caution when selecting in early generations and linkage's relation to ***heterosis***.

After making a cross or crosses to generate a new population, you need to be careful about selecting just a few of the best plants for the first few generations. To illustrate, let's continue with the tomato example where the linked genes that come from one parent are $\underline{A \quad b}$, and the genes from the other parent are $\underline{a \quad B}$. If we want to find plants that have the $\underline{A \quad B}$ genotype then we need to wait until the population has gone through enough generations to allow time for those particular chromosomes to have crossed over between those particular genes. Only then can we end up with *A* and *B* on the same chromosome. If selections are made too early on they can reduce the potential for certain gene combinations to occur, ultimately limiting what you have to work with.

Heterosis is the term used when the offspring of a cross are superior to their parents. Heterosis is also called hybrid vigor. There have been many arguments over the years about what causes heterosis. Recently, most scientists agree that the primary cause of heterosis involves two principles we have already discussed: dominance and linkage. To understand heterosis, let's look at the cross of two corn plants.

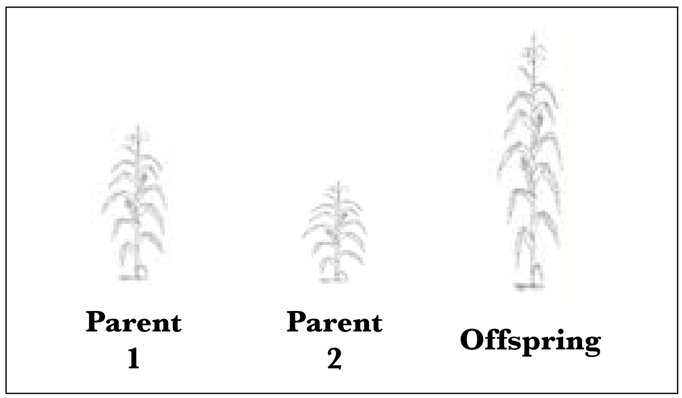


Figure 7. This diagram illustrating heterosis shows the cross of two corn plants that creates an offspring superior to its parents.

Why is the offspring so much taller? In these corn plants, there are two loci (location of a gene) that determine plant height: *A* and *B*. Plants with *A* are taller than plants with *a*, and plants with *B* are taller than plants with *b*. Both *A* and *B* are completely dominant genes, so as long as the plant has one copy of the dominant gene, it is as tall as if it had two copies. In this example parent 1 is *AAbb* and parent 2 is *aaBB*.

So what happens when we cross them? The offspring get *Ab* from parent 1 and *aB* from parent 2, so their genotype is *AaBb*. Because both *A* and *B* are ***dominant***, they affect plant height in the same way regardless of whether the genotype is ***AABB*** or ***AaBb***. The chart below shows that when parents 1 and 2 are crossed, their offspring gets a boost to height from parent 1's dominant *A* gene (shown as a "+") and a boost to height from parent 2's dominant *B* gene. This results in the hybrid offspring being taller than either parent.

	Parent 1	Parent 2	Offspring
Genes	AAbb	aaBB	AaBb
Effect of A	+		+
Effect of B		+	+
Overall height	+	+	++

In this case, the parents each had complementary genes. When they crossed, each parent contributed alleles that, through their dominant effects, masked the inferior recessive alleles of the other parent.

Heterosis is quite common in many crop plants. Why, then, between natural selection and the efforts of plant breeders, have we not been able to combine all of the best genes into one plant/variety? Why do we have to make hybrids to hide the poor genes of the parents? This is where linkage comes into play. Let's assume the ***loci*** for *A* and *B* are right next to each other on the chromosome and are tightly linked. In parent 1's case, *A b* will travel together until the chromosome crosses over into the region between the genes. Likewise, in parent 2's case, a B will travel together. Until a cross over occurs to break this linkage apart, the best we can do is keep remaking the hybrid. Most traits, such as plant height, are determined by multiple genes, not just one. Many of these genes, both desirable and deleterious/undesirable, are linked together. Since it is unlikely we will ever create or come across a plant with the perfect combination of genes for every trait we find desirable, we must continue to exploit the effect of dominant genes to produce superior offspring by finding parents whose gene combinations complement each other.

How genes operate in populations

Up until now we have been focusing on how genes pass from one generation to the next and how they affect the appearance of the plants we grow. To keep our discussion simple, we have presented examples where just one or two genes control a trait like plant height. Now, let us take a step closer to reality. Many of the traits that we care about – plant height, vigor, flavor, stress tolerance – are controlled by multiple genes. Rather than plants appearing either big or small, their height might exist along a spectrum. In this spectrum, a few of the plants will be very small, a few will be very large, and most will be somewhere in the middle. If you measured all the plant heights and graphed how common the various heights were, you might see them appear as a bell curve, as shown in figure 8.

When, as breeders, we work with these ***polygenic*** (multiple-gene) traits, our goal is to select the plants with the traits we want and slowly shift the whole population in the desired direction. Figure 9 shows the slight improvement you might expect from one generation to the next thanks to your selection.

To be successful as plant breeders, we want to improve plant populations for the traits we are interested in. Fundamentally, the way to improve a population is to find plants that will produce superior *offspring*. How do we find these plants? Let's look at figure 10 to see an example of a field planted with a population of corn that we are interested in improving for height.

