

Chapter 36

Heterosis in Vegetable Crops

T. C. Wehner

INTRODUCTION

Darwin's (1877) research on maize (*Zea mays* L.) demonstrated that cross fertilization was generally beneficial, and self fertilization was generally injurious. Later, McClure (1892) reported that hybrids made by crossing maize cultivars were generally superior to the midparent. In vegetable crops, some of the earliest research was by Hayes and Jones (1916) who reported hybrid vigor for cucumber (*Cucumis sativus* L.) fruit size and number. There has been much interest in hybrids in many breeding programs, although hybrids have not been exploited commercially as much in self-pollinated as cross-pollinated crops. The literature includes many estimates of hybrid advantage relative to the midparent, the high parent, or to the best standard (inbred or open pollinated) cultivars. The latter is most interesting to those evaluating the commercial potential of heterosis. In this chapter, I will use heterosis to mean hybrid vigor relative to the better parent, or where inbreeding depression is severe, to the comparable open pollinated cultivars.

Heterosis does not occur universally in vegetable crops. In fact, some self-pollinated vegetable crop species do not express any inbreeding depression or heterosis. Although there is heterosis expressed for yield traits in many of the vegetable crops, a primary advantage of hybrid cultivars is the protection they provide for proprietary lines developed by plant breeders, especially those working in seed companies. Commercial plant breeding programs have flourished in the USA through the use of hybrid cultivars to protect proprietary lines. In the future, the advantage offered by hybrids will be reduced because of patents and plant variety protection (PVP), especially as it becomes economical to distinguish among cultivars using molecular markers (DNA fingerprinting). Other advantages of hybrids include the ability to combine useful dominant genes available in different inbreds, optimizing the expression of genes in the heterozygous state, and the production of unique traits such as seedless triploid watermelons [*Citrullus lanatus* (Thunb.) Matsum. & Nakai].

The vegetable crops can be grouped according to how adaptable they are to hybrid production. For purposes of this chapter, I have divided them into self-pollinated crops with few or many seeds produced per cross, and cross-pollinated crops with a low or high rate of natural outcrossing. Important self-pollinated vegetable crops that have been researched extensively include the legumes [bean (*Phaseolus* sp.) and pea (*Pisum sativum* L.)], Solanaceae [eggplant (*Solanum melongena* L.), pepper (*Capsicum nigrum* L.), tomato (*Lycopersicon esculentum* Mill.)], and lettuce (*Lactuca sativa* L.). Important cross-pollinated vegetable crops

include the cucurbits [cucumber, melon (*Cucumis melo* L.), squash (*Cucurbita* sp.), and watermelon], the cole crops [broccoli (*Brassica oleracea* L.), cabbage (*Brassica oleracea* L.), and cauliflower (*Brassica oleracea* L.)], root and bulb crops [carrot (*Daucus carota* L.) and onion (*Allium cepa* L.)], asparagus (*Asparagus officinalis* L.), and spinach (*Spinacia oleracea* L.).

SELF-POLLINATED CROPS

Few Seeds Per Cross

Self-pollinated crops that produce few seeds per cross make it difficult to produce hybrids economically. Vegetable crops such as legumes and lettuce are important in the USA and will be used to represent this group.

Fabaceae (Leguminosae)

Phaseolus vulgaris L. is a hermaphroditic annual used for both green beans and dry beans. It is naturally self pollinated, and produces few seeds per cross. Commercially, 70 kg seeds ha⁻¹ (with 2900 seeds kg⁻¹) are required to plant a dry bean crop. If hybrid seeds were used, it would take 68 000 crosses to plant a 1 ha crop. Flowers must be emasculated before they open, and the work must be done by hand. Thus, it is not economical to produce commercial hybrids, but crossing could be facilitated by the transfer of genes for extrorse stigma from *Phaseolus coccineus* L. (a cross-pollinated species) to *P. vulgaris*; however, there are no reasons to produce hybrids, since little heterosis for yield has been observed.

