CURRENT DEVELOPMENTS IN THE BREEDING OF F₁ HYBRID ANNUALS

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There is a small group of companies, about 6 in the U.S. and perhaps 15 worldwide, that have caused a gardening revolution during the last 15 years. The revolution has been dramatic in the U.S. and is now rapidly spreading to the other more developed countries of the world. This revolution is the change by the gardening public from the existing open pollinated varieties is equally great.

ADVANTAGES OF HYBRIDS

Hybrid flowers offer the same advantages over open-pollinated sorts that are found in vegetables and field crops: Those of uniformity and increased vigor resulting in stronger plant growth; more abundant flowering and larger flowers blooming over a longer season; a generally all-around superior garden plant. Also in flowers the hybrid method can result in flower colors, flower types, and habits that are the result of the heterozygous condition for certain genes.

There are a truly amazing contrast between the small-flowered, poor-color, and usually rather weak-growing and loose-habit petunias that were sold before the F₁ hybrids, and the large-flowered, vigorous, compact-habit, very free-flowering, pastel and bright colored modern-habit hybrid petunias. The contrast between an open pollinated snapdragon mixture and vigorous hybrids like the Rockets; and the difference between the new F₁ semi-dwarf African marigolds and the existing open pollinated varieties is equally great.

Today one can purchase F₁ hybrid seed of at least eleven species of annual garden flowers, including Ageratum, Begonia (fibrous rooted), Geranium, Iceland Poppy, Impatiens, Marigold (Tagetes erecta), Pansy, Petunia, Salpiglossis, Snapdragon, and Zinnia. In addition, F₁ hybrid seed of four greenhouse pot plants is available: Calceolaria, Cyclamen, Gloxinia, and Saintpaulia. Fifteen years ago F₁ hybrids were only available in three of these species: Petunia, Begonia, and the greenhouse cut flower Snapdragon.

It is interesting to note that not only has the flower seed industry intensively used this method of breeding, but was one of the first to offer commercial seed of F₁ hybrids with the introduction of Begonia gracilis "Prima Donna" by Ernst Benary in 1909.

Economic as well as horticultural reasons have influenced the rapid and widespread use of F₁ hybrid flowers.

Because of the relatively small amount of seed needed when compared to a vegetable or field crop, hybrids can be hand produced in flowers that would be prohibitively expensive in some other crops. A large proportion of the hybrid seed is sold to professional growers who in turn market plants to the consumer. This system permits a high unit seed cost. Hybrid petunia seed may cost the grower hundreds of dollars per ounce but only represents a small part of his production costs. F₁ hybrid geranium seed was sold this spring for approximately $4 each but this still is economically feasible compared to the alternative of growing plants from cuttings.

The desire to protect one's product has also been a strong contributing factor to the rapid increase in the adoption of the F₁ hybrid method. Having this protection has permitted companies to invest more in their breeding programs, both in facilities and personnel.

RECENT DEVELOPMENTS

Some recent developments both in products and production methods in some of the more important flower crops are:
Petunia: The F₁ hybrid petunia is by far the most important bedding plant in the U.S. today. From 60 to 80% of the dollar volume sales of the seed companies selling to the plant grower trade is hybrid petunia. The double flower forms and the large-flowered or Grandiflora types of petunia are completely dependent upon the hybrid method for production. The double character is dominant to the single form and is essentially female sterile, producing only an occasional functional pistil. The tendency to produce this occasional pistil permits breeding work to proceed, but would be a limiting factor for seed production by open-pollinated means. The F₁ hybrid double-flowered petunias are produced by using a single-flowered line for the seed parent and a homozygous double clone for the pollen parent. The double-flowered lines produce variable amounts of pollen depending upon the individual inbred line, and are maintained by cuttings. Likewise, the popular large-flowered or Grandiflora class of petunias can only be successfully produced by the hybrid method. Like the double character, the Grandiflora flower type is dominant to the small or multiflora flower type. The Grandiflora character is a semi-lethal in the homozygous condition, giving a very weak plant.