There is obvious variation in the phenotypes of these plants. If the task is to pick out the tallest plants, it would be simple: plants 2, 4, 5, 6, and 12 are the tallest. However, what we really want to know is which of these plants will produce the tallest offspring. The first step in finding these plants is to understand that the phenotype (P) is influenced by two primary factors: the genetics, or genotype (G), of the plant and the environment (E). In breeding terms: P = G + E. The ***genotype*** is the sum of all the genetic information within the plant, although we generally use the term to refer to the genes in the DNA. The environment encompasses

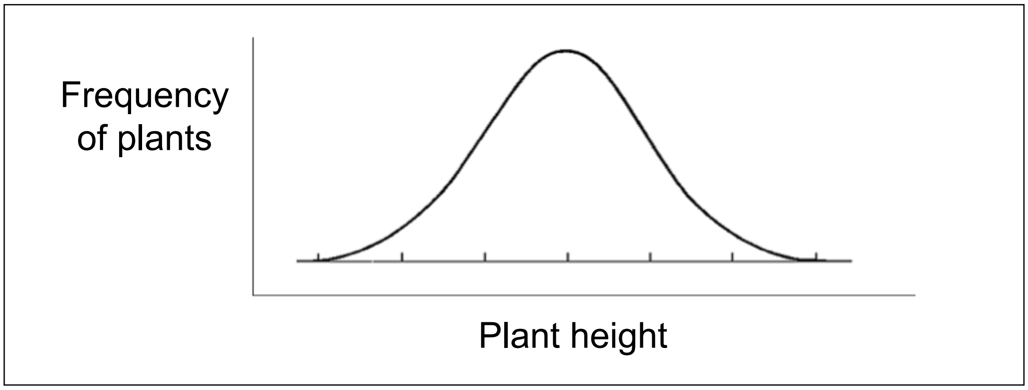


Figure 8. Rather than plants appearing either big or small, their height might exist along a spectrum. In this spectrum, a few of the plants will be very small, a few will be very large, and most will be somewhere in the middle as shown in this bell curve.

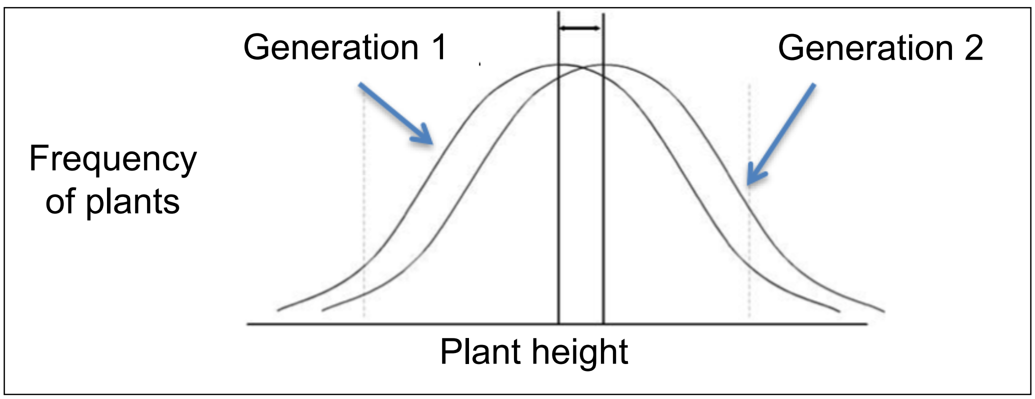


Figure 9. This graph illustrating how polygenic traits operate in populations shows the slight improvement you might expect from one generation to the next thanks to your selection.

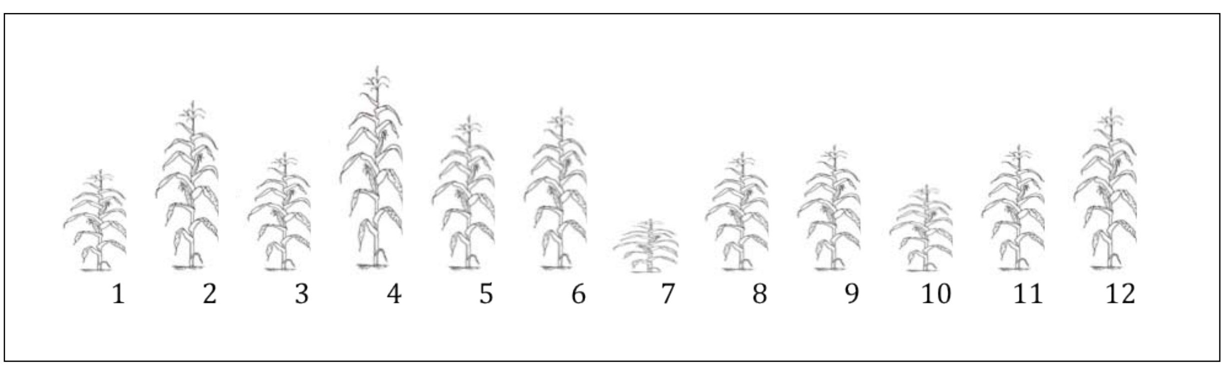
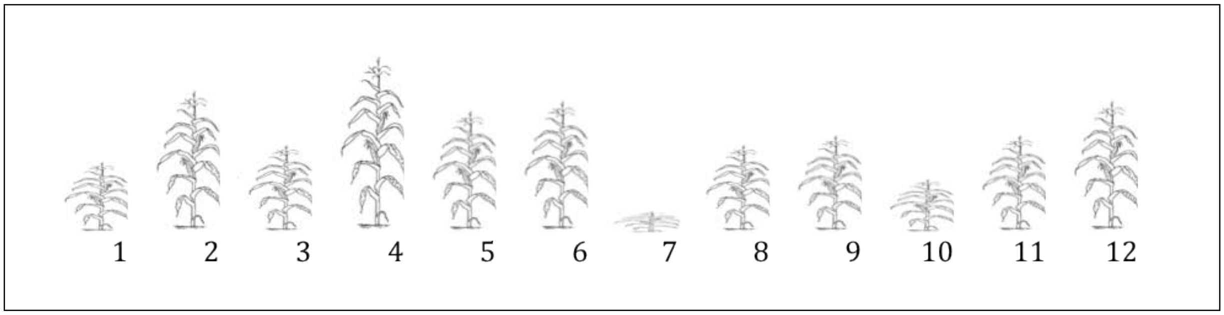