Like bean, pea is a hermaphroditic annual with little evidence of inbreeding depression. Although Gritton (1975) reported heterosis of 28% over the high parent for dry seed yield, for most traits there is no evidence of heterosis. Since there is no economical method for hybrid production, future cultivars will likely be inbred lines rather than hybrids.

Lettuce is considered a major U.S. crop with 130 000 ha in the USA in 1996, is a hermaphroditic annual, and is another good example of a crop where commercial use of hybrid cultivars is not feasible (Ryder & Waycott, 1993). Many seeds are required for planting (250 000 seeds ha⁻¹), but few are produced from hand pollinations (20 seeds cross⁻¹). The pollen is sticky, and cannot be carried by the wind and no insect pollinators are known. Heterosis is generally not important but may occur for secondary traits such as seedling size (E. Ryder, 1997, personal communication). The use of hybrids for protection of proprietary inbred lines has decreased in importance with the availability of plant variety protection and plant patents and the development of molecular markers.

Many Seeds Per Cross

Many crops in the Solanaceae are self pollinated and are adaptable to hybrid production. Eggplant, pepper, and tomato are examples of successful use of hybrids.

Solanaceae

Heterosis in eggplant is large, with hybrid yield advantage from 33% (Tiwari, 1966) to 97% (Dharme, 1977). Because eggplant flowers are perfect, and normally self pollinate, the natural outcrossing rate is near zero. Since hand pollination is easy and produces many seeds per cross, hybrid production has been commercialized widely. Many hybrid cultivars are now available, with half of the production area in the USA planted to hybrids (Table 36-1).

HETEROSIS IN VEGETABLE CROPS

Table 36-1. Use of hybrids and value of heterosis in 21 vegetable crops for the USA, 1996.

USA, 1996.						
Category	Crop area†	Crop area in hybrids†	Estimated % F ₁ inc. over OPs or inbreds	Amount agric. land saved by heterosis	Additional people fed by heterosis	
Group	ha	%	%	ha	%	
Crop						
Self pollinated, few seeds per cross						
<i>Legumes</i>						
Bean, Green	112 389†	0	0	0	0	
Pea, Green	134 737†	0	0	0	0	
<i>Other</i>						
Lettuce	131 151	0	0	0	0	
Self pollinated, many seeds per cross						
<i>Solanaceous</i>						
Eggplant	4 699	50	65	1 527	32	
Pepper, Hot	47 429	2	35	332	1	
Pepper, Sweet	86 616	36	35	10 914	13	
Tomato, Fresh	85 983	56	19	9 149	11	
Tomato, Proc.	166 235	74	19	23 373	14	
Cross pollinated, low outcrossing rate						
<i>Cucurbits</i>						
Cucumber, Pickle	46 128	100	5	2 306	5	
Cucumber, Slicer	43 638	76	5	1 658	4	
Melon	85 508	90	8	6 157	7	
Squash, Summer	57 655	52	44	13 192	23	
Squash, Winter	9 957	35	40	1 394	14	
Watermelon	126 802	33	10	4 184	3	
Cross pollinated, high outcrossing rate						
<i>Cole crops</i>						
Broccoli	94 480	100	65	61 412	65	
Cabbage	82 575	84	14	9 711	12	
Cauliflower	35 619	33	10	1 175	3	
<i>Root & Bulb</i>						
Carrot	78 462	56	28	12 303	16	
Onion	102 665	65§	40	26 693	26	
<i>Other</i>						
Asparagus	34 858†	90	106	33 254	95	
Spinach	8 908	100	18	1 603	18	
21-crop total or mean		1 576 494	-	27	220 337	18

† From Janick (1998).

‡ From USDA (1992).

§ Northern, USA is planted to 90% hybrids.

