

## Inheritance of leaf and fruit characteristics in *Cucurbita maxima* Duch. cv. Queensland Blue × *C. ecuadorensis* Cutler and Whitaker

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### Abstract

Inheritance of cotyledonary pattern of venation, bitterness of petioles and immature fruit, silver mottle on the leaf, hardness of rind and leaf shape (lobing) were investigated in parental, F<sub>1</sub>, F<sub>2</sub> and backcross progeny of *Cucurbita maxima* cv. Queensland Blue × *C. ecuadorensis*. Bitter fruit and silver mottle were inherited as dominant traits as in other *Cucurbita* spp. A dominant gene (Hi) occurred in *C. maxima* and inhibited the development of hard rind. Lobed leaf was controlled by a single dominant gene and linked to bitterness of fruit. Bitterness of the petiole and fruit were also linked. Two genes appeared to control pattern of venation. Petiole bitterness was controlled by more than one gene.

### INTRODUCTION

*Cucurbita ecuadorensis*, a wild South American species, is highly resistant to at least four viruses which infect cultivated pumpkin, *C. maxima* (Provvidenti *et al.* 1978, 1984; Pitrat and De Vaulx 1979; Greber and Herrington 1980). The two species readily hybridise. *C. ecuadorensis* is thus a valuable source of resistance, but the species also exhibits many undesirable characteristics including hard rind (Cutler and Whitaker 1969) and bitter flesh (Metcalf *et al.* 1982). Selection for a desirable trait or to eliminate undesirable traits would be easier if their inheritance was known. Wall and Whitaker (1971) investigated the inheritance of polymorphic enzymes but not other plant characteristics. Our work reports information on the inheritance of some fruit and leaf characteristics in the cross *C. maxima* × *C. ecuadorensis*.

### MATERIALS AND METHODS

Parental, F<sub>1</sub> hybrid and segregating populations were derived by controlled pollination of plants from commercial seed of *C. maxima* cv. Queensland Blue 'Selected Strain' and seed of *C. ecuadorensis*. Parents were inbred for three generations before use and were uniform for the characters investigated. Seed was sown on 22 August 1985 in pots in the glasshouse and transplanted to the field 28 days later. Originally the number of plants of P<sub>1</sub> (*C. maxima*); P<sub>2</sub> (*C. ecuadorensis*); F<sub>1</sub> (*C. maxima* × *C. ecuadorensis*); F<sub>2</sub>; BC<sub>1</sub>P<sub>1</sub> (F<sub>1</sub> × *C. maxima*) and BC<sub>1</sub>P<sub>2</sub> (F<sub>1</sub> × *C. ecuadorensis*) populations were 12, 12, 20, 144, 48 and 48, respectively. Because we wished also to determine the inheritance of resistance to papaya ringspot virus type W (PRV-W) from our population, all plants were inoculated with PRV-W at the cotyledonary stage.

The infection of plants with PRV-W was not expected to affect the results for the characters we studied, except that few fruit would set on P<sub>1</sub>. Prior to field planting the pattern of venation on cotyledons was recorded and in the field, silver mottle on the leaf, fruit and leaf bitterness, leaf shape, and rind hardness were classified as described later.

Segregation patterns of plants in parental,  $F_1$  and segregating populations were fitted to major gene models and goodness of fit tested using a Chi-square test (Srb *et al.* 1965). Associations among characters were investigated using contingency tables. Only the significant ( $P < 0.05$ ) associations are reported. Data on mature fruit characteristics were obtained only from plants with mature fruit, the number of plants being about 4, 20, 86, 35 and 45 for  $P_2$ ,  $F_1$ ,  $F_2$ ,  $BC_1P_1$  and  $BC_1P_2$  populations, respectively. Data on fruit characteristics of  $P_1$ , *C. maxima*, were collected from a separate plant since there was no fruit set on  $P_1$  in the trial area due to viral infection.

### **Venation**

The pattern of venation at the base of expanded cotyledons was classified as similar to *C. maxima* (separated veins) or *C. ecuadorensis* (fused veins) 11 days after sowing.

