Nectar Production of Cranberries: Genotypic Differences and Insensitivity to Soil Fertility

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ABSTRACT. Cranberry flowers (*Vaccinium macrocarpon* Ait.) require bee visitation for pollination. Bees visit cranberry flowers for nectar and sometimes pollen, but honey bees (*Apis mellifera* L.) in particular often work alternative co-flowering species for nectar, presumably because cranberry offers inferior nectar rewards. In a common garden setting, replicated plots of the cultivar Stevens were found to secrete significantly more nectar sugar (25% to 35% more) per flower than either 'Ben Lear' or 'Early Black', two other common commercial cultivars. The nectar secretion rate of 'Stevens' was unaffected by a 4-fold range of fertilizer application rates over the preceding 2 years. These results are compared to studies of other crops involving varietal differences and programs of selective breeding for nectar secretion.

Cranberries growing in managed or constructed bogs are reputedly weak competitors for the attentions of pollinating honey bees (Farrar and Bain, 1946; Kevan et al., 1983; Marucci, 1967). Although cranberries in such managed bogs produce a prodigious bloom (up to 50 to 80 million flowers/ha) (Eck, 1986; Farrar and Bain, 1946), individual flowers secrete a reportedly paltry quantity of nectar (Roberts, 1979). Individual flowers produce ample quantities of pollen, however [7000 pollen tetrads for 'Early Black' (Cane et al., 1996)], which is avidly harvested by a number of oligolectic as well as polylectic bee species that visit cranberries (Cane et al., 1996; Kevan et al., 1983; MacKenzie, 1994; MacKenzie and Averill, 1995). However, few honey bee foragers avail themselves of this resource (Cane et al., 1993; Farrar and Bain, 1946; MacKenzie, 1994), perhaps because they find the flower's poricidally dehiscent anthers difficult to manipulate (Cane et al., 1993). Hence, nectar is the floral reward of cranberries, whose enhancement is more likely to encourage the taxonomic fidelity of foraging honey bees.

In this study, we compare the total secreted nectar for individual flowers of several popular cranberry cultivars grown together in a common cranberry bog. In addition, we assess the effect that different fertilizer application rates have on nectar secretion in one cultivar.

Materials and Methods

Cranberry nectar production was studied during June 1995 on Bog 17 at Rutgers Univ. Blueberry/Cranberry Research Center near Chatsworth, N.J. The microclimate on this bog was monitored by a semipermanent automatic weather station. Three of the ten available cultivars on Bog 17 were used: 'Ben Lear', 'Early Black',

and 'Stevens'. Each cultivar was planted in four 3 × 10.5-m, 10-year-old replicate plots, one plot in each of the four randomized rows of plots that constituted Bog 17. These three commonly planted cultivars, like most traditional cranberry cultivars, are merely selections from wild clones that were first propagated vegetatively in the 19th century (Luby et al., 1991).

For the preceding 2 years, each rectangular plot had been subdivided into three 3 × 3.5-m subplots for soil fertility manipulations (J.R. Davenport, unpublished data). The minimum fertilizer treatment annually received was (in kg·ha⁻¹) 16.8N–36P–45K, divided among three seasonal application dates. These application rates were doubled or quadrupled for the moderate and high fertility plots, respectively. Only 'Stevens' was compared across all three fertilizer treatments. Differences between cultivars were compared for subplots receiving the moderate fertilizer treatments, as these correspond to the normal fertilization rates used on commercial New Jersey cranberry beds.

Nectar was removed from virgin flowers of equal age to measure total nectar accumulation. Each morning, beginning on 19 June 1995 (near the very end of the blooming season), equal numbers of each cultivar's upright terminals that still possessed flower buds were bagged in no-see-um netting. Each new flower was then marked on its morning of anthesis, and 72 h later its nectar was withdrawn using a 1-μL capillary micropipette. Only flowers with exerted styles were used to assure equivalent developmental stages. Volume was calculated from the length of the column of nectar in the pipette, measured to the nearest millimeter with calipers. The concentration of dissolved solids (sugars) was measured using a hand-held refractometer modified for small volumes (Bellingham and Stanley Ltd., Tunbridge Wells, U.K.). Total sugar was then calculated for each flower's accumulated nectar (Bolten et al., 1979).

