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Evaluation of Select *Monarda* Taxa in Montane and Piedmont Regions of Georgia: II. Floral Morphology and Nectar Production

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Abstract. **We analyzed the floral morphology and nectar production of several cultivars and species of *Monarda* representing five cultivars and four species grown in Georgia Piedmont and Montane regions. Over the course of two seasons, we detected significant differences among the samples in terms of inflorescence size, petal lobe and corolla widths and lengths, and total sugar content. *M. didyma* had larger glomerules, longer corollas and petal lobes, and higher nectar volume and total sugar content per flower. *M. fistulosa* and *M. punctata* had smaller glomerules, corolla and petal lobe lengths, and total sugar content per flower. Petal lobe and corolla length strongly correlated with sucrose and nectar production. Combined with data on horticultural performance, these results could be valuable in informing breeding goals for conservation-oriented landscape plants.**

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Breeding more floriferous, compact, and disease-tolerant native plants with high garden value that could also support an abundant and diverse insect community is an optimal goal. Breeders rely on a slate of desirable traits to select from various genotypes—larger and longer lasting flowers and tolerance to abiotic and biotic stressors being among the top characteristics. Until recently, little attention has focused on selection based on nectar production. Intentional landscape design can provide resources for wildlife across multiple seasons in human-dominated landscapes, providing refuge in spaces between natural areas.

Studying differences in floral morphology and nectar production among native plants and their cultivars provides empirical evidence to select plants that offer the most floral rewards to wildlife (Kalaman et al. 2022). Continued exploration of the subject is crucial due to the lack of consistent differences in floral rewards and pollinator preference between native and nonnative plants (Kalaman et al. 2022; Poythress and Affolter 2018; Torrez et al. 2023). Nectar is a primary floral reward important for wildlife and pollination (Dafini 1991), serving as an energy source for adult pollinating insects (Hill et al. 2001; Whitham 1977) and herbivorous hemipterans. The central role of nonprey, plant-derived food has also been shown for carnivorous arthropods (Patt and Pfannenstiel 2007). Several *Monarda* taxa are found in Georgia native to different regions in the state, and they are often included in seed mixes to provide summer forage to wildlife (Gray et al. 2007; Otto et al. 2017; Quinlan et al. 2021; Rubio et al. 2021; Weakley et al. 2022; Wolf et al. 2022).

There are many published comparisons concerning the relative nutrient value and pollinator attraction of nonnative cultivars and native plants (Braman et al. 2022; Native Plant Partnership 2014; Seitz et al. 2020; Tew et al. 2021; Williams et al. 2011). Nectar production and foraging visitors are well documented by Cruden et al. (1984) and Whitten (1981) among *M. fistulosa* and *M. didyma*, respectively, but to our knowledge, no research has been conducted assessing floral morphology and nectar production among cultivars and species within the genus. Due to the site- and species-specific nature of published research, there is a need to evaluate floral and nectar attributes among local plants (Kalaman et al. 2022), and in particular, Georgia-native plants. These properties are important from an applied perspective because *Monarda* taxa are often included in seed mixes to provide summer forage to wildlife (Gray et al. 2007; Otto et al. 2017; Quinlan et al. 2021; Rubio et al. 2021; Wolf et al. 2022).

Monarda species and cultivars provide an excellent opportunity to study the effect of floral morphology and nectar production because of their natural and intentional hybridization resulting in novel flower forms and color (Collicutt and Davidson 1999; Coombs 2016; Dudchenko et al. 2020; Hawke 1998; Mattarelli et al. 2017; Tabanca et al. 2013). The inflorescence of *Monarda* has individual flowers condensed into glomerules (head-like cyme), with varying sizes between species (Weakley et al. 2022). For instance, *M. didyma* has long corollas and deep red flowers compared with the short corollas and lavender to pink flowers of *M. fistulosa*.

Research has shown a general pattern that flowers with longer corolla tubes produce more nectar and vice versa (Dafini 1991; Gomez et al. 2008; Harder and Cruzan 1990; Kalaman et al. 2022; Petanidou et al. 2000). Specifically, the depth of corolla tubes has been associated with differences in nectar volume (Dafini 1991; Gomez et al. 2008; Harder and Cruzan 1990), largely due to differences in photosynthate secretion, nectar holding capacity, and nectar evaporation rates (Kalaman et al. 2022; Ornelas et al. 2007; Pleasants 1983). In addition, an earlier study by Dafini et al. (1988) found that within Labiatae, nectary size and nectar yield per flower were positively correlated.