The recent work has largely been that of making refinements in characters such as flower color, increased flower size, freedom of bloom, compactness of habit, and earliness to bloom. Hundreds of test crosses are made each year. These are tested in the greenhouse for petunia. At the time a plant grower would sell them and in the field for garden performance. Before a variety is introduced it is tested in trial gardens conducted by seed companies, public parks and universities. The University of Illinois and the Pennsylvania State University have been leaders in this type of testing. Varieties introduced in the last few years are far superior to older F₁ varieties. Botrytis cinerea, a fungal disease, is a serious problem in areas having summer rainfall. A Dutch seed house has made great progress in developing, by selection, varieties resistant to this disease.

Commercial F₁ hybrid Grandiflora petunia seed is produced by crossing multiflora and grandiflora lines, usually using the multiflora line as the seed parent.

The yield is low and has not proven to be useful.

Marigold: F₁ hybrids in the African marigolds (Tagetes erecta) have been available for about 10 years. The first were the Climax varieties. These were of the tall type as are the more recently introduced Gold Coin series. Both offer an abundance of large full-double flowers. The Jubilee varieties have been introduced. They are a semi-tall, hedge-type with excellent large full-double flowers. This season, First Lady, a semi-dwarf clear bright-yellow variety, has been added to the list of F₁ hybrid marigolds.

Very dwarf African marigolds, about a foot tall, have been in the trial gardens the last few years and should be on the market soon. For some time a variety named Red & Gold Hybrids, an F₁ hybrid between Tagetes erecta, the African or American marigold, and Tagetes patula has been available. Recently a great deal of interest has been shown in varieties produced by crossing these species. The most outstanding have been the Nugget varieties. The resulting hybrids are generally similar to T. patula but with many advantages over the French marigold. The flowers are larger, the plants bloom more heavily and over a much longer season. However, the triploid hybrid is rather difficult to make on a commercial scale, and the germination of the seed has been a problem. The result, though, is so outstanding that considerable effort is being expended to solve these problems.

F₁ hybrid marigolds are produced in field plots using alternating rows of seed and pollen lines. Two distinct forms of pollen sterility are used in the seed line. One method is to rogue a population segregating for full double (all ray flowers) and semi-double, leaving only the full double type. The other method is to incorporate a recessive apetalous character into the seed line. The line maintained in commercial hybrid production usually contains about 5% apetalous flowers.

**Fig. 1.** Two forms of male sterility are used to produce F₁ hybrid marigolds: Apetalous flowers (left), and full double-flower heads containing only pistillate ray flowers (right).

**Fig. 2.** F₁ hybrid petunia production in Guatemala. Most hybrid petunia seed is produced by hand emasculation and pollination in areas of the world with abundant and inexpensive labor.
a 50:50 normal to apetalous ratio is rogued to the apetalous type. Neither type of male sterility is without its problems. The full double method is difficult because age and environmental stress can cause plants that had been full double to produce some flowers with disc flowers. Pollination is a problem with the apetalous flower form. Not having petals, it is less attractive to pollinating insects.

Great strides have been made in zinnia with the recent introduction of F1 hybrids. At the present time hybrids are available only in the medium tall habit and cactus-flower form. The hybrid varieties are much superior, with stronger growth, a larger number of larger flowers with better doubling. A number of companies are working hard on zinnia hybrids in dwarf and semi-dwarf habit and other flower forms.

The apetalous character has been the source of pollen sterility, and the production methods are similar to those described for marigold. Pollination has been even more of a problem in zinnia, with some companies applying the pollen from the male part by hand.

Geranium: 1967 and 1968 have seen the most recent species to be offered for sale as an F1 hybrid. The Moreton and Carefree series of single-flowered geraniums have greatly expanded the use of geranium as a bedding plant. Several breeding programs are in progress which would yield important additional advantages in this crop as earlier blooming, larger flowered, dwarfer, and double-flowered forms are introduced.

