About Our Cover

On The Emergence of *B* Cultivars in Squash

The names squash and pumpkin are used interchangeably for fruit vegetables that belong to several cultivated species of *Cucurbita*. The species *C. pepo* consists of different groups of edible cultivars and a small group of inedible ornamentals known as yellow-flowered gourds. In 1939, while leafing through L.H. Bailey's *The Garden of Gourds* (1937), I was fascinated by the illustrations of some bicolor gourd fruits. It occurred to me that the biocolor fruit pattern (Fig. 1) might be useful experimentally for studies of polarity in biology. However, the opportunity to initiate such studies did not come until about 10 years later.

Origin of gene *B*

The gourd plant on the cover (top row, left) was grown and photographed in 1948. This plant (pedigreed 168–5) was selected in 'Pear', an ornamental cultivar. As can be seen, plant 168-5 produced both green and bicolor fruits. The bicolor fruits appeared irregularly during plant development and they varied considerably in extent of yellow pigmentation. Furthermore, unlike standard fruits, which turn from green to yellow at different times following anthesis, the onset of yellow pigmentation in bicolor fruits is limited to early bud stages prior to anthesis. This phenomenon is known as precocious fruit pigmentation.

Results of self-reproduction of 168-5 and its offspring for several generations showed that many segregates were unpredictable in their breeding and phenotypic behavior with respect to precocious fruit pigmentation. The unpredictable behavior was due to nuclear instability as well as to phenotypic plasticity. Selection for increase in extent of precocious fruit pigmentation led to the development in 1953 of Precocious Pear, a genetically stable pure line of gourds. The precociously pigmented fruits of this breeding line were completely yellow in one environment and almost completely yellow (i.e., the fruits tended to exhibit green at the very tip of their distal region) in another environment. A study of crosses between standard cultivars and Precocious Pear demonstrated that standard and precocious fruit pigmentation are conditioned by a pair of genes, B^+ and B (for potential bicolor fruit pattern), respectively. It is believed that plant 168–5 carried gene B^w, a weak B, and that B originated from B^w through mutation.

Transfer of *B* from gourd to squash

One of the standard cultivars used in the above crosses was 'Fordhook Zucchini', a vegetable cultivar whose fruits are dark green at early stages of development, gradually turning "black" at maturity. It was evident in 1958 that some *BB* segregates of the cross involving this cultivar produced fruits that were intensely golden externally and internally. Similar segregates were not found in the other crosses. The data suggested that interaction of B and L genes for dark green fruit color (the recessive l genes are for light pigmentation) can markedly increase the level of carotenoids in the flesh, and that a higher level of carotenoids in the flesh would improve the quality of summer squash cultivars, which are extremely low in fruit carotenoids.

Fig. 1. Bicolor fruit pattern of the yellow-flowered gourds.

From 1958 to 1982, we substituted B for B^+ in 13 different genetic backgrounds: in four gourd and nine vegetable cultivars; some of the resulting vegetable lines (*BB*) were used as parents or germplasm for the development of 15 new B cultivars (Table 1). These cultivars represent the major groups of summer and winter squash in *C. pepo*. Five of them are illustrated on the cover. From top, left to right, following the gourd plant, are 'Sunburst' (courtesy of All-America Selections), 'Goldfinger' (courtesy of Asgrow Seed Co.), 'Butterstick' (courtesy of W. Atlee Burpee Co.), 'Jersey Golden Acorn' (courtesy of Hollar & Co.), and 'Autumn Gold' (courtesy of All-America Selections).

Use of gene *B* in breeding

The progress of breeding B cultivars has been slow largely because gene B is often associated with undesirable manifestations.

The phenotypic effects of B can be divided tentatively into two categories: a primary effect and secondary effects. The primary effect is precocious depletion of chlorophyll in fruit; chlorophyll depletion is associated with precocious yellow pigmentation. This effect is manifested in all known genetic backgrounds. In contrast, a secondary effect is manifested in some genetic backgrounds and not in others. Breeding experiments showed that the B effects, both primary and secondary, may be either deleterious, nondeleterious, or beneficial, depending on the combinations or interactions of B and other genetic elements.

