

Natural Outcrossing in Watermelon - A Review

Rakesh Kumar and Todd C. Wehner

Department of Horticultural Science, North Carolina State University, Raleigh, NC 27695-7609

Watermelon [*Citrullus lanatus* (Thunb.) Matsum. & Nakai var. *lanatus*] belongs to the family *Cucurbitaceae* and subtribe *Benincasinae* (24). Other members of the *Cucurbitaceae* are cucumber, melon, pumpkin, and gourd. The genus *Citrullus* has been divided taxonomically into four species: *C. lanatus* (Syn. *C. vulgaris*), *C. ecirrhosus*, *C. colocynthis*, and *C. rehmii*. Diploid watermelon has 22 chromosomes ($2n=22$, $x=11$) with a genome size of 420 million base pairs (9, 18). It is native to southern Africa, mainly the Kalahari Desert area (2). The secondary center of origin is China. Watermelon can be found growing wild in various parts of western hemisphere, particularly in India (13) and in the Mediterranean region, including Iran and Egypt.

The way plants reproduce depends on their sex expression. This is important in cucurbits because of their different types of sex expression, such as monoecious (staminate and pistillate flowers on the same plant) and andromonoecious (staminate and perfect flowers on same plant) (17). Sex expression in cucurbits besides being genetically controlled is also highly affected by environment (temperature, humidity, light, and nutrition). A single pair of alleles determines sex expression in watermelon. The andromonoecious gene *a* controls monoecious (*AA*) vs. andromonoecious (*aa*) sex expression (9, 14, 15). Watermelon is considered allogamous because both andromonoecious and monoecious sex forms promote cross-pollination. However, both sex forms show varying degrees of self-pollination. The andromonoecious sex form promotes autogamy because of the presence of hermaphroditic flowers, whereas the monoecious sex form promotes allogamy. Allard (1) reported that domesticated cucurbits are more autogamous than allogamous because they originated populations consisting of only a few individuals during domestication. Furthermore, because of their vining growth habit, outcrossing among related individuals may be common, increasing the level of inbreeding, and leading to the purging of deleterious recessive genes. That, in turn, may explain the lack of inbreeding depression in watermelon.

Estimation of natural outcrossing rate is useful for plant breeders especially when experiments are run to estimate components of genetic variance. The genetic structure of plant populations is determined in part by the rate of natural outcrossing. However, consideration of the rate of self-pollination is also important to calcu-

late precise estimates of genetic variances and heritability. In general, individuals within a family in allogamous (cross-pollinated) crops are assumed to be half-sibs, but that is not necessarily the case if self-pollination occurs. As a result of inbreeding, coancestry among half-sibs will be greater than expected (5). Due to self-pollination, variability within families decreases and variability among families increases. The breeding methods applied to self-pollinated crops are distinct from that for cross-pollinated crops. Common methods for crop improvement employed in watermelon are: pedigree breeding and recurrent selection (23). If the natural outcrossing rate is found to be high, watermelon populations can be improved by intercrossing selected families in isolation blocks by recurrent selection. Intercrossing can play an important role in genetic gain.

The factors that influence the rate of natural outcrossing in watermelon are insect pollinators, plant spacing, genotype (cultivar), and climatic conditions. Cross-pollination in watermelon is mediated by honeybees (*Apis mellifera* L.) and bumblebees (*Bombus impatiens* Cresson) that visit the flower to collect pollen and nectar (4, 7, 12). Although >85% of watermelon pollinators are honey bees, bumble bees have been reported to be a better pollinator than honey bees in watermelon (21). Most of the pollen is removed in 2 hours after anthesis in watermelon (20) by pollinators. Gingras et al. (8) suggested that a single visit is enough to induce fruiting. The movement of insect pollinators in a field is strongly directional, with pollinators moving to the nearest neighboring flowers within the same row (3, 10, 22, 26). In addition to insect pollinators, the outcrossing rate is also reported to be influenced by staminate flower and pollen production as affected by the genotype and environment. Pollen movement was restricted to 3 m from the donor plant in muskmelon (10) and 2 to 3 m in cucumber (11). Stanghellini and Schultheis (19) reported variability in pollen grain production in 27 watermelon cultivars.

In watermelon, the rate of natural outcrossing (measured between-row only) was near zero for rows separated by 6 m or more (16) and averaged 0.8% for rows 3 to 6 m apart. Walters and Schultheis (23) recorded an outcrossing rate near to zero in plants spaced more than 10 m apart. Ferreira et al. (5) reported an outcrossing rate of 65% and inbreeding coefficient as high as 0.41 in andromonoecious families of watermelon. When aver-

aged over monoecious and andromonoecious families, the outcrossing rate was 77% (5, 6). However, these authors did not report the plant spacing adopted in the experiment. The rate of natural outcrossing has been measured for cucumber families planted in isolation blocks. Wehner and Jenkins (24) reported that natural outcrossing rate (mean and range over replications) was 36% (29-43%) cross-, 17% (0-42%) sib-, and 47% (23-77%) self-pollination. Thus, 64% of pollinations were self- or sib-, but not crosspollination among families. Watermelon was expected to have a mixed mating system since it is similar to cucumber in plant growth and sex expression. Moreover, there was no significant inbreeding depression in watermelon (23), indicating a high rate of self-pollination in the species. Self-pollination can occur in both monoecious and andromonoecious populations (6). Allard (1) suggested that cucurbits evolved as small populations in nature, thus having high levels of inbreeding.

Watermelon breeders often calculate estimates of genetic variance and covariance among family members (e.g. half-sibs) in their populations. Estimates are often miscalculated if the mating system is not well studied. The coancestry of individuals is higher when parents are spaced widely, due to an increase in self-pollination. Genetic variance may be calculated as: $\hat{\sigma}_G^2 = (1+F)\hat{\sigma}_A^2 + (1-F)\hat{\sigma}_D^2 + 4FD_1 + 4FD_2 + F(1-F)H$, where $\hat{\sigma}_G^2$ is genetic variance (25). F , $\hat{\sigma}_A^2$, $\hat{\sigma}_D^2$, D_1 , D_2 , and H are inbreeding coefficient, additive variance, dominance variance, covariance between additive and homozygous variance effects, variance of homozygous dominance effects, and measure of inbreeding depression, respectively.

Further studies are needed to measure the amount of self- and cross-pollination in watermelons at different plant spacings. If the rate of self-pollination is high in widely-spaced plants, it would be possible to use open pollination for the initial generations of selection during the development of lines without the expense of controlled pollination.

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