Pepper is an annual, self-pollinated crop with a natural outcrossing rate of 25%. Dikil et al. (1973), reported yield heterosis of 28 to 47%, with the higher levels occurring when different ecological groups with different growth patterns were crossed. In a study done in Israel where peppers are grown for export, hybrids had a 9% advantage over inbred cultivars for total yield, but a 75% advantage in export-quality yield (Shifriss & Rylski, 1973). Although cytoplasmic male ste-

rility systems exist, they are not reliable for hybrid production. Thus, commercial hybrids are produced through hand emasculation and hand pollination. In the USA, 36% of the production area of sweet pepper is in hybrid cultivars, but only 2% of the hot pepper is in hybrids (Table 36-1).

Tomato is a hermaphroditic annual (or perennial in the tropics). Heterosis was reported 90 years ago by Hedrick and Booth (1907), and many researchers since then have reported heterosis for yield and earliness. Heterosis has been reported in numerous research articles, and hybrid advantage ranges from 0 to 300% over the best inbreds. In one series of studies (Yordanov, 1983), heterosis averaged about 19%, with 50% for early yield (harvests 1-5) and 4% for late yield (harvests 6-15). East and Hayes (1912) suggested that F_1 hybrids could be made easily and have practical value, but hybrid cultivars have become important only since the 1970s when seed companies needed a way to protect their research investment in inbred lines. Besides heterosis, hybrids permit the combination of traits controlled by dominant alleles present in one or the other parent. Several important dominant genes used for tomato improvement include resistance to fusarium wilt, verticillium wilt, root-knot nematode, tobacco mosaic virus, and tomato spotted wilt virus. Also, performance of some genes, such as ripening inhibitor (*rin*) and non ripening (*nor*), is optimum in the heterozygous state: homozygous recessives produce fruits that have poor flavor and no red color, but heterozygotes become red and flavorful while keeping longer. Griffing (1990) showed that heterosis in a cross of two tomato inbreds (one with few large fruits and one with many small fruits) was not due to mock heterosis (a mathematical phenomenon described by Richey, 1942), but rather to faster growth rate in the hybrid.

The natural outcrossing rate in cultivated tomatoes is 0.5 to 4% in temperate areas (Scott & Angell, 1998), but higher in tropical areas. Insects are the main vector, although wind also is a factor. Most hybrids are produced by hand emasculation and hand pollination; however, it may be possible to produce seeds less expensively using male sterility or exerted stigma genes to increase the number of seeds and reduce the time required per cross. Hand emasculation resulted in 27 to 50 seeds per cross depending on year and location, and took 64 to 120 hours to produce 1 kg of seeds (Oba et al., 1945). In field evaluations, Shakya and Scott (1983) obtained 32 to 92 seeds per pollination with hand emasculation, and 118 to 145 seeds per pollination using a male sterile inbred; however, Scott and Angell (1998) made a case for hand emasculation rather than using male sterility because of the additional time required to convert inbred lines relative to the amount of labor saved. Although hybrid seeds are more expensive than seeds of standard (inbred) cultivars, their improved performance, uniformity, and protection of proprietary lines has made them very popular in the USA. Transplants in Florida cost the grower \$185 ha⁻¹ for hybrid cultivars and \$12 ha⁻¹ for inbred cultivars (Scott & Angell, 1998). However, the cost of hybrid seed was only 2 to 3 % of the total production and marketing cost for the grower (Smith and Taylor, 1993). Currently in the USA, 56% of fresh market and 74% of processing tomato crop area is planted to hybrid cultivars (Table 36-1).