Figure 10. This figure represents a field planted with a population of corn that we are interested in improving for height.

all of the non-genetic influences on the phenotype. Examples of environmental factors affecting plant growth include fertility, temperatures, water, weed competition, planting density, and pest and disease pressure. Say we are able to grow these same twelve plants with very little water and they all grow 10 inches shorter than before as seen in the below figure:



Clearly, the environment affected the plant phenotypes, but did it affect them in a way that changes our ability to pick the best parents? In this case, no. We would still pick 2, 4, 5, 6, and 12 as our favorites. If all effects from environmental stresses were uniform like this example, it would be simple for us to pick the best parents based on their phenotypes. Unfortunately, life is not so simple. There are environmental effects that make it more challenging. These effects are basically classified into two types: error and genotype by environment interaction (GxE). Error is a catch-all term for effects that we cannot, or did not, measure or account for. For example, imagine that additional fertilizer was accidentally applied to the soil under plant 4, providing a fertility boost that none of the other plants experienced. This fertility boost would be an effect that was not replicable, and would influence our selection in an unpredictable and probably unhelpful way. This is error. Some error we can reduce through good experimental design, especially the use of replication and randomization. To illustrate, let's take another look at the corn plants. What if plants 7 through 12 are smaller overall because the field is drier on the right? To test this we could split the field into two sections and replicate the experiment by planting each corn randomly on each side of the field as shown in figure 11.

By replicating our trial, we see the plants on the right are consistently smaller than those on the left. Replication allows us to measure this effect and correct for it. Unlike any of the other effects on plant phenotype, we are able to account for and remove effects that are captured by replication.

The second effect that confounds our ability to pick the best parents is the GxE interaction. GxE is a statistical term that accounts for the fact that different genotypes sometimes respond differently to

