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Inheritance of sex forms in watermelon (*Citrullus lanatus*)

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ABSTRACT

Inheritance of sex forms in watermelon (*Citrullus lanatus*) is not well described. In this study, we made five pairs of crosses of watermelon plants with different sex forms and grew progeny in two different seasons to investigate the inheritance of sex forms and the seasonal effect on sex expression. We showed that environmental factors have no effect on sex forms, but they affect sex expression on individual flowers as more pistillate flowers were observed in spring than in autumn. This suggests that short photoperiod and low temperatures promote formation of pistillate flowers in watermelon. In the F_2 population of the cross of andromonoecious (SL3H or AKKZW) × monoecious (XHB), the segregation ratio is 9 monoecious: 3 trimonoecious: 4 andromonoecious, and the segregation ratio in BC_1P_1 (F_1 × andromonoecious parent) is 1 monoecious: 1 trimonoecious: 2 andromonoecious. The segregation ratio in the F_2 population of the gynoecious (XHBGM) × monoecious (XHB) is 3 monoecious: 1 gynoecious whereas the segregation ratio in the BC_1P_1 (F_1 × gynoecious parent) is 1 monoecious: 1 gynoecious. The segregation ratio in the F_2 population of gynoecious × andromonecious cross is 27 monoecious: 12 andromonoecious: 9 gynoecious: 9 trimonoecious: 4 hermaphroditic: 3 gynomonoecious. The segregation ratio in the BC_1P_1 population (F_1 × gynoecious) is 1 monoecious: 1 gynoecious whereas the segregation ratio in the BC_1P_2 (F_1 × andromonoecious) is 1 monoecious: 1 trimonoecious: 2 andromonoecious. Taken together, the results suggested that three recessive alleles, *andromonoecious* (*a*), *gynoecious* (*gy*) and *trimonoecious* (*tm*) control the sex forms in watermelon, and *a* allele is epistatic to the *tm* allele. The following phenotype-genotype relationships are proposed for each of the sex forms in watermelon: monoecious, *A_Gy_Tm_*; trimonoecious, *A_Gy_tmtm*; andromonoecious, *aaGy_Tm_* or *aaGy_tmtm;* gynoecious, *A_gygyTm_*; gynomonoecious, *A_gygytmtm*; and hermaphroditic, *aagygyTm_* or *aagygytmtm*.

1. Introduction

Three types of flowers, staminate, pistillate and hermaphroditic were found in angiosperms (Lewis, 1942). The sex form of a plant is the result of the presence/absence and distribution pattern of these three types of flowers on an individual plant (Dellaporta and Calderon-Urrea, 1993; Tanurdzic and Banks, 2004). In Cucurbitaceae, andromonoecism is the predominant sex form in cultivated melon, producing separate perfect (hermaphroditic) and staminate flowers in one plant. Monoecism is the predominant sex form in cultivated cucumber and watermelon, producing separate pistillate and staminate flowers in one plant. In watermelon, trimonoecy which produces all of the three types of flowers, i.e., staminate, pistillate and hermaphroditic flowers in one plant has been occasionally observed (Rosa, 1928). But unlike cucumber and melon, gynoecious watermelon has not been found until 2007 when Jiang and Lin discovered a natural gynoecious mutant in China and studied the genetic basis of gynoecism. Still, the genetic relationship of andromonoecism and gynoecism has not been described well in watermelon. A better understanding of the inheritance of sex form in watermelon would help us to develop gynoecious cultivars and to ultimately uncover the molecular mechanism underpinning sex determination in watermelon.

Inheritance of sex forms has been clearly described in major Cucurbitaceae crops including cucumber and melon. Rosa (1928) has stated that andromonoecism is a recessive character, and monoecism is a dominant character. Furthermore, through the

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1960s, great improvements were made in unveiling the cucumber sex determination mechanism. Briefly, there are three genes, the *female* (*F*) gene, the *male* (*m*) gene and the *androecious* (*a*) gene that control the sex form in cucumber (Kubicki, 1969a,b,c,d). Moreover, the inheritance of sex form in melon has been well described (Poole and Grimball, 1939; Kenigsbuch and Cohen, 1987, 1990). These authors have shown that the sex form in melon is controlled by three genes, *g* (*gynoecious*), *a* (*andromonecious*) and *m* (*male*). The *m* gene controls the presence of trimonoecy and gynomonoecy.

Unlike cucumber and melon, the sex determination mechanism in watermelon is not clear. The andromonoecious sex form has been reported a long time ago, and the monoecy is dominant to andromonoecy (Rosa, 1928). In addition, Porter (1937) has supported this result on his research. Furthermore, Poole and Grimball (1944) have described the correlation between fruit shape and hermaphroditic flowers, and also supported that andromonoecism is a recessive character. However, until now, little progress has been made in the research on inheritance of sex form in watermelon. One of the challenges in studying sex inheritance in watermelon is that besides the genetic elements, environmental conditions and hormone levels also influence sex expression in watermelon (Rudich and Peles, 1976; Rudich and Zamski, 1985; Salman-Minkov et al., 2008; Manzano et al., 2014).