### **Silver mottle on leaf**

Silver mottle in the axils of veins was considered present if leaves of any age showed this character 75 days after sowing. A general uniform light silvering present over the entire leaf of some plants was considered as a separate character.

### **Bitterness**

Bitterness of petiole of a plant was classified by tasting one (if bitter) or two (if non-bitter or uncertain) petioles at the junction of lamina and petiole of the sixth leaf from the terminal apex 89 to 92 days after sowing. Placental tissue (Jaworski *et al.* 1985) of one or two (if non-bitter or uncertain) immature fruit was similarly classified for bitterness, within five days and in most cases within one day of the flower's opening, 95 or 103 days after sowing. Bitterness of mature fruit was assessed on a sample of 55 fruit about 60 days later. To avoid fatigue (Andeweg and DeBruyn 1959) when assessing bitterness of petiole or fruit, the mouth was rinsed four times between samples, each rinse was with 45 mL of water; only 25 to 50 samples were assessed at each session of 40 to 90 minutes; and there was a break of at least one and usually two hours between tasting sessions.

### **Leaf lobing**

Leaf shape (lobing) was described as a 'lobe index', ( $L$ ), from measurements on the tenth leaf from the terminal apex of each of two branches on each plant;  $L = 2D / (A + B)$  where  $A$  is the distance from leaf base to the tip of the midrib lobe,  $B$  is the distance from leaf base to the tip of next lobe and  $D$  is distance from leaf base to the closest point of the depression between the lobes. Where only one branch was available measurements were made on leaf 10 and 11, 84 to 88 days after sowing. A leaf was lobed when  $L < 0.8$ .

### **Hardness of rind**

Soft rind (skin) of fruit was readily cut by a knife when the fruit was mature. Hard rind was very difficult to cut and was usually 3 mm to 5 mm thick.

## **RESULTS AND DISCUSSION**

Thayer (1934) found the pattern of venation on the blade of cotyledons of *C. pepo* was controlled by more than one gene. In the present study the pattern of venation at the base of cotyledons was similarly not controlled monogenically but was consistent with duplicate dominant epistasis with dominance of the phenotype of *C. maxima* ( $P$  of  $F_2$  Chi-square=0.49). However this needs confirmation with larger populations as there was an apparent deviation from expectation ( $P$  of Chi-square=0.047) in the backcross to the recessive parent.

The segregation pattern, with respect to the presence or absence of silver mottle in the vein axils, among plants in populations derived from *C. maxima* × *C. ecuadorensis* is consistent ( $P$  of  $F_2$  and  $BC_1P_1$  Chi-squares=0.11 and 0.47 respectively) with previous reports in other species of *Cucurbita* spp. Silvering is conferred by a single dominant gene (Robinson *et al.* 1976) although modifiers occur (Shifriss 1982). Leaves of *C. ecuadorensis* have the silver mottle. This character could provide a useful marker to test the extent of cross pollination in attempted hybridisations.

Bitterness of immature fruit was conferred by a single gene with bitterness dominant. This is consistent ( $P$  of  $F_2$  and  $BC_1P_1$  Chi-squares=0.43 and 0.65 respectively) with inheritance of bitterness in *C. pepo* (Robinson *et al.* 1976). By contrast segregation pattern of bitterness of petiole was consistent ( $P$  of Chi-squares=0.81) with bitterness being conferred by recessive complementary epistasis in the  $F_2$  but segregation in the backcross was not consistent. The degree of bitterness differed between plants (data not shown). This aspect requires further investigation.

Bitterness of immature fruit was completely associated with bitterness of mature fruit in the 55 plants assessed. Thus selection for fruit bitterness could be achieved at early flowering. Further, the strong association ( $P$  of Chi-square=<0.01) of bitter petiole and bitter fruit in  $F_2$  and  $BC_1P_1$  populations may allow selective elimination, even before the female flower opens, of more than two thirds of the plants destined to produce bitter fruit.

