The majority of modern potato cultivars suffer from male sterility; they either produce little to no pollen or the pollen that they produce is not viable. Male sterility is part of a complex of traits that makes life difficult for potato breeders. Some varieties rarely flower at all, others will flower but rarely form berries even if cross pollinated, and others will drop their berries before they mature, particularly if the climate is not just right. Together, these traits add a lot of challenges to potato breeding, but male sterility is arguably the worst of them because it is, in most cases, a trait that will be inherited by all the progeny of a male sterile variety. In this post, we will discuss the causes of male sterility, strategies for working with it, and, most importantly, methods for detecting it so that you can eliminate male sterile varieties from your breeding pool.

You might wonder, quite reasonably, how male sterility could evolve in the first place. Potatoes can still reproduce asexually from tubers, but asexual reproduction slows the speed at which evolution can work the plant. Most male sterility in potatoes is the result of an interaction between a cytoplasmic gene found in some wild potatoes and a nuclear gene that is found in nearly all Andean potatoes. These traits probably evolved independently in different populations of potato and only came together to cause problems later. Male sterility is rare in Andean potatoes, which have M, A, or P type cytoplasm, and very common in modern and Chilean potatoes, which mostly have T or W type cytoplasm. Chilean potatoes descended from Andean potatoes, so what happened? Most likely, there was hybridization with a wild species early on in the development of Chilean potatoes. That may have introduced some adaptation for long day photoperiods, but also introduced male sterility. Unfortunately, the modern potato is primarily descended from Chilean potatoes, so male sterility came along with it.
Most Andean potatoes and some Chilean and modern potatoes carry a dominant male sterility allele, \textit{Ms}. This gene does not function in Andean potatoes because they have a compatible cytoplasmic genome. The consequence of this gene only appears when a variety that carries the dominant \textit{Ms} allele is used to pollinate Chilean and modern domesticated potatoes and many wild potato species. Most of those types of potatoes carry a cytoplasmic incompatibility and when they also have a dominant allele of \textit{Ms}, they become male sterile. The cytoplasmic genome is always inherited from the female parent, so all the progeny of a variety that carries this cytoplasmic incompatibility will also carry it. Even when starting with modern varieties that are male fertile, crossing with Andean varieties typically produces male sterility. Hanneman (1981) found 19 to 69\% sterile progeny when performing tetraploid tuberosum \times diploid andigenum crosses using six male fertile tuberosum varieties.

It isn’t easy to breed your way out of male sterility, but it is not a completely hopeless situation. You can’t get rid of the cytoplasmic incompatibility because it is always inherited from the mother. You can try to breed for a homozygous recessive (quadruplex) configuration of \textit{ms}. It isn’t easy to breed for a quadruplex configuration in tetraploids, but if you can achieve it, that will eliminate the incompatibility that produces male sterility. In addition, some potatoes carry another gene, \textit{Rf}, that restores fertility in male sterile varieties (Iwanaga 1991b). The problem is that this gene does not appear to be very common and doesn’t always restore full fertility. The amount of viable pollen produced can still be pretty low, although any viable pollen is much better than none. The biggest problem with trying to rely on fertility restoration is that you might not be able to get the \textit{Rf} gene into the varieties that you want to breed without multiple crosses, which may unacceptably dilute the other genes that you want to work with. Neither of these strategies is easy, but if you select unfailingly for male fertility, you can increase the prevalence of these genes in your population over time.

