Chemical and Sensory Comparison of Tomatoes Pollinated by Bees and by a Pollination Wand

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ABSTRACT Tomato flowers (Solanum lycopersicum L.) in greenhouses require assisted pollination. Compared with pollination using a vibration wand, pollination by buzz pollinating bees results in improved seed set and consequently, higher fruit weight. We investigated whether there are further chemical and sensory differences between bee- and wand-pollinated cherry tomatoes, Solanum lycopersicum variety Conchita. The pollination method did not result in significant differences in concentration of soluble solids and titratable acidity. However, the concentration of soluble solids was significantly positively correlated with seed number. We suggest that an increase in the amount of soluble solids in the locular area, due to increased seed numbers, is counteracted by the effects of seed numbers on the growth of the walls, which occurs through cell elongation. In the sensory part of this study, a large, untrained panel significantly preferred bee-pollinated over wand-pollinated tomatoes and classified bee-pollinated tomatoes as having more depth of flavor than wand-pollinated tomatoes. Thus, bee-pollinated tomatoes taste better than wand-pollinated tomatoes, and it is likely that the sensory differences between the two groups of tomatoes are mediated through effects of pollination treatment on seed numbers. Future chemical and sensory studies of fresh tomatoes should take into account the effects of seed numbers and their possible effect on the distribution of chemical compounds within tomatoes.

KEY WORDS horticulture, pollination, Amegilla, seeds, flavor

Tomatoes, Solanum lycopersicum L., grown in greenhouses require assisted pollination to ensure successful pollen transfer to the stigma, because fruit set is generally poor when natural pollination agents such as wind and insects are withdrawn (Verkerk 1957, Tüzel et al. 1999). Pollination in greenhouses is generally achieved either by using a hand-held vibrating tool to vibrate the petiole of open flowers or by introduction of buzz-pollinating bees, such as bumblebees (Bombus spp.) (Velthuis and van Doorn 2006, Dogterom et al. 1998), carpenter bees (Xylocopa spp.) (Hogendoorn et al. 2000), or bluebanded bees (Amegilla spp.) (Bell et al. 2006; Hogendoorn et al. 2006, 2007). Buzz-pollinating bees sonicate flowers through vibration of the thoracic muscles, which causes a large number of pollen grains to be released (King and Buchmann 2003). Some of these pollen grains will end up on the sticky stigma.

Compared with pollination using a pollination wand, buzz pollination by bees results in an increased number of pollen landing on the stigma, which causes increased seed set (Banda and Paxton 1991, Hogendoorn et al. 2000). Because there is a correlation between the number of seeds and the weight of a tomato (Dempsey and Boynton 1965, Imanishi and Hiura

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1975), bee-pollinated tomatoes are, on average, heavier than wand-pollinated tomatoes (Banda and Paxton 1991, van Ravenstijn and van der Sande 1991, Hogendoorn et al. 2006). In addition, the presence of seeds is related to the activity of endogenous hormones, which influences fruit size (Mapelli et al. 1978, de Jong et al. 2009).

Both fruit weight and the presence or absence of seeds have been associated with sensory and chemical attributes of tomatoes, including concentration of soluble solids concentration (SSC), titratable acidity (TA), and sweetness, sourness, overall aroma, and various component volatiles (Janes 1941, Saliba-Colombani et al. 2001, Causse et al. 2002). A negative correlation between fruit weight and the concentration of SSC or TA has been found in some studies (Goldenberg and von der Pahlen 1966, Saliba-Colombani et al. 2001, Causse et al. 2002) but not in others (Ibarbia and Lambeth 1971, Cuartero and Cubero 1982, Tanksley et al. 1996, Carmi et al. 2003, Prudent et al. 2009).

The presence of seeds increases both SSC and levels of acidity (Janes 1941). Neither Prudent et al. (2009) nor Carmi et al. (2003) found a significant correlation between the sugar concentration of the pericarp and seed number. Therefore, the overall effect of seed number on SSC and acidity may be related to the

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content of locules, and in particular the pulp around the seeds, having the highest concentration of both sugars and acids (Janes 1941, de Bruyn 1971).

The number of seeds directly influences the amount of pulp, as well as the growth and ripening of tomatoes (Dempsey and Boynton 1965), which is probably mediated through effects of auxin production in the ovaries (Varga and Bruinsma 1976, Mapelli et al. 1978, de Jong et al. 2009). This could influence volatile aromatic compounds of tomatoes. Among other factors, consumer preference is influenced by volatile substances, TA, and SSC (de Bruyn 1971, Stevens et al. 1979, Jones and Scott 1983, Malundo et al. 1995, Auerswald et al. 1999, Serrano-Megías and López-Nicolás 2006).