As part of a larger study of horticultural performance of *Monarda* in cultivation (Smith

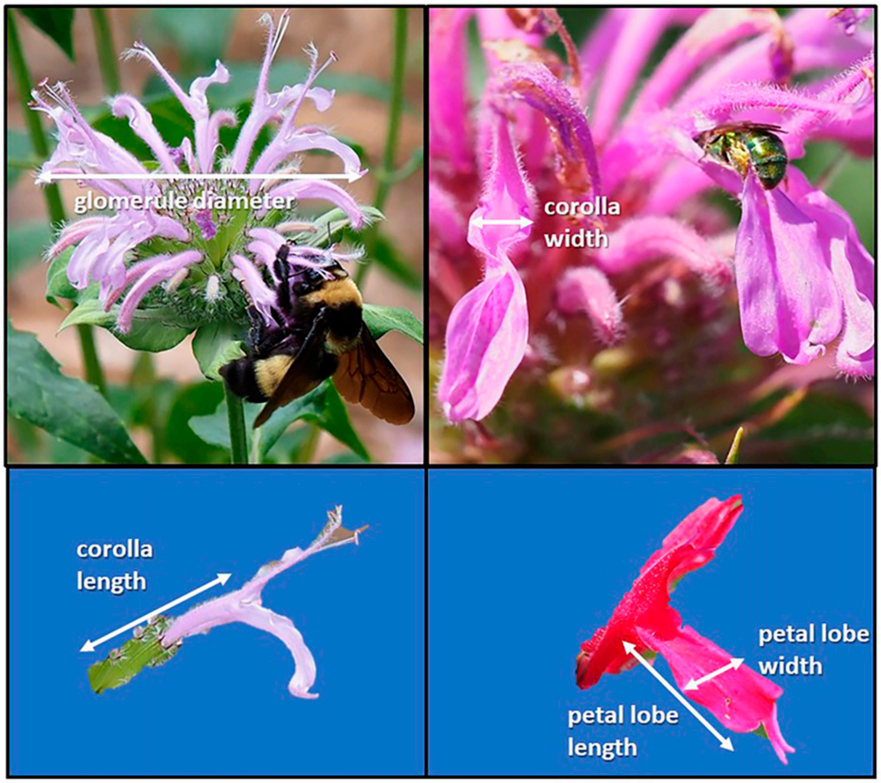

Fig. 1. Flower morphology of *Monarda* and measurements of floral characteristics.

et al. 2024), here we report on the second part of the work, namely flower morphology and nectar production. We used the same Athens and Blairsville, GA, USA, study sites described in Part I to test if floral morphology and nectar yield differed among selected *Monarda*. We measured perianth diameter, corolla length and width, and petal length and width to assess floral morphology. To study nectar production, we measured nectar volume, sucrose concentration, and total sugar content per flower. We hypothesized that floral morphology and nectar production would vary among *Monarda*.

Materials and Methods

Plant data

Floral morphology measurements. Plant material sourcing, descriptions, and at the Georgia Mountain Research and Education Center (GMREC) site in 2020 and at the Mimsie Lanier Center for Native Plant Studies (MLCNPS) site in 2021 are described in Smith et al. (in review). In short, 10 taxa, *Monarda* 'Raspberry Wine', *M. punctata* (GA, Georgia provenance), *M. didyma* 'Jacob Cline', *M.* Sugar Buzz® Grape Gumball Bee Balm, *M. punctata* (NJ, New Jersey provenance), *M. didyma*, *M.* 'Judith's Fancy Fuchsia', *M. fistulosa*, *M. bradburiana*, and *M. fistulosa* 'Claire Grace', were evaluated during the 2020 and 2021 growing seasons. Glomerule size/width (millimeters) was measured from the tip of one corolla across the head to the tip of another (Fig. 1). Two random glomerules per plant were measured in 2021 at the GMREC and MLCNPS. In 2020, at the GMREC, 12 to 32 random flowers per *Monarda* sample were measured for corolla and petal lobe length and width (millimeters). The length of the corolla was determined from where the nectary meets the receptacle to the opening where the lobes (the open part of the petals) fuse. The width of the corolla was the opening measured lengthwise from each union of the upper to lower petal lobe. Length of the lower petal lobe was measured from the corolla opening to the tip of the lip. The width of the lower petal lobe was measured at the widest horizontal point (Fig. 1). Measurements were made with digital calipers during peak bloom.

Nectar production. Nectar volume (microliters) and sucrose concentration (as % w/w sucrose) were measured at the GMREC in 2020 and at both sites in 2021. For each repetition and treatment, a random glomerule was bagged for 24 h to exclude visitors, after which the flowers were probed for nectar. The samples were taken between 9 and 10 AM to collect nectar after it had been secreted and before significant evaporation had taken place. In total, 50 random flowers were sampled per *Monarda*. One flower per inflorescence was used per nectar sample. Volume was measured by inserting a microcapillary tube into the corolla. The nectar was then deposited onto a handheld refractometer (Bellingham Stanley Limited Delta Refractometer Code Range 0% to 50% sucrose w/w) to measure the percent sucrose per flower. The refractometer was rinsed with deionized water and dried after each sample. As microgram sucrose per flower, the total sugar content was the product of volume times concentration times nectar density, the latter taken from reference tables. At micro volumes, nectar density is negligible and for the purpose of this study was considered 1 µL/µg (Bolten et al. 1979; Dafini 1991; Petanidou et al. 2000).