**Most Likely Fertility Results from Crosses Between Potato Populations**

<table>
<thead>
<tr>
<th>Female Parent</th>
<th>Cytoplasm Group</th>
<th>Male Parent</th>
<th>Cytoplasm Group</th>
<th>Likely Outcome</th>
</tr>
</thead>
<tbody>
<tr>
<td>Chilean/Modern Potato</td>
<td>T</td>
<td>Andean Potato</td>
<td>M, A, P</td>
<td>Male sterile, with T type cytoplasm</td>
</tr>
<tr>
<td>Chilean/Modern Potato</td>
<td>T</td>
<td>Chilean/Modern Potato*</td>
<td>T</td>
<td>Male sterile, with T type cytoplasm</td>
</tr>
<tr>
<td>Chilean/Modern Potato</td>
<td>T</td>
<td>Wild Potatoes</td>
<td>W</td>
<td>Male sterile, with T type cytoplasm</td>
</tr>
<tr>
<td>Andean Potato</td>
<td>M, A, P</td>
<td>Andean Potato</td>
<td>M, A, P</td>
<td>Fertile, with M, A, or P type cytoplasm</td>
</tr>
<tr>
<td>Andean Potato</td>
<td>M, A, P</td>
<td>Chilean/Modern Potato*</td>
<td>T</td>
<td>Fertile, with M, A, or P type cytoplasm</td>
</tr>
<tr>
<td>Andean Potato</td>
<td>M, A, P</td>
<td>Wild Potatoes</td>
<td>W</td>
<td>Fertile, with M, A, or P type cytoplasm**</td>
</tr>
<tr>
<td>Wild Potatoes</td>
<td>W</td>
<td>Andean Potato</td>
<td>M, A, P</td>
<td>Male sterile, with W type cytoplasm</td>
</tr>
<tr>
<td>Wild Potatoes</td>
<td>W</td>
<td>Chilean/Modern Potato*</td>
<td>T</td>
<td>Fertile, with W type cytoplasm</td>
</tr>
</tbody>
</table>
* If you can find one that produces viable pollen.
** Fertile progeny are possible, but with about 100 wild species, it is hard to make generalizations. Some species have incompatible cytoplasm.

My solution was more severe. With just a couple of exceptions like Ozette, I have eliminated all male sterile varieties from my breeding pool. This was a painful decision, as it entailed discarding a lot of potatoes that I had selected over many years and really liked. I figure that plant breeding takes a long time and, if you feel like things aren’t going the way you want them to, there is no better time to restart than now. My original breeding strategy was to cross Andean potatoes to modern potatoes, hoping to get some of the flavors, colors, and unusual forms of Andean potatoes along with the better tuberization and disease resistance of modern potatoes. That works, but the problem is that the majority of the progeny will be male sterile or poorly fertile. Trying to plan crosses where few of your varieties produce viable pollen quickly becomes an exercise in frustration. In contrast, when Andean potatoes are used as the parent, fertility is the norm; Ross (1964) found 100% male fertility among 60 diploid andigenum x dihaploid tuberosum hybrids.

Relationships Between Domesticated Potatoes and Some of Their Wild Progenitors

Whether you want to breed modern potatoes or Andean potatoes, it is best to evaluate your varieties and narrow them down to where they are at least mostly male fertile. This will preserve your options for crosses years down the road, whereas male sterility will increasingly box you in. The real trick is when you want to cross between the modern and Andean gene pools. The best option here seems to be always or almost always using the varieties with Andean cytoplasm as the female parents. That means that you need to track your varieties at least well enough to know the female parent of each. Even if you don’t want to do pedigree breeding, you can at least save seed only from varieties with Andean cytoplasm.

There are several different ways that you can determine male fertility in potatoes. The method that is easiest for amateurs is probably just self-pollination. In general, you won’t need to test Andean varieties. While their fertility will vary, none of them are likely to be carrying cytoplasmic male sterility. It is the modern and Chilean potatoes that need to be tested and they are almost all tetraploid. Because they are tetraploid, they will generally be self compatible. So, to test for male fertility, you can bag some flower blossoms just before they open. Once the flowers open, you can flick the bag several times each day to dislodge some of the pollen. (An electric toothbrush is much more effective and you really ought to have one if you are doing potato breeding.) If you get berries, that is usually an indication that the variety has fertile pollen. On rare occasions, you may get parthenocarpic berries from varieties that have defective pollen. A more certain method is to stain the pollen. You just collect some pollen on a microscope slide, stain it with acetocarmine, and then look at the pollen under the microscope. Viable pollen will take up the stain, while non-viable pollen will not. For full instructions, see the CIP Technical Manual of Potato Reproductive and Cytological Biology. In male fertile varieties, the majority of the pollen will be stained and less than 25% stained pollen is probably a good indication that the variety will be difficult to use as a pollen parent. Unfortunately, there is an exception even to this method: some varieties have a high percentage of stainable pollen but are still nearly sterile in practice (Carroll 1975).

As is so often the case with plant breeding, this subject does not easily simplify. The goal of this post has
been to highlight the kinds of crosses that are most likely to yield fully fertile progeny. You can break all the rules in this post and still get some fertile plants. The only question is whether or not the number of such progeny that you obtain will be worth the effort required to produce and identify them.

*For a great overview of male sterility in general, check out Genetics of Male-Sterile Plants at The Biologist is In.*