Thus, due to the interrelatedness of seed number, tomato weight, ripening, and chemical and potentially sensory attributes, the differences in seed content and fruit weight of bee-pollinated versus wand-pollinated tomatoes could cause correlated differences in both sensory and chemical attributes of tomatoes.

We explored how the pollination method influences a number of chemical and sensory attributes of cherry tomatoes. With respect to chemical attributes, we investigated whether bee-pollinated tomatoes contain higher concentrations of soluble solids and titratable acids than wand-pollinated tomatoes, and whether this is related to their seed number. In a separate assay, we investigated whether untrained subjects tastes differences between bee- and wand-pollinated tomatoes in sweetness and "tanginess," and whether there is a perceived difference in depth of flavor between beeand wand-pollinated tomatoes. Furthermore, we performed a consumer preference test to find out whether there is a preference for cherry tomatoes that are the result of either method of pollination.

Materials and Methods

Bees. Bluebanded bees (*Amegilla murrayensis* Rayment) were used as buzz pollinators in each of the experiments. The bees were all produced in the long-term breeding program of this species at the University of Adelaide (Adelaide, Australia) (Hogendoorn et al. 2006, 2007). Female bluebanded bees were kept in a glasshouse compartment (40 m²) and provided with clay nesting material and with feeders that contained 1:1 honey/water (vol:vol). The bees were maintained according to protocols described in Hogendoorn et al. (2007). During the experiment, at least eight females were actively nesting in the compartment and collecting pollen for their offspring. The experimental tomato plants were moved into the glasshouse compartment for pollination.

Plants and General Experimental Protocol. For both the chemical and the sensory experiments, cherry tomatoes (*Lycopersicum esculentum* variety Conchita) were grown from a single batch of seeds. The plants were grown in pots with 20-cm-diameter and depth. Each plant received a label with a unique number, and these numbers were randomly assigned to bee- or wand-pollination treatment. The day before the plants were moved into the glasshouse compartment that contained the bees, the plants were cut back to a single shoot with a single truss with three unopened flowers.

The plants were moved into the glasshouse compartment, where half of each batch of plants received bee pollination, and the other half received pollination by using a pollination wand. To achieve this, the plants were placed on two adjacent tables. One table held the wand-pollinated plants, which were protected by a tent of coarse white gauze that let through light and air but no bees. The other table held the bee-pollinated plants, which were freely accessible by bees.

The flowers of the wand-pollinated plants were pollinated by vibrating the petiole with a pollination wand. This was done twice a week between 10 a.m. and 11 a.m., following industrial protocol. After all three flowers had dehisced on each plant, all plants were moved into a greenhouse away from the bees, where they were placed randomly on tables. They were watered every other day, fertilized weekly, and all additional shoots and trusses were pruned back every other week. The person performing the plant maintenance was not aware of the pollination treatment that each plant had received.

Tomatoes were picked once they were fully red, according to the USDA (1975) tomato ripeness color chart for maturity and ripeness of cherry tomatoes and weighed using a balance with an accuracy of 0.01 g.

Chemical Analysis. This study involved 48 tomato plants, 24 bee-pollinated plants, and 24 wand-pollinated plants, with a single truss of three flowers each, which received treatments according to the general protocol described above. Fully red tomatoes were picked over a 15-d period.

The first tomato on the truss of each of the plants was used for the chemical analysis. The tomatoes were weighed and halved. The seed mass was removed and the seeds were counted following methods in Hogendoorn et al. (2006). Then, the flesh and pulp of each tomato were reunited and the tomato was homogenized using a Polytron homogenizer (Kinematica, Bohemia, NY) for 30 s at 3,000 rpm. The homogenate was spun down for 5 min at 4,000 rpm, and the clear internatant was removed with a syringe and tested for SSC and TA.

The soluble solids were measured in Brix, using a handheld refractometer for measurements between 0 and 50% (Eclipse, Bellingham and Stanley model 45-03, Turnbridge Wells, Kent, United Kingdom). Titratable acidity was determined by titrating 10 ml of the filtered tomato internatant diluted in 50 ml of MilliQ water (Millipore, Billerica, MA) to pH 8.2 with 0.1 M NaOH.