The objective of this study is to study the genetic control of sex forms in watermelon by using crosses of gynoecious line with monoecious or andromonoecious line, and also by using crosses of andromonoecious line with monoecious line. We expect this study would facilitate the development of elite gynoecious lines that will be useful for producing F_1 hybrids economically, thus revolutionizing watermelon hybrid seed production. Furthermore, it will lay the groundwork for research aimed at discovering the molecular mechanism that controls sex expression in watermelon.

2. Materials and methods

2.1. Germplasm

Four cultivars of *Citrullus lanatus* var. *lanatus*, SL3H, AKKZW, XHB and XHBGM were used in this study. SL3H is an andromonoecious line, producing separate staminate and hermaphroditic flowers on the same plant. SL3H produces dark green and round fruits with pink flesh and large white seeds. The ratio of hermaphroditic flowers to staminate flowers is about 1:7. AKKZW, another andromonecious line used in this study produces pale green and oval fruits with plum flesh and large black seeds. The ratio of hermaphroditic flowers to staminate flowers is about 1:6 in AKKZW. XHB, a monoecious line, producing separate staminate and pistillate flowers on one plant, has small, pale green and round fruit with red flesh and small black seeds. The ratio of pistillate flowers to staminate flowers is about 1:4 in XHB. XHBGM, a gynoecious line derived from a natural mutant from XHB, develops the first pistillate flower in the first node and continues to develop normal pistillate flowers at each node until nodes 25–30 from which staminate flowers develop occasionally. The phenotype of the XHBGM plants is otherwise the same as XHB except for the sex form. All cultivars were obtained from China National Engineering Research Center for Vegetables (NERCV), Beijing, China.

2.2. Crosses

Plants used for crossing were grown in plastic greenhouses at NERCV. Five crossing groups were used to study the inheritance of sex form of a plant and sex expression of individual flowers in watermelon (Table 1). The andromonoecious parent, SL3H or AKKZW was crossed with either the monoecious XHB or the gynoecious XHBGM. The gynoecious XHBGM was also crossed with the monoecious XHB, its progenitor. The flowering patterns in F_1, F_2, BC_1P_1 and BC_1P_2 generations of each cross were carefully examined, either in the field (Spring from March to July) or in the greenhouse (Autumn from June to October).

Table 1
The crossing groups, parents and their sex forms.

Hybridizing group	Maternal parent (sex form)	Pollen parent(sex form)
Group 1	SL3H(andro)	XHB(mono)
Group 2	AKKZW(andro)	XHB(mono)
Group 3	XHBGM(gyno)	XHB(mono)
Group 4	XHBGM(gyno)	SL3H(andro)
Group 5	XHBGM(gyno)	AKKZW(andro)

Note: andro, andromonoecious; mono, monoecious; gyno, gynoecious.

Table 2
Sex form, putative genotype and flowering pattern in *Citrullus lanatus*.

Phenotype	Putative genotype	Flowering pattern
Monoecious	*A_Gy_Tm_*	♂,♀
Andromonoecious	*aaGy_Tm_* or *aaGy_tmtm*	♂, ⚥
Gynoecious	*A_gygyTm_*	♀
Trimonoecious	*A_Gy_tmtm*	♂,♀,⚥
Hermaphrodite	*aagygyTm_* or *aagygytmtm*	⚥
Gynomonoecious	*A_gygytmtm*	♀⚥

Note: The following symbols are assigned to flower types: ♂, staminate flower; ♀: pistillate flower; ⚥ : hermaphroditic flower.

2.3. Identification of the sex forms

Flowers were examined daily for 3 months. The sex of flowers in the first 30 nodes of all plants was recorded during the growing period. Plants were then classified into the following six sex forms (Table 2):

(1) Monoecious: In monoecious plants, both staminate and pistillate flowers are observed in the first 30 nodes, although hermaphroditic flowers and abnormal flowers may be observed after the 30th node.XHB, one of the parents used in crosses 1–3 is a typical monoecious plant and its flowering phenotype is very stable in spring and autumn.
(2) Andromonoecious: In andromonoecious plants, only staminate flowers and hermaphroditic flowers, but not pistillate flowers are observed in the first 30 nodes. AKKZW and SL3H, two parents used in crosses 1, 2, 4 and 5 are typical andromonoecious plants and their flowering phenotypes are stable in spring and autumn.
(3) Gynoecious: In gynoecious plants, at least 95% of the flowers are pistillate in the first 30 nodes. XHBGM, a parent used in crosses 3–5 is a gynoecious plant.
(4) Hermaphrodite: Hermaphrodite is defined if at least 95% of flowers are hermaphroditic flowers in the first 30 nodes.
(5) Gynomonoecious: If pistillate flowers and hermaphroditic flowers make up 95% or more of the total flowers in the first 30 nodes of a plant, the plant is defined as gynomonoecious.
(6) Trimonoecious: Plants with pistillate flowers, staminate flowers and hermaphroditic flowers in the first 30 nodes are defined as trimonoecious.

In this study, flowers producing fertile pollen and having an ovary are defined as hermaphroditic flowers, and the other flowers which have an ovary with or without non-functional stamens are defined as pistillate flowers. Sex form was assigned to each plant after the flowering pattern of each plant was determined.