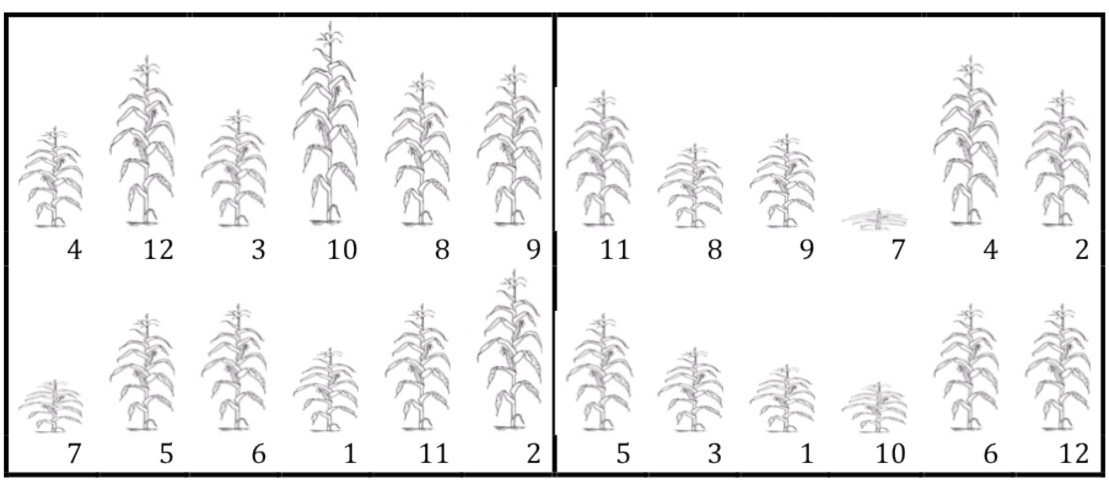


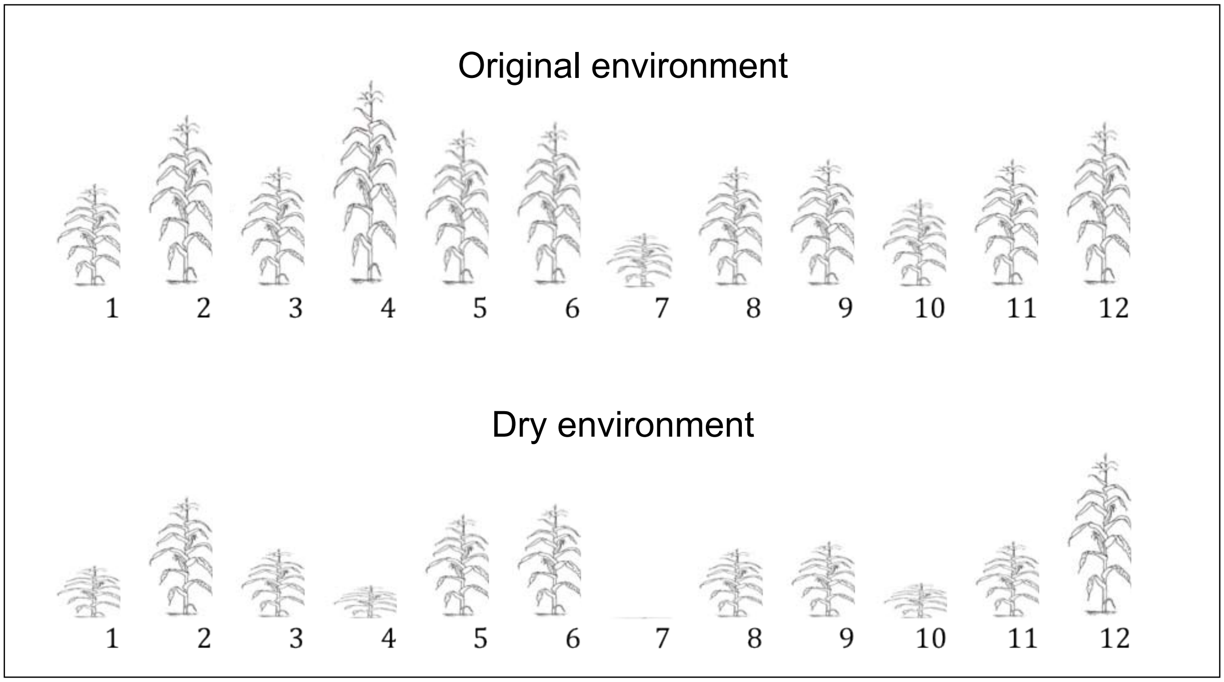
Figure 11. Here is the above field split into two sections and the experiment replicated by planting each corn randomly on each side of the field.

the same environment. To continue with our corn example, say that we grew our corn both in the environment and in a much drier environment as shown below.

In this example, the height of most plants was reduced in the dry environment relative to the original environment. However, the plant heights were not uniformly reduced. Number 4 is much smaller than in the original environment, and number 12 is the same height in both environments. This unequal response from different genotypes to different environments is captured by the concept of GxE. As breeders, we have two choices of what to do with this information. We can focus our breeding efforts toward a certain environment – in this case to select for a dry environment. This method is called selecting for specific adaptation. Alternately, we can select for the genotypes that, on average, perform best in all environments. This method is called selecting for ***general adaptation***. In reality, breeding often mixes these two approaches by breeding for adaptation within a certain specified ***target population of environments*** (TPE).

As plant breeders, we are interested in the plants that are most likely to produce the best offspring, not simply perform the best themselves. Here is another key to plant breeding: The plants with the best genotypes may not produce the best offspring. This is because, unless they are clonally reproduced, plants pass on genes, not genotypes. The next section will explain why, including the implications.

Dominance effects confound our efforts to find the best parents because they are genetic effects that are not transferable from parent to offspring. To understand dominance effects, we will return to our tomatoes (see next page).



Again, given identical environments, tomatoes 1 and 2 have the same appearance, because they both have at least one copy of the dominant *Sp* allele. However, while tomato 1 will only produce indeterminate offspring, tomato 2 has a chance of producing determinant offspring.

Since tomato 1 (*Sp Sp*) and tomato 2 (*Sp sp*) are indistinguishable from each other, you are equally as likely to choose them as parents. This is problematic because you may prefer one or the other for your breeding work. The dominance effect that allows *Sp sp* plants to appear the same as the *Sp Sp* plants is a genotypic effect that is not reliably transferable to its offspring. The bottom line is that genotypic effects due to dominance are not transferable to offspring.

In summary, genetic effects and environmental effects influence plant phenotypes. If proper experimental designs are used we can account for

Tomato 1
Sp Sp

Tomato 2
Sp sp

Tomato 3
sp sp

environmental effects. These experimental designs allow us to achieve one of our primary goals as plant breeders, which is to minimize and account for the variability caused by non-genetic effects.

One more important plant breeding term is ***heritability***. Heritability describes how predictably a trait is passed on from parent to offspring. Plant breeders often talk about the heritability of a trait and how to increase it. Some traits are naturally high in heritability. Often these traits are relatively unaffected by environment, like seed color or flower shape. We can increase the heritability in all traits by using mating designs that increase or maintain additive genetic variance, and by using experimental designs that reduce the variance of other effects.

How to see the genetic differences between plants

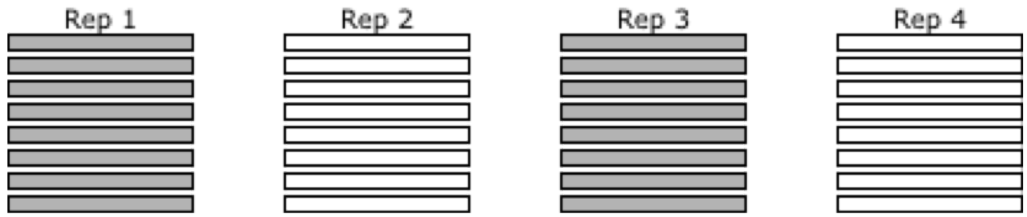
Earlier we talked about the importance of reducing environmental error. We briefly mentioned replication as one tool to help reduce this error. Next we'll go into more depth about how to use replication and other tools of ***experimental design*** to help make more effective selections in our breeding work.