Sensory Pilot Study. The plants used to produce the tomatoes for the chemical analysis also produced the tomatoes used for a pilot sensory study. These were the second and third tomatoes from each truss. The outcome of this pilot study was used to design the questions for the final sensory trial, and to perform a power analysis for a preference study. Bee- and wand-pollinated tomatoes were harvested when red and weighed within an hour referred to the bee- or the wand-pollinated tomato. Adult subjects were approached during different times of the day and were asked to partake in a tomato taste trials involving two cherry tomatoes. If they agreed, they were invited to taste the tomatoes in whatever order they preferred, they were allowed to compare bites, and they were asked the following questions: 1) Do you taste a difference between these tomatoes? 2) If so, can you describe the difference? 3) Do you have a preference for any of these two tomatoes?

Of the 28 respondents, 26 tasted a difference between the tomatoes. They described this differences as differences in sweetness (n = 16), and/or acidity or tanginess (n = 6) and in depth of flavor (or equivalents statements; n = 11). Because these untrained subjects predominantly identified three characteristics, the final sensory study included questions about sweetness, tanginess, and depth of flavor (see below). Of the respondents, 61% indicated preference for beepollinated tomatoes. Power analysis indicated that 98 respondents would be required to achieve an acceptable type II error (80%).

Sensory Study. This study involved 124 tomato plants grown from seeds planted on 24 December 2008, which received treatments according to the general protocol described above. The plants were randomly assigned to bee- or wand-pollination treatment (n = 62 plants per treatment).

To ensure all ripening tomatoes could be processed, the plants were moved into the glasshouse compartment in two batches of 62 plants. Half of each batch of plants (n = 31 plants) received bee pollination, and the other half received pollination by using a pollination wand. The first batch of plants was moved into the glasshouse compartment on 7 February and out on 20 February, and the second batch was moved in on 20 February and out on 6 March 2009. Both batches received the same treatment according to the general protocol described above.

Picking and Pairing of Tomatoes. To prevent any bias that could arise due to consistent numbering of the treatments, the person who picked the tomatoes numbered the treatments 1 and 2 at the toss of a coin. The two tomatoes were then handed over to a person who was unaware of the treatments they had received. This person formed pairs of tomatoes on the basis of physical attributes according to the protocol outlined in the pilot study. Whenever a counterpart from the other treatment could not be found, e.g., because of noticeable differences in color, firmness or blemishes, or extreme size differences, the tomato was discarded. In total, 113 pairs of tomatoes were included in the sensory test.

Sensory Test. The sensory testing was performed within a time span of 3 wk. The subjects (n = 113)were all adult employees or visitors at the Waite Campus, and they were allowed to participate once only. Subjects were approached individually between 10 a.m. and 12 p.m. (noon) and asked whether they were willing to participate in a tomato taste trial involving two cherry tomatoes. If the answer was affirmative, they were then asked to decide which tomato they should taste first by coin toss. It was pointed out that although they had to start with one tomato, they were allowed to compare individual bites. The guestions put to the subjects were as follows: 1) Which tomato tastes sweeter? 2) Which tomato tastes more tangy? 3) Which tomato has more depth of flavor? 4) Which tomato do you prefer? To answer each of these questions, the subjects were asked to tick a box ("tomato 1," "tomato 2," or "none").

After they had answered these questions, the palate of the subjects was tested using four aliquots of ≈25 ml of tomato juice (Berri tomato juice, National Foods, Melbourne, VIC, Australia). The juice was presented in two pairs. Each pair came from the same bottle. The first pair had one aliquot straight from the bottle, whereas the other had been sweetened by adding 12.5 g of sucrose per liter of juice. The subjects were asked to identify which of the two juices tasted sweeter. The second pair had one aliquot straight from the bottle, whereas the other aliquot had been acidified using 0.5 g of citric acid per liter of juice. The amount of sugar and citric acid added was derived from recommended additions in Lawless (1999), and adjusted to a level where an informal panel of three could just taste the difference between the adulterated and unadulterated juices.

The subjects were asked to identify the juice of the first pair that tasted sweeter, and the juice of the second pair that tasted tangier. The data would allow later exclusion of the subjects that showed no palate for the gustatory attributes of tomato flavor.