Total nectar sugar per marked flower was statistically compared for the three cultivars and for the three fertilizer treatments using two separate general linear models ANOVAs. When treatment or cultivar differences were significant ($P \leq 0.05$), Tukey's test was used to contrast all pairs of comparisons between fertilizer treatments or cultivars (SAS Institute, Cary, N.C.). Means are given ± 1 standard deviation. Degrees of freedom are given for the F values.

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Results

Climatic variables known to influence nectar secretion and evaporation [e.g., air temperature (Jakobsen and Kristjansson, 1994)] were remarkably uniform over the 4 days of nectar sampling. Hourly mean relative humidity ranged from $91\% \pm 4\%$ to $98\% \pm 2\%$ each day (hourly minimum was 84%). Hourly mean temperature ranged from $19 \pm 0.3^\circ\text{C}$ to $23 \pm 2.3^\circ\text{C}$ each day. Canopy wind speed remained $<6.5\text{ km}\cdot\text{h}^{-1}$. There was no rain, but persistent and complete cloud cover and occasional fog kept mean solar radiation $<200\text{ W}\cdot\text{m}^{-2}$.

The fertilizer treatments did not affect nectar sugar production per flower for 'Stevens' (16 to 20 flowers per treatment) ($F_{[2,53]} = 1.4, P > 0.20$). Each flower's nectar contained an average of $383 \pm 106\text{ }\mu\text{g}$ of sugar. The concentration of dissolved solids averaged $23\% \pm 4\%$ contained in $1.4 \pm 0.5\text{ }\mu\text{L}$ of nectar. As expected, the high fertilizer treatment yielded vigorous vegetative growth but a noticeable sparsity of flowers.

Nectar production differed among cultivars grown with moderate fertilization in the common bog ($F_{[2,63]} = 6.45, P \leq 0.003$). Only 'Stevens' produced significantly more nectar sugar per flower, which was on average 25% to 35% more nectar sugar per flower than the other two cultivars. Each 'Stevens' flower accumulated nectar containing an average of $411 \pm 89\text{ }\mu\text{g}$ of solids dissolved in $1.4 \pm 0.6\text{ }\mu\text{L}$ of nectar. 'Early Black' produced $301 \pm 84\text{ }\mu\text{g}$ sugar per flower; 'Ben Lear' produced $329 \pm 133\text{ }\mu\text{g}$ per flower. Average concentrations of nectar solids ranged only from 21% to 24% for the three cultivars during this period of uniform, damp local weather conditions, so the differences between cultivars were primarily attributable to differences in nectar volume.

Discussion

Our values for nectar sugar production per cranberry flower agree closely with those of Roberts (1979). He also found that 3-day-old flowers of 'Early Black' yielded a little $>300\text{ }\mu\text{g}$ of sugar in New Jersey bogs despite sampling and analytical methods that differed radically from our own. He also reported that nectar sugar available per flower increased linearly and additively for flowers up to 5 days in age. Nevertheless, the cool, overcast weather experienced during this study may have depressed cranberry nectar production: in alfalfa (*Medicago sativa* L.), flowers produce nearly twice as much nectar in fair weather than when it is cloudy (Pedersen, 1953a).

Supplemental fertilizer application did not affect nectar sugar accumulation by 'Stevens' flowers. Nectar secretion rates of alfalfa (Pedersen, 1953a), red clover (*Trifolium pratense* L.) (Ryle, 1954), and mustard (*Brassica* sp.) (Shuel, 1957) likewise did not respond to modest changes in soil fertility. In two of the few carefully controlled experiments to relate soil fertility to nectar secretion, it was reported that excess phosphorus could reduce nectar secretion, but excessive nitrogen fertilization or suboptimal supplies of potassium generally elicited more gross responses, such as reduced flower production or vegetative growth (Ryle, 1954; Shuel, 1957). Modest alterations of fertilizer application rates in commercial cranberries are not likely to change the attractiveness of individual flowers to foraging bees.