Experimental design refers to how the experiment is set up or arranged in the field. One of the more common designs for breeding is called "randomized complete block design," or RCBD. A RCBD is replicated using multiple blocks, with each block containing the complete set of breeding lines within it. To create a RCBD, assign each breeding line to a plot in each block and arrange the plots in a randomized order within each block. The breeding trial should ideally be located where there is as little variability as possible. Where variability exists, try to orient the blocks so the variability is between blocks rather than within them, because breeding lines are compared to each other within each block. Replication, randomization, and blocking are the essential elements of the experimental design that helps to separate out the genotypic effects from the environmental effects.

Understand the effects of the environment

Environmental effects refer to the influence that variable field conditions have on the performance of plants. For example, if the field is on a slope and the soil is richer on the downhill side, then plants on the downhill side may grow larger because of better soil conditions, not because they have superior genetics. Likewise, plants grown on the southwest side of a field may grow larger because they receive more afternoon sun, or smaller if they are sun-sensitive and their roots are easily dried out by afternoon sun. Natural variability often exists in the field that affects crop growth, including variations

Example of RCBD, where all varieties would be in each block or "rep"



in soil quality, soil texture, soil pH, soil fertility, drainage, pest pressures (insect, weed, disease, and animals), sun exposure, irrigation, and temperature (both warm and cold pockets). Some sources of environmental variation are relatively stable, like soil type and production practices, while others vary from year-to-year, like weather and climate. Pests (diseases, insects, and weeds) may be stable or variable depending on the organism. For example, the soil insects known as symphylans are usually found in the same spot year after year and would be regarded as stable, whereas aphids blown into the plots from another region would be more variable. Stable sources of variability can be compensated for by the use of randomization whereas seasonally variable sources of variability require testing over multiple locations and/or seasons. "Seasons," as used here, may be different times of year or different years. The objective is to obtain data in a number of different growing environments. The goal of the experimental design is to minimize the effects of environmental variability on trial results by blocking replications so field variation is minimized within blocks. In essence, replication in the breeding trial accounts for stable effects and repeating the experiment over time compensates for variable effects.

Ensure that plants receive consistent treatment
Management practices should be consistent across all breeding plots, including irrigation, soil fertilization, pest management, staking, cultivation and weeding, or any other horticultural aspect of crop production. If practices are not consistent, differences in performance may be the result of unequal treatments as opposed to genetic differences in varieties. For example, if half the field was cultivated and the other half left uncultivated, the plots in the uncultivated section would have an unfair disadvantage, as they would likely be subjected to greater weed competition.

Randomize the plots
Randomizing plots within each block helps to increase the confidence that the evaluation results are due to genetic difference between varieties rather than variation in the environment. The more replications used the greater the assurance that measurements will reflect differences in the varieties rather than variation in the field. Randomizing is also important to minimize the influence that varieties have on one another. For example, if each breeding line was planted in the same order in each block rather than if one line is planted next to another very tall, vigorous line, it might be unfairly affected by the competition for light and nutrients.

The order of plots may be randomized using any basic randomization tool, as basic as drawing numbers from a hat. An easy method is to mark all of the plant stakes for each block and then mix them up, walking the block and inserting whichever stake comes to hand first to mark the first plot. Continue down the row marking plots in this manner.

Use sufficient population and plot sizes
The size of plots in the trial should be large enough that the resulting number of plants provides a good representation of the whole family or population. The greater the plot size, the more representative it will be of the population. However, the larger the plot the more difficult it may be to manage, especially if you are dealing with a large number of varieties and three or more replications. In general, when evaluating open-pollinated varieties of self-pollinated crops, fewer plants are necessary to get a representative sampling than in cross-pollinated crops. This is due to the generally greater inherent

genetic variability in cross-pollinated populations.

Ideally plots should be large enough that you can treat them the same as the rest of your farm and maintain them with your normal farming practices. For example, if you usually plant your cabbage on 36-inch centers and field cultivate with a tractor, you will likely get different results then someone with a small garden trial on 24-inch spacing using hand hoeing. Similarly, if you usually apply drip irrigation, then overhead irrigation may skew results. For best results, locate your breeding trial within your production field of the same crop so that all production practices are the same as for commercial production. Plot size may be dictated by your normal planting and management practices. For example, a minimum amount of seed may be required to plant with a seed drill or vacuum planter, and the planting equipment may need to run a certain distance to function properly. Mechanical harvesting equipment may also require a certain minimum scale to operate appropriately.

Another variable to consider when determining plot size is the number of rows to include per plot. Single row plots allow you to place more lines or families in your trial, but may give more variable results because of fewer plants per plot and potential competition between varieties in adjacent plots. With three or four row plots, the center one or two rows can be evaluated without concern of competition effects with neighboring plots. While this approach takes more space, it does minimize inter-plot competition and produces more accurate data. As with plot length, a minimum number of rows may be determined by equipment. For example, you may be limited by the setup of your planting equipment. Border rows around your experimental plots will minimize what is known as the edge effect, whereby plots on the edge experience slightly different growing conditions relative to the rest of the trial. Without borders, plots on the edge may be more productive because they lack competing plants around them or less productive because they are next to a more competitive crop or damaged by field operations occurring in adjacent crops. As such, data from un-bordered plots around the outside of the trial will be biased relative to the center of the field. Border rows should be planted at the front and back of a trial as well as along the sides.