Statistical Analysis. Statistical Analysis of Chemical Data. A multiple analysis of variance (MANOVA) was performed to investigate the relationship between the pollination method, seed number, weight, and the measured chemical characteristics. The MANOVA was followed up by a Roy–Bargmann stepdown analysis (Tabachnick and Fidell 2001, p. 350) using Bonferroni correction. This procedure uses stepwise analysis of covariance (ANCOVA) to investigate the effect of treatment on multiple potentially correlated dependent variables, by prioritizing the dependent variables on the basis of theoretical and practical considerations. Because the pollination treatment initially influences seed number, the latter variable was used as the highest priority dependent variable in the first step of the analysis. For the remaining steps, the priority of the dependent variables was decided by the significance of their association with seed number. In the next step, because it showed the most significant association with seed number, and for similar reasons, SSC was included as covariate in the third step. For

Table 1. Average \pm SE physical and chemical attributes of tomatoes pollinated by bees and by a pollination wand

| Attribute ^a | Wand $(n = 24)$ | Bee $(n = 24)$ | |
|------------------------|------------------|------------------|--|
| Wt (g) | 27.58 ± 0.39 | 30.31 ± 0.42 | |
| No. of seeds | 91.08 ± 2.56 | 99.13 ± 2.49 | |
| SSC (Brix) | 10.79 ± 0.11 | 10.60 ± 0.09 | |
| TA (g/liter) | 3.91 ± 0.09 | 4.01 ± 0.07 | |

significant associations, we also indicate whether the correlation coefficient was positive or negative.

Statistical Analysis of Sensory Data. In the sensory analyses, some of our subjects gave a response of "no difference" or "no preference." It is important to take such data in consideration (Bailey 1980, Lawless 1999). Comparison of the confidence intervals for the preferences of alternatives (Lawless 1999) provides an unbiased approach for the analysis of such nonforced preference data. Using continuity correction (Bailey 1980, equation 6), we calculated confidence intervals of each alternative at the type I error probability of 0.05. Nonoverlapping confidence intervals indicate a preference for the choice with the highest frequency. Furthermore, we conducted two-tailed binomial test in which half of the undecided votes were added to each of the preference votes.

Factors that contributed to preferences were analyzed in a backward stepwise logistic regression. These factors included the weight difference between the paired tomatoes and whether, compared with the beepollinated tomato, the subject perceived the wandpollinated tomato as less, more or equal in sweetness, tanginess, and depth of flavor. SPSS version 17 (SPSS Inc. Chicago, IL) was used for all statistical analyses.

Results

Chemical Analysis. Overall, there was a significant difference between bee- and wand-pollinated tomatoes in the variables measured (Table 1; Hotelling's $T^2 = 0.63$; $F_{4, 43} = 6.78$; P < 0.0001). To investigate the effect of the treatment on the potentially correlated dependent variables we performed a Roy-Bargmann stepdown analysis with Bonferroni correction (Table 2). Univariate analysis of variance (ANOVA), the first step in the analysis, showed that the number of seeds (the highest priority dependent variable) differed sig-

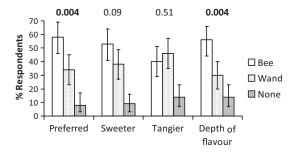


Fig. 1. Results of the comparison of paired bee- and wand-pollinated tomatoes by a large inexperienced panel (n = 113). Each participant compared two tomatoes with respect to preference, sweetness, tanginess, and depth of flavor. The columns show the percentage of respondents with 95% confidence intervals (CI), calculated using Bailey's continuity correction. A nonoverlapping CI indicates a significant difference. *P* values, resulting from two-tailed binomial tests with half of the undecided votes allocated to each of the categories "bee" and "wand" are shown above the columns. Significant *P* values are indicated in bold.

nificantly between treatments. In subsequent ANCO-VAs, the effect of the pollination treatment was not significant (Table 2), and there were no significant interactions between treatment and any of the covariates. However, seed number, which was entered as a covariate after the first step, had a significant positive association with weight in the second step, and a significant positive association with soluble solids content in the third step. In the last step, there were no significant associations between titratable acidity and any of the covariates.

Sensory Study. When presented with a choice, 66 subjects indicated a preference for the bee-pollinated tomato, 38 preferred the wand-pollinated tomato, and nine had no preference (Fig. 1). Thus, 58% of subjects preferred the bee-pollinated tomato compared with 34% who preferred the wand-pollinated tomato. There was a significant preference for bee-pollinated tomatoes, because the 95% confidence intervals for the preferences were nonoverlapping (Fig. 1). The binomial test also supported an overall preference for bee-pollinated tomatoes (P = 0.004).