Hard rind in *C. pepo* and *C. andreana* × *C. maxima* is conferred by a single dominant gene (Robinson *et al.* 1976). By contrast, in the cross *C. maxima* × *C. ecuadorensis* hard rind was recessive to soft rind in the 20 plants of the  $F_1$ . Plants of *C. moschata* × *C. ecuadorensis* have hard rind (M. E. Herrington unpub. data 1983). Therefore we conclude that *C. maxima* cv. Queensland Blue has a dominant gene ( $H_i$  is proposed) which inhibits the expression of hard rind. None of the 35 plants of  $BC_1P_1$  had hard rind but 27 of 45 plants of  $BC_1P_2$  produced hard rind. The lack of fit in the  $F_2$  population where 44 plants produced hard rind, may be due to incomplete expression of  $H_i$ , or linkage of  $H_i$  with sterility (Wall and Whitaker 1971) or some unknown factor which prevented maturation of fruit; only 86 of 144  $F_2$  plants matured fruit. These unknown factors may also have contributed to the association (for  $F_2$ ,  $P$  of Chi-square=0.03) between an absence of silver mottle on the leaf and hard rind. The phenotype of *C. maxima* was lacking.

Table 1. Segregation pattern for lobing\* of leaf in plants of *C. maxima* × *C. ecuadorensis*

|                                  | Numbers of plants |       |           | Expected ratio of Lobed: not lobed | $\chi^2$ | $P$  |
|----------------------------------|-------------------|-------|-----------|------------------------------------|----------|------|
|                                  | Total             | Lobed | Not lobed |                                    |          |      |
| $P_1$ ( <i>C. maxima</i> )       | 11                | 0     | 11        | 0:1                                | n.a.     | n.a. |
| $P_2$ ( <i>C. ecuadorensis</i> ) | 12                | 12    | 0         | 1:0                                | n.a.     | n.a. |
| $F_1$                            | 20                | 20    | 0         | 1:0                                | n.a.     | n.a. |
| $F_2$                            | 141               | 105   | 36        | 3:1                                | 0.02     | 0.88 |
| $BC_1P_1$                        | 47                | 17    | 30        | 1:1                                | 3.6      | 0.06 |
| $BC_1P_2$                        | 48                | 47    | 1†        | 1:0                                | n.a.     | n.a. |

\* Ratio ( $L$ ) of length of depression between lobes: average length of midrib and next lobe. A plant is classed as 'lobed' when  $L < 0.8$ .

† This entry is believed due to a misclassification as under the proposed hypothesis it should not exist.

n.a. = not available.

Lobed leaf (Table 1) was dominant to entire leaf, controlled by a single gene and linked to bitterness of immature fruit (Table 2). By contrast, lobed leaf in *C. maxima* is

controlled by a single recessive gene (Dyutin 1980). This difference indicates more than one genetic system controls leafshape in *Cucurbita* spp.

**Table 2. Association of bitterness of immature fruit and lobed leaf**

| Bitterness of<br>immature fruit | F <sub>2</sub> Leaf lobe* |              | Total |
|---------------------------------|---------------------------|--------------|-------|
|                                 | Lobed                     | Not<br>Lobed |       |
| Not-bitter                      | 10                        | 16           | 26    |
| Bitter                          | 64                        | 31           | 95    |
| Total                           | 74                        | 47           | 127   |

$\chi^2_1 = 7.18; P = 0.01$

\* 1 (Lobed) when  $2D/(A+B) < 0.8$ , and not lobed when  $2D/(A+B) > 0.8$ . Where A is the distance from leaf base to tip of midrib lobe, B is distance from base to tip of next lobe and D is the distance from leaf base to closest point of depression between lobes. P<sub>1</sub> (*C. maxima*) =not-bitter, not lobed and P<sub>2</sub> (*C. ecuadorensis*)=bitter, lobed.

These results indicate that inheritance of some characters in *C. maxima* × *C. ecuadorensis* differs from those reported elsewhere for *Cucurbita* spp. Such information on inheritance should be useful in choosing breeding strategies when it is desired to transfer characteristics from *C. ecuadorensis* into *C. maxima*.

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