V. Examples of Farmers Breeding for Organic Systems

'Abundant Bloomsdale' organic spinach breeding project

What were the goals of this project?

There is a strong demand for more open-pollinated savoy spinach varieties, which are important to diversified organic farms. The goal of the Abundant Bloomsdale project was to develop a dark green, open-pollinated savoy spinach variety with high nutritional content, good flavor, and superior bolt resistance. The variety needed to have an upright plant habit and be useful at all stages from baby leaf to fully mature bunching types.

The Pacific Northwest is a prime spinach seed producing region, yet there is little organic spinach seed produced there, as most seed companies have ignored the organic spinach seed market. An end result of this breeding project will be to help both organic farmers and small organic seed companies by supplying them with an alternative to the spinach hybrids that are largely bred for conventional systems.

Breeding procedure

The project began with a cross of 'Winter Bloomsdale' and 'Evergreen.' 'Winter Bloomsdale' is a cold hardy, open-pollinated spinach variety with dark green leaves, deep curl, and good flavor. The variety was originally bred for winter and early spring harvest in coastal Virginia. It is the last of the old fully savoy spinach varieties that is still widely grown in North America. 'Evergreen' is a semi-savoy spinach variety developed by Dr. Teddy Morelock of the University of Arkansas for winter production in Arkansas and Texas. The variety has strong horizontal resistance to many of the major diseases of spinach.

In the first year of breeding, OSA breeder John Navazio made a 'strain cross,' where approximately 20 plants of both parental varieties were planted side-by-side and allowed to cross through open-pollination. By making the cross in this manner, rather than pollinating by hand, more crosses between the varieties could occur and more of the genetic variability of the two parents is retained.

After that initial cross, the resulting population was grown for five generations on various farms in Western Washington. This intermating process broke up some of the genetic linkages (see *linkage* description in previous section) and allowed the genes of the two parents to thoroughly mix. During this process, a low intensity of mass selection was applied for appropriate leaf shape and vigor.

In the sixth season, after five generations of intermating, Navazio and local farmer Marko Colby planted a 2,000 plant "space plant nursery," where each plant was spaced far enough from all others so they could be evaluated individually. From these 2,000 plants they selected intensely for the traits already mentioned, and ended up with 130 spinach plants. These selected plants were allowed to openly pollinate.

As spinach is dioecious, with plants containing either male flowers or female flowers, only about half of the selected plants were seed bearing. Ultimately, seed from 67 female plants were harvested into separate bags that were numbered sequentially from 1 to 67. Seven families were subsequently dropped because of their poor seed quality or yield.

In the following year (year seven), seed of the remaining 60 families were planted in family rows and evaluated at several stages of growth between the baby leaf and mature bunching stages. Of these 60 families, only five proved to be superior through all growth stages. The other 55 undesirable families were eliminated and the remaining five selected families were allowed to intermate through open-pollination. The resulting seed of each of the five families were harvested separately into five family bags.

In year eight, Navazio and Colby planted seed from these five families as family rows, with the goal of identifying the best of these selected families to comprise the final population that would be released as 'Abundant Bloomsdale.' The five families were again evaluated at all stages of growth between the baby leaf and mature leaf stage. In this final evaluation, only one of the five families was uniform in all of the traits that satisfied the breeding goals. This family had dark green, fully savoyed leaves on a very upright, vigorous plant, and a rich, sweet flavor and superior cold hardiness. The other four families were eliminated and the chosen family was rogued for off types. The remaining plants were allowed to intermate and produce the stock seed of 'Abundant Bloomsdale.'

Winter sprouting broccoli

What were the goals of this project?

This breeding project is ongoing, and the goals are to develop a purple sprouting broccoli variety that reliably overwinters in the Pacific Northwest and produces good yields of tender, flavorful, 6 to 8 inch shoots with purple florets. The purple winter sprouting broccoli varieties that are commonly available to Pacific Northwest growers generally come from Western Europe and most are not consistently cold hardy to temperatures below 18°F (-8°C). Some Pacific Northwest winters provide low temperatures between 8° and 14°F (-13 and -10C). Also, many of the European open-pollinated varieties have sprouts that are inconsistent in the length and size of their florets.

This project is a collaboration with Organically Grown Company, the largest all-organic produce distributor in the Pacific Northwest. Organically Grown Company is investing in the project to expand access to regionally grown, organic produce.

Breeding procedure

OSA began this breeding project by conducting a trial with ten sprouting broccoli varieties. Six of these were open-pollinated varieties and four were hybrids. This trial was planted in Port Townsend, Washington, in the mid-summer of 2010 and grown through the cold winter of 2010 and 2011. Temperatures got down to 14°F (-10°C) during several of these nights. We evaluated the varieties throughout the winter for frost damage. Several varieties were damaged to the point where plants died or where the damage severely reduced the yield of sprouts in spring. Five of the ten varieties were found to survive the cold at higher rates than the others. Of those five, only two varieties had many of the required quality characteristics, including large sprout size, deep purple colored florets, and good stem length.

In the spring of 2011, approximately 25 plants from each of the two best performing varieties were selected as parents to make a strain cross. All of the other plants from these two varieties were removed from the field, as were the other varieties. These 50 selected plants were allowed to cross-pollinate and set seed. During flowering, eight additional plants were eliminated based on poor flowering characteristics. In the summer of 2011, seed was harvested from each plant and saved separately, representing 42 half-sib families. After harvest, two of the families were eliminated based on poor seed set.