Similar analyses indicated that the difference between bee- and wand-pollinated tomatoes in perceived sweetness or tanginess was nonsignificant, but

Table 2. Roy-Bargmann stepdown analysis of the association between pollination treatment and the four dependent variables (DV; in order of priority: seed number, weight, soluble solid content (SSC, Brix), and titratable acidity (TA, g/liter)

| Step | DV | df1, df2 | | | Associations with covariates | | | | | |
|------|-------|----------|-----------|------|------------------------------|---------|------|------|------|------|
| | | | Treatment | | Seed no. | | Wt | | SS | |
| | | | F | Р | F | Р | F | Р | F | Р |
| 1 | Seeds | 1,46 | 5.47 | 0.02 | | | | | | |
| 2 | Wt | 1,45 | 0.64 | 0.80 | 26.89 | < 0.001 | | | | |
| 3 | SSC | 1,44 | 2.22 | 0.14 | 9.50 | 0.004 | 0.88 | 0.35 | | |
| 4 | TA | 1, 43 | 1.91 | 0.17 | 5.69 | 0.02 | 4.92 | 0.03 | 0.35 | 0.55 |

Significance levels were adjusted using stepwise Bonferroni correction. All significant correlations were positive. Significant F and P values are indicated in bold.

 Table 3. Backward stepwise logistic regression analysis of the factors associated with preference

| Variable | В | SE | Exp (B) | Wald statistic | Р |
|--------------------------|-------|------|---------|-------------------|---------|
| Relative depth of flavor | -4.73 | 0.88 | 0.01 | 29.04 | < 0.001 |
| Relative sweetness | -2.45 | 0.83 | 0.09 | 8.81 | 0.003 |
| Wt difference | -0.15 | 0.15 | 0.86 | 0.92 | 0.34 |
| Relative tanginess | -1.29 | 0.99 | 0.28 | 1.68 | 0.28 |
| Constant | 2.79 | 0.75 | 16.22 | 13.87 | < 0.001 |

Significant P values are indicated in bold.

a significant difference was perceived in depth of flavor (Fig. 1).

Subjects who did (n = 88) and who did not (n = 25)classify the sweetened and unsweetened tomato juices correctly, did not differ in their classification of bee- and wand-pollinated tomatoes with respect to sweetness ($\chi^2 = 0.77$, P = 0.38), tanginess ($\chi^2 = 0.77$, P = 0.38), depth of flavor ($\chi^2 = 0.61$, P = 0.74), or preference ($\chi^2 = 0.54$, P = 0.82). Subjects who did (n = 61) and who did not (n = 52) classify tomato juices correctly according to acidity did not differ in their classification of bee- and wand-pollinated tomatoes with respect to tanginess ($\chi^2 = 0.10, P = 0.75$) or depth of flavor ($\chi^2 = 2.93$, P = 0.23). However, the subjects that incorrectly classified the acidity of the tomato juices significantly identified the bee-pollinated tomatoes as sweeter ($\chi^2 = 7.14, P = 0.03$) and preferred bee tomatoes over wand tomatoes significantly more often ($\chi^2 = 9.42, P = 0.01$) than the group who classified acidity correctly.

Excluding subjects who had no preference for either bee- or wand-pollinated tomatoes, a backwards stepwise logistic regression of preferences was performed with weight difference between the paired tomatoes as a continuous covariate and perceived relative sweetness, tanginess, and depth of flavor as categorical covariates. This showed that depth of flavor and sweetness significantly contributed to the preference (Table 3), whereas tanginess and weight difference between the two tomatoes had no influence on preferences.

Discussion

An inexperienced panel of >100 participants significantly preferred bee-pollinated over wand-pollinated cherry tomatoes. This indicates that the pollination method influences the sensory characteristics of tomatoes. Bee-pollinated tomatoes were perceived as having more depth of flavor than wand-pollinated tomatoes, but no significant differences were perceived with respect to sweetness and tanginess.

It is likely that the sensory differences between the two groups of tomatoes are caused by differences in seed numbers. Tomatoes that are pollinated by buzzpollinating bees are heavier and have more seeds than wand-pollinated tomatoes (Banda and Paxton 1991; van Ravenstijn and van der Sande 1991; Hogendoorn et al. 2000, 2006; Morandin et al. 2001). Although the relationship between fruit weight and chemical and sensory aspects of tomatoes has often been investigated (Baldwin et al. 1995, Baldwin et al. 1998, Auerswald et al. 1999, Causse et al. 2002, Prudent et al. 2009), the effects of seed numbers are mostly not included in these analyses. The relationship between seed number and chemical and sensory aspects of tomatoes should be further explored.