CROSS-POLLINATED CROPS

Low Outcrossing Rate

Cucurbitaceae

Cucumber is an annual outcrosser with monoecious (first staminate, then pistillate flowers) sex expression. Several genes control sex expression to produce gynodioecious (all pistillate flowers), andromonoecious (staminate, then perfect flowers), and hermaphroditic (all perfect flowers) types. No inbreeding depression was found in inbred lines developed from a pickling cucumber population (Rubino &

HETEROSIS IN VEGETABLE CROPS

Wehner, 1986), perhaps because cucumbers are often grown in small groups of plants where there is little outcrossing. Wehner and Jenkins (1985) measured a natural outcrossing rate of 53% (36% between row). Some have reported heterosis from specific hybrid combinations (Ghaderi & Lower, 1979), especially when crossing diverse parents (Hayes & Jones, 1916). However, others have found no heterosis when parents were of similar type (Hayes & Jones, 1916). In a study involving three years, two replications, and eight locations in the USA (Wehner et al., unpublished data), the total once-over harvest yield of the popular gynoecious hybrid 'Calypso' was 60 fruits per plot, while the gynoecious inbred parent Gy 14 had 61 fruits per plot. Where breeders have worked to develop elite hybrids, heterosis may average only a 5% advantage.

Hybrids are produced commercially using a gynoecious inbred as the female parent crossed with a monoecious inbred as the male parent, and honey bees as pollen vectors. Gynoecious inbreds can be developed by self pollination of plants that have been treated with silver nitrate or other ethylene inhibitors (Tolla & Peterson, 1979). One advantage of producing gynoecious by monoecious crosses is that the resulting hybrid will be gynoecious, having pistillate flowers at every node. A monoecious pollenizer must be mixed in with the hybrid if it is not parthenocarpic. Gynoecious cultivars have earlier, and sometimes higher, yield than monoecious cultivars since they have pistillate flowers at every node (Wehner & Miller, 1985).

Melon has no inbreeding depression, but some crosses were reported to express heterosis of 3% for earliness and 8% for yield (Lippert & Legg, 1972). Andromonoecious lines had only 20 to 35% natural outcrossing (Whitaker & Bohn, 1952), so the lack of inbreeding depression might be explained in the same way as for cucumber. Hybrids are produced by hand pollination of emasculated perfect flowers on the female parent using staminate flowers from the male parent. Gynoecious inbreds have been produced, but fruits from pistillate flowers are oval, rather than round like those produced from perfect flowers. Also, gynoecy is controlled by several genes and is complex to work with. The use of cytoplasmic-genic male sterility would reduce hand labor requirements for crossing in hybrid production blocks.

Summer squash (*Cucurbita pepo* L.) has been shown to have heterosis for yield, with 11 to 84% hybrid advantage over open pollinated cultivars in zucchini types and 0 to 82% advantage for yellow types (Elmstrom, 1978). Hybrids are produced by crossing two monoecious inbred lines using honey bees as the pollen vector. One of the inbreds is made gynoecious for the first two to three weeks of flowering by spraying the plants with ethephon at the two and four-leaf stage. Hybrids are used in 52% of the U.S. crop. On the other hand, winter squash (*Cucurbita maxima* Duch and *C. moschata* Duch) is difficult to cross using monoecious inbreds since ethephon does not work well to change sex expression. Heterosis for yield in hybrid cultivars may be 40% higher than for the open pollinated ones, and an increasing proportion of the crop is planted to hybrids (Table 36-1).

Watermelon is a monoecious, annual outcrossing species with little inbreeding depression. Heterosis is expressed for yield in some parental combinations, perhaps averaging 10%; however, the main use of hybrids has been to protect the parental inbreds, and to produce seedless fruits. Seedless hybrids are triploids produced by crossing a tetraploid female parent with a diploid male parent. Tetraploids are produced by doubling the chromosome number of elite diploid inbred lines. A diploid cultivar must be planted in alternating rows with the triploid cultivar to provide the pollen required for fruit set, so seeded watermelons are produced along with the seedless ones.

High Outcrossing Rate

The ideal crops for purposes of hybrid production are those where there is a high rate of natural outcrossing, and methods for economical control of self and cross pollination. The cole crops, root and bulb crops, asparagus, and spinach are good examples.