In the summer of 2012, seed from each of these 40 families were planted as family rows in two locations: Port Townsend, Washington, and Ashland, Oregon. Each location had 40 family rows, with 30 plants in each family. Each of the families was evaluated in the winter and spring of 2012 and 2013 at both locations based on sprout characteristics, upright growth, yield, vigor and cold-hardiness. Families needed to have a rate of good plants greater than 60% to be considered acceptable. Eight of the 40 families were found to be superior at both the Washington and Oregon locations. The other 32 families were eliminated from the field, as were up to 40% of the inferior plants within the eight selected families. The selected plants in the eight selected families were then allowed to intermate. Seed was saved separately from each of the eight families.

As of the writing of this publication, the eight selected families are being grown as separate family rows in both Washington and Oregon. Selection will occur in the winter and spring of 2013 and 2014. We anticipate a finished variety will be ready for release in 2015.

Glossary and Index

Additive genetic effect: the linear phenotypic change in a trait that occurs from the substitution of one allele for another at a given locus.

Allele: one of a number of possible genes that could occupy a given locus.

Anther: the pollen bearing male reproductive structure in a flower.

Artificial selection: (see ***Selection***)

Breeding value: the expected average value of the offspring of a given plant for a given trait.

Broad adaptation: (see ***Wide adaptation***)

Chromosome: a single, organized piece of DNA that contains many genes, as well as non-genetic elements.

Cross-pollination: the pollination (and, as a general rule, fertilization) of an ovule of one plant by the sperm of another plant. Cross-pollinating plants rely on cross-pollination for a significant amount of their mating.

Crossing over: the exchange of segments between chromosomes during meiosis.

Crossover interaction: a type of genotype by environment interaction where certain varieties are superior to other varieties in one environment while being inferior to those same varieties in another environment.

Dioecious plants: species where a fraction (generally half) of the plants in the population will have only male flowers, while the others will have only female flowers.

Dominant allele: an allele that produces a given phenotype regardless of whether it is present as a heterozygote or a homozygote (one or two copies at a locus). Dominant alleles, if present as a heterozygote, mask the presence of recessive alleles.

Dominance effect: the difference in the genetic performance of a heterozygote from what would be expected from the average value of the homozygous parents (the additive effects). Heterosis is a type of dominance effect.

Drift: (see ***Genetic drift***)

Environment: the external, non-genetic conditions that affect the phenotype of an organism. In a given location, these can include fixed conditions such as soil type and daylength, as well as variable conditions such as available water, fertility, cultivation practices, and pest and disease pressure.

Experimental design: the process of planning a study with the goal of meeting specific objectives in an efficient manner.

F1 (F2, etc.): abbreviation for first filial generation, i.e. the first generation of plants to come from a cross.

Family: a group of genetically related plants. Often the nature of the relationship is specified. As examples, see half-sib families, full-sib families, and S1 families.

Family selection: selecting plants or families based on the overall performance of a family.

Fertilization: fertilization is the process by which sperm cells travel through the pollen tube to the ovary. Fertilization is complete when the sperm fuses with an ovule, eventually leading to the formation of a seed.

Full-sib family: a family structure where the plants in the family share the same mother and the same father.

Gamate: sperm or egg cells resulting from meiosis, containing half the number of chromosomes as the parental plant.

Gene: a unit of inheritance that controls, in whole or in part, a given trait. Genes are located at fixed loci in a series of alternative forms called alleles.

Gene pool: the set of genetic information shared by a population.

General adaptation: (See ***Wide adaptation***)

Genetic drift: the random (non-intentional) change in the frequency of genes in the population as it reproduces over generations.

Genetic variability: the range and distribution of alleles that are contained in a population. Genetic variability is important because it determines the ability of the population to be improved and to adapt to variable environments. Genetic variability can exist in a population as heterozygosity and as heterogeneity.

Genetically Modified Organisms (GMOs): Organisms with human mediated genetic alteration resulting from the direct uptake, incorporation and expression of foreign genetic material.

Genotype: the genetic makeup of an organism.

Genotype by environment interaction (GxE): the variability in phenotypes that occurs when genotypes perform differently in different environments.

Germplasm: a collection of genetic resources in a species.

Half-sib family: a family structure where the plants in the family share the same mother.

Heirloom: for the purposes of this text, pre-World War II open-pollinated varieties that were selected, adapted, and maintained over generations within families or agricultural communities.

Heritability: the proportion of observed variability that is heritable.

Heterosis: the increased performance of hybrid beyond that predicted based on parental performance (also known as hybrid vigor).

Heterozygous: having non-identical alleles at one or more loci.

Homozygous: having identical alleles at one or more loci.

Hybrid: the product of a cross between genetically distinct parents.

Ideotype: for the purposes of this text, an imagined crop variety representing the ideal to be reached through a breeding project.

Inbreeding: mating between related individuals.

Inbreeding depression: the decrease in varietal fitness due to inbreeding.

Intermate: cross-pollination between individual plants.

Isolation distance: the required distance to isolate seed crops from other crops of the same species that may be a source of pollen or seed contamination.

Landrace: a genetically and physically diverse variety that has developed over time by adaptation to the natural and cultural environment in which it exists.

Line: a nearly completely homozygous variety or breeding parent produced by continued inbreeding.