Cranberry cultivars differed in the quantities of nectar sugars that accumulated in individual flowers. The individual stems of these defined cultivars actually represent ramets of a single self-fertile clone, as cranberries are propagated vegetatively from cuttings. In Bog 17, environmental heterogeneity was minimized by our sampling design. In addition, randomization of the replicate

plots of cultivars within the four rows of Bog 17 also lessened the likelihood that differences between cultivars could be attributable to environmental gradients. As a result, we conclude that the differences in nectar production among the three cranberry cultivars grown in these plots in Bog 17 must be heritable and therefore susceptible to selective breeding.

Consistent, presumably heritable, differences in nectar secretion have been reported for clones or cultivars of other agricultural crops, primarily forage legumes. These include alfalfa (Pedersen, 1953b), birdsfoot trefoil (*Lotus corniculatus* L.) (Murrell et al., 1982), red (Ryle, 1954) and white (*T. repens* L.) clover (Oertel, 1961), and others (Szabo and Najda, 1985). Nectar sugar production of selected alfalfa clones, for instance, ranged from 350 to $1050\text{ }\mu\text{g}$ of sugar per floret (Pedersen, 1953b), or one to three times that produced per cranberry flower. Through selective breeding, nectar secretion rates or volume of individual flowers have been successfully enhanced in these leguminous crops (Hawkins, 1971; Murrell et al., 1982; Teuber et al., 1990). For example, nectar height in corolla tubes of singlecut red clover was increased 1.5-fold in four generations of selective breeding (Hawkins, 1971). Significant differences in nectar volume of three alfalfa cultivars were obtained after just two generations of intensive selective breeding (Teuber et al., 1983).

Nectar is the floral reward commonly sought by most pollinators, including bees (Baker and Baker, 1983; Bentley and Elias, 1983; Kevan and Baker, 1983). Nectarivores such as the social bees can readily evaluate the sugar concentration of nectar (von Frisch, 1967; Waddington, 1983, 1985) and learn to associate it with a flower's appearance, scent, spatial location, and schedule of nectar secretion (Barth, 1985; Free, 1970; Real et al., 1982; von Frisch, 1967; Waddington, 1983, 1985; Waddington and Holden, 1979). Honey bees might also respond to the modest differences in nectar accumulation reported here for cranberry. In laboratory foraging trials, they preferentially visit artificial flowers providing 2 vs. $1\text{ }\mu\text{L}$ of 20% sucrose solution, and can be trained to mere one-half microliter rewards (Waddington, 1985). Alfalfa cultivars that secreted more nectar attracted 2- to 3-fold more visits from foraging honey bees (Pedersen, 1953b), which led to a 1.4-fold increase in seed yields per hectare (Teuber et al., 1983, 1990). It should be noted, however, that individual alfalfa plants produce many flowers [$x = 11,020$ flowers (Pedersen, 1953b)], which is as many flowers as cranberries might produce in 2 m^2 of managed bog. Hence, although floral nectar production in cranberry compares well with alfalfa, reward density will be less in cranberry, which might temper forager's evaluation of any nectar improvements in cranberry clones.

Cranberry breeding programs that take advantage of heritable differences in nectar production may be able to improve the attractiveness of commercial cranberries to pollinating bees seeking nectar rewards, as has been demonstrated for alfalfa. Superior nectar production can enhance pollination success through ways that alter the efficiencies, visitation intensities, and taxonomic fidelities of pollinators. First, pollinators linger at individual flowers that offer more nectar, during which time they may inadvertently transfer more pollen to the stigma (Thomson, 1986). In addition, pollinators are likely to return (or recruit) to more rewarding patches, where they may repeatedly visit receptive flowers (Pedersen, 1953b; Real and Rathcke, 1991; Teuber et al., 1990; Waddington, 1983). Finally, species rarely bloom in isolation: as pollinators forage, they compare nectar resources available at competing flower species, preferentially visiting the more rewarding taxa (Free, 1968; Heinrich, 1979; Rathcke and Real, 1993). For all of these reasons, enhancing the nectar production of

bee-pollinated crops such as the cranberry is desirable, as it can directly boost fruit and seed yields (Holtkamp et al., 1992; Real and Rathcke, 1991; Teuber et al., 1990). Such improvements could help stabilize the annual fruit set and marketable yields experienced by growers, especially in years during which marginal weather for pollinator activity prevails, or when alternative bloom is abundant.

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