Chemical Analysis. Sensory analysis has shown that sweetness and sourness are among the main determinants of tomato preference (Stevens et al. 1977) and that these sensory characters correlate with soluble solids content and titratable acidity (Kader et al. 1977, Auerswald et al. 1999, Serrano-Megías and López-Nicolás 2006). Therefore, we investigated effect of pollination treatment on these chemical characteristics. No differences between wand- and bee-pollinated tomatoes were found with respect to either SSC or TA. However, further analysis points to a more complex relationship between seed number, fruit weight, and chemical characteristics. The correlation between seed number and fruit weight was significant, and when controlling for fruit weight, a significant positive correlation was found between seed number and SSC. The latter result may be partly counteracted by marginally nonsignificant negative relationship with fruit weight. Further work is required to fully elucidate these interactions.

The effects can be understood in the light of the physiology of tomatoes and tomato growth. The highest levels of soluble solids and TA of tomatoes are found in the locules, i.e., in the gelatinous substance around the seeds, whereas the lowest values are found in the outer wall of the tomato (Janes 1941, de Bruyn 1971). Growth of tomato walls occurs in response to the number of seeds and is mainly the result of cell elongation rather than cell division (Mapelli et al. 1978, de Jong et al. 2009). This elongation of cells could dilute the concentration of soluble solids and TA in the cell walls (Causse et al. 2002, Serrano-Megías and López-Nicolás 2006). Thus, a higher seed number would cause an increase in the amount of titratable acidity and soluble solids in the seed area, but a decrease of both in the outer wall. The overall effect on chemical characters would then depend on the increase in locular volume relative to the increase in wall volume. In addition, it is possible that localized chemical and sensory differences within a tomato, e.g., between the locules and the walls, interact to influence the sensory characteristics.

Sensory Analysis. Overall, our large untrained panel preferred bee-pollinated tomatoes over wand-pollinated tomatoes, and described bee-pollinated tomatoes as having more depth of flavor. These results confirmed the outcome of the pilot study. Preference correlated with classifications of more depth of flavor and sweeter tomatoes but did not correlate with perceptions of tanginess.

Sweetened and acidified juices, used to check the palate of the subjects were classified correctly by 78 and 54%, respectively. Therefore, in the case of acidity, the differences were possibly too subtle. Interestingly, compared with subjects who correctly classified the acidified and nonacidified tomato juices, the subjects who failed to do so significantly more often preferred bee-pollinated tomatoes over wand-pollinated tomatoes and classified bee-pollinated tomatoes more often as sweeter. A possible explanation for this finding lies in the fact that perceptions of sweetness and acidity interfere (Schifferstein and Frijters 1990). Sucrose suppresses the sourness of citric acid (Fabian and Blum 1943, Pangborn 1960, McBride and Johnson 1987, Schifferstein and Frijters 1990), whereas suprathreshold concentrations of citric acid suppress the perceived sweetness of a sugary solution (Gordon 1965, McBride and Johnson 1987, Schifferstein and Frijters 1990). For tomatoes, the same mechanism was demonstrated by Causse et al. (2002), who found a positive correlation between SSC and TA, but a negative correlation between perceived sweetness and sourness. Among tomatoes, cherry tomatoes have very high levels of acidity (Hobson and Bedford 1989), and this is particularly true for Conchita, the variety used in this study (J. Altmann, personal communication). It is therefore possible that increases in levels of acidity in the locular area, caused by the presence of more seeds in the bee-pollinated tomatoes, were not appreciated by subjects who were better able to perceive this higher acidity and that this lowered the perception of sweetness and the bee-biased preference of this group.

To date, the size of tomatoes was the only known advantage of buzz pollination by bees over the use of a vibrating pollination wand. This study shows that there are more benefits of having tomatoes pollinated by bluebanded bees rather than by a vibrating wand, because the bee-pollinated tomatoes were preferred by an untrained panel. It is likely that other buzzpollinating bee species have similar effects on the sensory characters of tomatoes, because all buzz-pollinating bees tested so far for their ability to pollinate tomatoes increased the number of seeds in a similar manner (Banda and Paxton 1991; Hogendoorn et al. 2000, 2006).

This study clearly demonstrates that seed number should be taken into account as a factor that potentially influences the sensory characteristics of fruit, in particular tomato. In addition, future sensory analysis of fresh tomatoes should accommodate for the fact that chemical compounds are not distributed homogenously throughout a tomato and that this can influence the sensory characteristics.

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