Linkage: the tendency of genes that are located near each other on a chromosome to be inherited together.

Linkage disequilibrium: the occurrence of combinations of linked alleles in a population in frequencies difference from what would be expected based on random assortment.

Locus: the position occupied by a gene on a chromosome.

Mass selection: a form of selection where individual plants are selected based on their individual performance.

Meiosis: the process of cell division that produces sperm and egg cells.

Monoecious plants: a type of plant that has stamens and pistils in different floral structure on the same plant.

Monogenic: a trait that is controlled by a single gene.

Multiline: a variety formed by the combination of two or more lines.

Natural selection: the process by which populations change due to individuals within the population that are better adapted to their environment tending to survive and produce more offspring.

Negative selection: selection against undesired traits, typically removing only a small fraction of the population.

Nursery: a field designated for rearing and testing breeding stock, performing crosses and other breeding activities.

Open-pollinated: more narrowly, a cross-pollinated crop allowed to intermate freely during seed production; or, more broadly, a non-hybrid crop variety.

Ovule: the structure that contains the eggs.

Perfect flowers: a flower having both male and female organs.

Phenotype: the appearance of an individual, as contrasted with its genetic makeup or genotype.

Pistil: a complete female organ within a flower, containing a stigma, style, and ovary.

Pollen: the structure that contains and conveys the sperm cells during pollination.

Polygenic: traits that are controlled by many genes.

Population: a community of individuals within a species that can intermate. A population shares a common gene pool.

Positive selection: selection for beneficial traits, typically removing a majority of the population.

Randomization: the process by which varieties, families, etcetera are randomly assigned to locations within a field.

Recessive allele: an allele that produces a given phenotype only when it is present as a homozygote (two copies at a locus).

Recombination: formation of new combinations of genes due to crosses between genetically distinct parents.

Rogue: removal of a small fraction of undesirable individuals from a population.

S1 (etc): symbol designating the first generation after a self-pollination.

S1 family: a family structure where the plants in the family all resulted from the same self-pollination.

Selection: the process of determining which individuals in a population will genetically contribute to the next generation.

Self-incompatibility: a general name for several genetic mechanisms that prevent self-fertilization. Self-incompatibility can also limit cross-fertilization between closely related plants.

Selection intensity: the difference between the average of the original population and the average of the selected population.

Self-pollination: the pollination (and, as a general rule, fertilization) of an ovule of one plant by the sperm of the same plant. Self-pollinating plants rely on self-pollination for a significant amount of their mating.

Space plant nursery: a nursery where plants are widely spaced so that they may be easily evaluated as individuals.

Specific adaptation: the ability of a given genotype or population to be superior in a specific environments.

Stigma: the upper part of the pistil that receives the pollen.

Stock seed: seed used by a seed grower or seed company to produce the seed that is grown for commercial sale and distribution.

Strain cross: a technique to produces multiple crosses between two or more populations, wherein the populations are allowed to openly pollinate.
Style: is the part of the pistil that connects the stigma and the ovary.

Target population of environments (TPE): is the set of environments (farms and future seasons) in which the varieties produced by a breeding program will be grown.

Trial: a systemic comparison of a set of varieties or families.

Unisexual flower: flowers that contain either all male or all female parts.

Variety: a named group of plants of the same species that shares a set of traits that differentiates it from other varieties.

Wide adaptation: the ability of a given genotype or population to perform in a stable fashion across many different environments.

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Germplasm and information resources

National Plant Germplasm System. A searchable listing of the USDA plant germplasm collections. Much of the material is available in small quantities for research purposes. http://www.ars-grin.gov/npgs/index.html

Seed Saver's Exchange. A membership organization that facilitates gardener-to-gardener exchange of open-pollinated seeds. http://www.seedsavers.org/

Organic Seed Finder. A searchable listing of organic vegetable and field crop seed from a wide array of vendors. http://www.organicseedfinder.org/

Organic Variety Trial Database. A collection of reports from organic variety trials conducted around the nation. http://varietytrials.eorganic.info/
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Selected Organizations and University Programs Involved in Organic Breeding

Mandaamin Institute. http://www.mandaamin.org/

Michael Fields Agricultural Institute. http://michaelfields.org/

Northern Plains Sustainable Agriculture Society Farmer Breeder Club. http://npsas.org/about-us/farm-breeding-club.html

Organic Seed Alliance. http://seedalliance.org

Cornell Department of Plant Breeding and Genetics. http://plbrgen.cals.cornell.edu/

North Carolina State University Plant Breeding Program. http://cuke.hort.ncsu.edu/breeding/

Oregon State University Plant Breeding and Plant Genetics Program. http://plantbreeding.oregonstate.edu/

Texas A&M Department of Soil and Crop Sciences. https://soilcrop.tamu.edu/programs/research-programs/plant-biotechnology/plant-breeding/

University of Iowa Plant Breeding Program. http://www.plantbreeding.iastate.edu/

University of Minnesota Plant Breeding/ Molecular Genetics Program. http://www.appliedplantsciences.umn.edu/PlantBreedingMolecularGenetics/

University of Nebraska Plant Breeding, Genetics and Molecular Physiology Program. http://agronomy.unl.edu/pg-plantbreed

University of Wisconsin Plant Breeding and Plant Genetics Program. http://plantbreeding.wisc.edu/

Washington State Department of Crop and Soil Sciences. http://css.wsu.edu/research/crop_genetics/breeding/

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