

Challenges Faced by Day-neutral Strawberry Breeders in the Continental Climates of the Eastern United States and Canada

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Day-neutral strawberry cultivars of *Fragaria × ananassa* Duch. ex Rozier now play a dominant role in the Mediterranean climate of California, but day-neutrals have had little commercial success in the continental climates of the eastern United States and Canada. It has been over 30 years since a new day-neutral cultivar has been released outside of California, although a number of breeding programs have sought new day-neutral (DN) types (Dale et al., 2000; Galletta et al., 1981). Several factors have limited the development of day-neutral cultivars for the east, including: 1) uncertainty about the genetics of the day-neutral trait; 2) genotype × environment interactions related to temperature; and 3) a narrow germplasm base. In this article, we discuss these limitations and suggest a potential shift in breeding focus.

UNCERTAINTY ABOUT THE GENETICS

Several different models have been proposed on the genetics of day-neutrality, including: 1) regulation by a single dominant gene (Ahmadi et al., 1990; Bringhurst and Voth, 1978; Sugimoto et al., 2005); 2) regulation by dominant complementary genes (Ourecky and Slate, 1967); and 3) quantitative inheritance (Hancock et al., 2001; Powers, 1954; Serçe and Hancock, 2005). The usefulness of simple backcrossing strategies to develop day-neutral cultivars is dependent on the genetics of the trait being monogenic. Based on the most recent research, it appears likely that at least one strong quantitative trait loci (QTL) is regulating day-neutrality (Shaw and Famula, 2005); however, numerous other QTL with varying additive effects influence the trait (Weebadde et al., 2008). This suggests that quantitative approaches to genetic improvement will need to be undertaken.

Part of the reason why the previous studies have generated such different hypotheses is that they used different sources of day-neutrality and were undertaken in different environments. The studies of Bringhurst and Voth (1978) and Ahmadi et al. (1990) were

done in California using parents carrying day-neutral gene(s) from a Wasatch Mountain genotype of *F. virginiana* Mill. subsp. *glauca* (S. Watson) Staudt. The studies of Powers (1954) and Hancock et al. (2001) were done in Wyoming and Michigan, respectively, using day-neutral parents that carried genes from *F. × ananassa* and wild clones of *F. virginiana* Mill. that were different from the Wasatch source. The study of Ourecky and Slate (1967) was performed in New York using parental material that did not contain any recently incorporated *F. virginiana* germplasm.

GENOTYPE × ENVIRONMENT INTERACTIONS

The expression of day-neutrality has been shown to vary greatly in different environments, which complicates the development of widely adapted day-neutral types. Hancock et al. (2001) observed a significant difference in the expression of day-neutrality across locations when they crossed short-day and day-neutral representatives of native *F. virginiana* with short-day and day-neutral *F. × ananassa* cultivars and evaluated the progeny in Michigan, Minnesota, and Ontario. The average percentage of day-neutral progeny ranged from 26% in Michigan to 44% in Ontario. In the same segregating population of 'Honeoye' × 'Tribute', Weebadde et al. (2008) found the proportion of day-neutral plants to be ≈50% in Maryland, Michigan, and Minnesota, whereas percentages were over 80% in California and Oregon.

This environmentally induced variation in the percentage of day-neutral progeny could relate to temperature, although this possibility has not been rigorously tested. Eastern breeders must contend with summer temperatures that are often high enough to inhibit flower bud formation. Flower bud formation has been shown to be generally limited by temperatures exceeding 28 °C, which are not unusual midsummer temperatures in continental climates (Darrow, 1966; Durner et al., 1984; Serçe and Hancock, 2005). Eastern breeders may need to identify and incorporate two types of genes to generate commercial DN cultivars, those associated with photoin sensitivity and those providing heat tolerance.

In the study by Weebadde et al. (2008), a strong QTL for day-neutrality was identified

on linkage group 17 in Maryland, Michigan, and Minnesota that was not found in Oregon or California. We speculate that this QTL may be required for floral initiation under the hot summer conditions found in eastern continental climates. In the cooler western states, this gene may not play a role in regulating day-neutrality, because temperatures are too mild to need its expression for the trait.

LIMITED SOURCE OF THE DAY-NEUTRAL TRAIT

Eastern breeders have used the same source of day-neutrality that was used in California by Bringhurst and Voth (1978). The gene(s) for day-neutrality entered the eastern breeding material through an advanced selection, Cal. 65.65-601. Thus, the eastern breeders of day-neutrals began with germplasm that was much better adapted to Mediterranean than Continental climates.