One of the deleterious effects of B is abnormal fruit growth, which results in poor seed production. Another deleterious effect is vulnerability of leaf blades early in plant development to precocious depletion of chlorophyll, a defect that tends to depress yield. Fortunately, the known deleterious effects can be eliminated through gene substitutions at loci other than *B*. For example, the

Table 1. List of B cultivars in summer and winter squash of *Cucurbita pepo*.

Cultivar	Awards	Year of introduction	Introduced by
Autumn Gold	AAS	1987	Musser Seed Co.
Blondie	---	1986	Asgrow Seed Co.
Butterstick	---	1987	W. Atlee Burpee Co.
Eldorado	---	1977	Harris Moran Seed Co.
Golden Zucchini	PVP	1973	W. Atlee Burpee Co.
Goldfinger	---	1986	Asgrow Seed Co.
Goldilocks	PVP	1984	Musser Seed Co.
Gold Rush	AAS	1980	PetoSeed Co., Inc.
Goldy	---	1983	ARO, Israel[z]
Jersey Golden Acorn	AAS,PVP	1982	Rutgers Univ.[y]
Multipik	---	1981	Harris Moran Seed Co.
Orangetti	---	1986	ARO, Israel[z]
Sunburst	AAS	1985	Goldsmith Seeds, Inc.[x]
Superpik	---	1987	Harris Moran Seed Co.
Supersett	---	1987	Harris Moran Seed Co.

[z]Agricultural Research Organization. Seed is produced by Hazera, P.O. Box 1565, Israel.
[y]Produced by Hollar & Co., Inc.
[x]Produced by Northrup King & Co.

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vulnerability of leaf blades to precocious chlorophyll depletion early in plant development can be eliminated by substituting *Ses-B* for *Ses-B*$^+$. Gene *Ses-B* selectively suppresses the expression of *B* in leaves but not in fruits.

The idea that interaction of *B* and *L* genes can markedly increase the level of fruit carotenoids (including β-carotene) has been confirmed in both summer and winter squash. However, this interaction is effective only in the absence of pigment-inhibiting genes such as *W*. The *B* and *L* interaction acts as an enhancer system of carotenoid accumulation. A similar enhancer exists in *C. maxima*. The potential increase in fruit carotenoids by the enhancer system varies from less than two to more than 10 orders of magnitude, depending on the *L* genes involved and the initial carotenoid level in the comparable B^+B^+ background. It is generally known that β-carotene is the precursor of vitamin A. In addition, several reports suggest that adequate consumption of carotenoids during human life tends to reduce the incidence of certain types of cancer.

The fruits of some *B* cultivars have firmer texture and improved flavors. There are also suggestions that *B* can enhance female expression and reduce fruit damage caused by CMV and WMV-2. Thus the high marketable yield of 'Multipik', *BB*, is attributed in part to its strong female expression and relative fruit tolerance to these viruses.

Gene *B* is being used in breeding dual-purpose cultivars of increasingly higher fruit quality. The fruits of such cultivars can be harvested at different stages of their growth as summer (early stages) and winter (full maturity) squash. 'Jersey Golden Acorn' represents the first small step in this development.

Finally, gene *B*, in concert with other known genes, can bring about a wide range of variations in fruit color expression, some of which may be of special aesthetic and commercial interest. For example, a combination of golden and green fruits of 'Zucchini' is quite attractive in culinary use. More strikingly colorful would be bicolor 'Zucchini' fruits, one-half golden and one-half green (details on the control of the bicolor fruit pattern will be discussed elsewhere).

Future evolution

The cultivated species of *Cucurbita* harbor valuable genetic resources. Based on these resources, squash may evolve into a major food crop through recombination of genes for efficient habit of growth and reproduction, pest tolerance, and high fruit quality. One of the anticipated products is powdered meal obtained from processing of whole fruits, nutritious flesh and seed combined.

OVED SHIFRISS
Rutgers Univ.
New Brunswick, NJ 08903