Brassicaceae (Cruciferae)

Broccoli, cabbage, and cauliflower are hermaphroditic annuals with a high degree of outcrossing enforced by sporophytic self incompatibility. Significant inbreeding depression and heterosis is present. The exception is summer cauliflower (the most recent and modern crop of the species) where there is no inbreeding depression and no self incompatibility. Heterosis of hybrids over open pollinated cultivars may be only 10%. Cabbage hybrids were 12 to 15% better yielding than open pollinated cultivars (Pearson, 1983). In broccoli, hybrid cultivars yielded 40 to 90% better than open pollinated ones (Morelock et al., 1972), but that comparison was not entirely due to heterosis. High rates of natural outcrossing and heterosis in the cole crops has made them ideal for hybrid production, with 84% of cabbage and 100% of broccoli land in hybrid cultivars (Table 36-1). Another significant factor in the adoption of hybrids has been their greater uniformity in yield and quality relative to open pollinated cultivars. Single cross hybrids are produced by crossing two self incompatible inbred lines in an isolation block. Self incompatible inbreds can be self pollinated using bud pollination, since flowers are self compatible before they open. The system permits economical production of hybrid seed, but is "leaky". Occasional self- or sib-pollinations result in seeds of the parental inbreds being sold in the hybrid cultivar. One solution has been to use four-way hybrids (with occasional two-way hybrids mixed in). Cytoplasmic male sterility is being phased in for hybrid production since it is more reliable in protecting the proprietary inbred lines used as parents.

Root and bulb crops

Carrot (*Daucus carota* L.) is a monoecious biennial outcrosser with much inbreeding depression and essentially no naturally self pollination. Heterosis for marketable yield was measured at 25 to 30% over open pollinated cultivars (Bonnet, 1978; Bonnet and Pecaut, 1978). Most cultivars are two- or three-way hybrids and are produced by cytoplasmic male sterility (either the brown anther or petaloid type). Inbreds are difficult to develop because of inbreeding depression, but can be advanced to S_3 to S_6 by alternating each generation of self pollination with open pollination. Hybrids are produced in isolation blocks with eight rows of the female parent alternating with two rows of the male parent. Hybrids are produced on 56% of the carrot land in the USA.

Onion is a hermaphroditic biennial outcrosser. There is significant inbreeding depression, making the development of inbred lines difficult. Heterosis is large, with hybrids 14 to 67% higher yielding than the best open pollinated cultivars (Dowker & Gordon, 1983). Hybrid production was made economical by the discovery of cytoplasmic male sterility by Jones and Emsweller (1936), and a hybrid production method was described by Jones and Clarke (1943). Commercial hybrids are produced by planting 24 rows of the female parent line alternating with two rows of the male parent line. Bees are used to move pollen from the pollen parent to the male sterile parent for seed production. Europe has a lower proportion of hybrids used (15%) than in the USA (56%), perhaps because of the extra effort required to develop hybrids, and the extra legal protection provided to developers of cultivars in Europe (Dowker & Gordon, 1983).

Other crops

Asparagus is a dioecious perennial outcrosser having genetic control of sex expression through the *m* gene. Male (androecious) cultivars have a 38% higher spear yield than female (gynoecious) cultivars because they do not use photosynthate in seed production each year (Franken, 1970). Androecious (all male) hybrids (*Mm*) have been produced by crossing a super male (*MM*) inbred with a female (*mm*) inbred. Super males are developed by self pollination of occasional perfect flowers on male plants, and test crossing the resulting progeny with a female tester to identify individuals having all male progeny. In the USA, super male hybrids now occupy 45% of the production area, with dioecious hybrids occupying another 40 to 50%. Inbreeding depression results from self pollination, with inbreds yielding 45% that of open pollinated cultivars (Ito & Currence, 1965). Heterosis is important, with the best hybrids yielding 64 to 149% more than open pollinated cultivars (Thevenin & Dore, 1976). The hybrid advantage is expressed mainly in the first four years of production. Asparagus requires two to four years to become established, and has a productive life of 10 to 20 years.