Efforts have been made only recently to incorporate new sources of day-neutrality from native strawberries that might be more closely adapted to continental climates (Dale et al., 2000). In a number of recent germplasm surveys in Continental climates, several elite day-neutral clones of *F. virginiana* have been selected for their horticultural characteristics, including *F. virginiana* ssp. *glauca* from Utah (LH 50-1; PI 612491) and *F. virginiana* ssp. *virginiana* from Alberta (N 8688; PI 612496), Ontario (Frederick 9; PI 612493), New York (RH 30; PI 612499), and Minnesota (RH 23; 612498) (Hancock et al., 2001; Serçe and Hancock, 2005; Hancock et al., 2002). These should be useful as breeding parents, because they may contain a wide array of genes determining day-neutrality and have trialed well in eastern conditions.

CONCLUSIONS

Eastern breeders have had to contend with ambiguous genetics, strong genotype × environment interactions and a limited germplasm base in their efforts to develop new day-neutral cultivars. The dramatic differences in the inheritance patterns of day-neutrality found in previous studies is likely the result of variation in the test environments and the specific QTL carried by the parents.

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The test environment is particularly critical, because very different levels of expression have been observed across test locations.

There is likely a major QTL that determines day-neutrality, but there are also a wide array of genes determining day-neutrality that have differing strength. One or more of these genes could be associated with heat tolerance, whereas others may be associated with variations in rates of floral development, rest period requirements, and patterns of vegetative growth. It is suggested that eastern breeders continue to broaden their germ-plasm base to incorporate more native, well-adapted genes into their day-neutral breeding programs.

Eastern breeders may also want to shift their focus from developing day-neutral types that produce multiple crops throughout the season to generating day-neutrals that produce a single crop later in the summer when short-day genotypes will not work. It should be easier to breed new day-neutral types that perform well across a few months of the growing season than over the whole summer. The day-neutrals could be planted a few months before the desired harvest date as is done in California with their day-neutral cultivars. These genotypes would still have to

contend with midsummer heat, but we wonder if part of the poor performance of our current day-neutral cultivars in midsummer has more to do with the lingering physiological strain of the spring crop rather than summer heat per se.

Literature Cited

- Ahmadi, H., R.S. Bringham, and V. Voth. 1990. Modes of inheritance of photoperiodism in *Fragaria*. J. Amer. Soc. Hort. Sci. 115:146–152.
- Bringham, R.S. and V. Voth. 1978. Origin and evolutionary potentiality of the day-neutral trait in octoploid *Fragaria*. Genetics 90:510 (abstr.).
- Dale, A., J.J. Luby, and J.F. Hancock. 2000. Breeding day-neutral strawberries for northern North America. Acta Hort. 567:133–136.
- Darrow, G. 1966. Interaction of temperature and photoperiodism in the production fruit buds and runners in strawberries. Proc. Amer. Hort. Soc. 34:360–363.
- Durner, E.F., J.E. Barden, D.G. Himelrick, and E.B. Poling. 1984. Photoperiod and temperature effects on flower and runner development in day-neutral, Junebearing and everbearing strawberries. J. Amer. Soc. Hort. Sci. 109: 396–400.
- Galletta, G.J., A.D. Draper, and H.J. Swartz. 1981. New everbearing strawberries. HortScience 16:726.
- Hancock, J.F., J.J. Luby, A. Dale, P.W. Callow, S. Serge, and A. El-Shiek. 2001. Utilizing wild *Fragaria virginiana* in strawberry cultivar development: Inheritance of photoperiod sensitivity, fruit size, gender, female fertility and disease resistance. Euphytica 126:177–184.
- Ourecky, D.K. and G.L. Slate. 1967. Behavior of the everbearing characteristics in strawberries. J. Amer. Soc. Hort. Sci. 91:236–241.
- Powers, L. 1954. Inheritance of period of blooming in progenies of strawberries. Proc. Amer. Soc. Hort. Sci. 64:293–298.
- Serge, S. and J.F. Hancock. 2005. Inheritance of day-neutrality in octoploid species of *Fragaria*. J. Amer. Soc. Hort. Sci. 130:580–584.
- Shaw, D.V. and T.R. Famula. 2005. Complex segregation analysis of day-neutrality in domestic strawberry (*Fragaria ×ananassa* Duch.). Euphytica 145:331–338.
- Sugimoto, T., K. Tamaki, Y. Matsumoto, K. Shiwaku, and K. Watanabe. 2005. Detection of RAPD markers linked to the everbearing gene in Japanese cultivated strawberry. Plant Breed. 124:498–501.
- Weebadde, C.K., D. Wang, C.E. Finn, K.S. Lewers, J.J. Luby, J. Bushakra, T.M. Sjulín, and J.F. Hancock. 2008. Using a linkage mapping approach to identify QTL for day-neutrality in the octoploid strawberry (*Fragaria ×ananassa* Duch ex Rozier). Plant Breed. 127:94–101.