This has been the beginning—the future promises much more for the gardening public. New crops are being added almost every year, and significant advances made in existing hybrids. There is much to look forward to from the flower seed industry.

UNSTABLE GENE SYSTEMS IN VEGETABLE CROPS AND IMPLICATIONS FOR SELECTION

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The mutation rate in higher plants depends on the gene considered; some change more easily than others. Stadler, as summarized by Srb (34), reported in corn a range from 492 per million gametes to less than one, according to the gene involved; most of them averaged about two per million (2 x 10^-6). In man (34) the rate is about 2 x 10^-5. This speaks well for the stability of the gene replicating system. With present understanding of the replicating mechanism involved -- DNA serving as a template for the RNA synthesis, or collection of the required bases and their arrangement uniquely, usually when the trouble appeared to be species wide. This fragmentary, and in only a few cases have they been studied in detail.

The terms are not restricted to off-types resulting from such series. Meiotic irregularities, characteristic of the Japanese introduction. Jensen (20) emphasizes the rapid degeneration of a variety which has a steady input of variation.

Sorghum:
In sorghum, four recessive cumulative factors condition the dwarf habit. In some varieties that are homozygous for three of these, tall plants spontaneously occur at the rate of about one in 600 (1.6 x 10^-3). (30). These tall plants occur only in varieties of the kafir type; the mild based varieties are stable. There is no decrease in yield, but these tall plants create doubt in the farmer's mind about the purity of the seed and suggests careless seed production. Several approaches toward substituting a more stable allele from the milo types have been suggested, from irradiation to the conventional convergent improvement program. Roguing is not effective.

Maize:
In corn, in spite of intensive study, no unstable rogue plants are found, but instability does occur in color patterns. Emerson (14) in 1919 described the erratic inheritance of variegation in corn kernels. Corn has been used extensively for studying gene mechanisms in several forms of instability and some of the patterns described in it may be useful in understanding what may be involved in the crops we will consider (4, 8, 14, 17, 24, 25, 27, 32).

Lettuce:
Great Lakes and 45 lettuce varieties have been widely accepted. There is a rogue in these varieties that keeps recurring in commercial stock. Unfortunately the variant is easily recognized and thorough roguing will restrict these types in commercial seed to those which occur spontaneously. Originally this rogue occurred only in these two varieties which have "Brite Ice" in their pedigree, but in the development of newer varieties both Great Lakes and 456 have been used, and there are indications that the rogue is appearing in them.

These changes seem to follow a pattern of a change in a gene complex, because the variant acts as a unit and often segregates in a definite pattern. The following examples are less predictable, and other systems are possibly involved.

SOME CROPS WHICH ARE UNSTABLE

Small Grains

Jensen (20) has recently discussed the nature and origin of variation in the grains, the cause of an apparently never ending struggle by grain breeders to keep their stocks at high levels of varietal purity. He distinguishes between variation due to "procedures", largely the result of contamination, and that due to errors in the plant "system", where the variation arises spontaneously as the result of errors in the reproductive process. The plant parts affected in the grains range from height and maturity to seed and chaff color. Cytological studies have demonstrated that aneuploidy or deletions can explain some of these changes in wheat, but in oats, especially those tracing to Avena byzantina (9, 20), the major source seemed to be in tiller differences within a given plant. Similarly in wheat, the new dwarf varieties based on Norin 10 are retaining a high degree of reversion to tall plants, and also show the high percentage of meiotic irregularities characteristic of the Japanese introduction. Jensen (20) emphasizes the rapid degeneration of a variety which has a steady input of variation.

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Tomato

Lewis (22) has described a rogue in tomato that appears only in certain European varieties, not in American. He was not able to establish a homozygous rogue line, which would be characterized by short internodes, smaller leaves and a more freely branching habit.

1Presented at a special session, organized by the ASHS Committee on Vegetable Breeding and Varieties, during the Society's 65th Annual Meeting. It is being published as a part of the Horticultural Plant Breeding Symposium proceedings because of its relevance to the subject.