Spinach (*Spinacea oleracea* L.) is normally dioecious, but monoecious flowering also exists. It is an annual outcrosser that is wind pollinated, with a natural outcrossing rate of 60% (near 100% in dioecious populations). Although spinach has been described as having sex chromosomes (Dressler, 1958), sex expression is simply controlled by three alleles at one locus (Janick & Stevenson, 1954, 1955), with *XX* gynoecious, *XY* and *X^mY* androecious, *XX^m* monoecious (highly pistillate), and *X^mX^m* monoecious (highly staminate). Inbreeding depression occurs, with a 2 to 6% reduction in yield relative to open pollinated cultivars (Thompson, 1956). Hybrid cultivars outyield open pollinated cultivars by 16 to 20% (Thompson, 1956). Hybrids are produced by planting a monoecious inbred with a high percentage of pistillate flowers (gynoecious inbred) alternating with rows of a monoecious or androecious inbred. The gynoecious inbred is maintained in an isolation block, using the late-appearing staminate flowers for natural self pollination. Hybrid cultivars have been adopted rapidly since their introduction by Jones et al. (1956), occupying 100% of production area in the USA (Table 36-1).

CONCLUSIONS

Benefits of Hybrids

Although many vegetable crops have significant heterosis, some of the major benefits of hybrids relate to other issues. A primary benefit is the protection of parental inbreds used in the production of elite hybrids. This has become more important with increased involvement of private companies in the development of vegetable cultivars. Hybrids can be sold in commerce without making the parental inbred lines available, so the parents are protected under the "trade secrets" provision of the laws of the USA.

A second important benefit of hybrids is uniformity of trait expression among plants of a cultivar. Uniformity was an especially attractive selling point in broccoli and cabbage when they became available as alternatives to open pollinated cultivars. Uniformity of harvest provided earlier and higher yield, and uniformity of the harvested product resulted in higher prices per kg.

Hybrids offer additional advantages for those crops where important traits are controlled by dominant genes. Hybrids make it easier to produce a cultivar with many useful traits by combining dominant alleles from the two parents. A good example is tomato, where single dominant genes control resistance to fusarium wilt, verticillium wilt, root-knot nematode, tobacco mosaic virus, and tomato spotted wilt virus.

There are cases where hybrids may offer additional benefits that are not possible in inbred or open pollinated cultivars. For example, the ripening inhibitor (*rin*) gene in tomato must be in heterozygous condition for it to work partially to allow the fruits to turn red and gain flavor while keeping longer. In homozygous recessive condition, the fruits keep well but stay green and do not develop flavor. Another example of unique traits is the production of seedless triploid watermelons using one tetraploid and one diploid parent. Neither parental inbred has the appropriate chromosome number for seedlessness, but the odd number produced in the triploid hybrid does.

Finally, heterosis may be sufficient by itself to justify the production of hybrids. In spinach, large amounts of heterosis permit higher yielding cultivars to be developed than the open pollinated alternatives. Over the 21 crops summarized here, heterosis averaged 27% improvement for yield of the hybrid cultivars over the inbred or open pollinated ones.

Benefits of Heterosis

The benefit provided to the world by heterosis in the vegetable crops is dependent on the crop. In the case of bean, pea, and lettuce, there has been no effect of heterosis. In other cases, such as tomato, onion, cabbage, and asparagus, there have been significant savings of agricultural land and a large increase in our ability to feed people as a result of heterosis. In the USA, the 21 vegetable crops discussed here occupied 1 576 494 ha of agricultural land, with an average of 63% (not weighted by ha for each crop) of the crop in hybrid cultivars (Table 36-4). Heterosis was estimated to have saved 220 337 ha of agricultural land per year, or to have fed 18% more people without an increase in land use.

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