Statistical analysis

To determine which *Monarda* had the most desirable flower morphology and nectar production, we fit linear models using the *lm* function in R software (R Core Team 2023) with taxa as the independent variable. Years and sampling locations were analyzed separately. Through testing the assumptions of ordinary least squares, we found evidence of heteroskedasticity among a subset of the models that was confirmed by the Breusch–Pagan test (Zeileis and Hothorn 2002). These models were refit with generalized least squares using the *gls* function on R (Pinheiro et al. 2023). Following the satisfaction of all model assumptions, we completed post hoc tests using the *emmeans* function (Lenth et al. 2022) and Tukey's honestly significant difference test. In the event of a singular fit where the Satterthwaite parameters could not be estimated using the *emmeans* function, the approximate Satterthwaite mode was used to calculate the degrees of freedom correctly. Data visualizations were completed using ggplot (Wickham 2016) and show the estimated marginal means and the confidence intervals around each mean. The raw data are also plotted for reference.

Additional multivariate analyses using principal component analysis were performed on the flower morphology and nectar production data. Years and sampling locations were analyzed separately. The analysis and visualization of the data were completed using the *princomp* (R Core Team 2023) and *fviz_pca_biplot* (Kassambara and Mundt 2020) functions respectively.

Table 1. Results of the linear modeling comparing the floral morphology parameters and nectar production among the different *Monarda* tested.

Model	Num *df*	Den *df*	*F* value	*P* value
Corolla width	7	150	13.268	<0.0001
Corolla length	7	150	536.794	<0.0001
Petal lobe width	7	150	20.148	<0.0001
Petal lobe length	7	150	118.212	<0.0001
Blairsville glomerule	9	60	275.913	<0.0001
Athens glomerule	8	54	16.115	<0.0001
Blairsville 2020 sugar content	7	150	11.0326	<0.0001
Blairsville 2021 sugar content	9	60	38.8501	<0.0001
Athens 2021 sugar content	8	54	12.41377	<0.0001

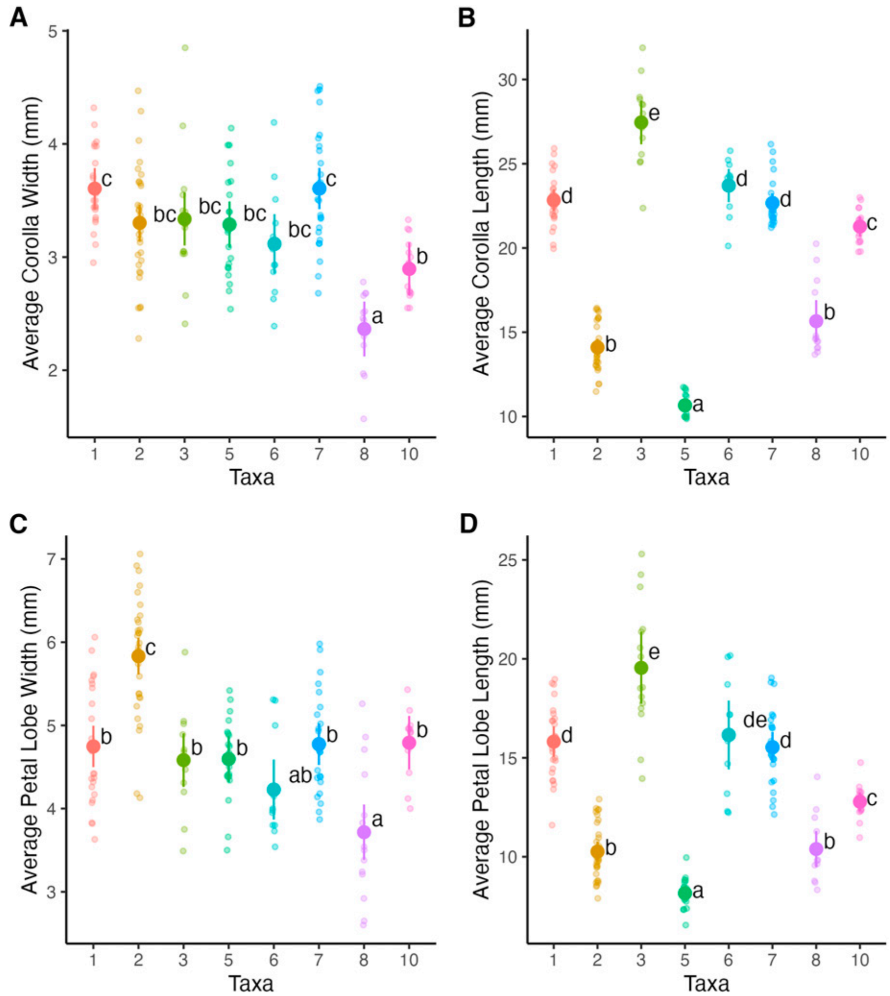

Fig. 2. Average corolla width (**A**), corolla length (**B**), petal lobe width (**C**), and petal lobe length (**D**) for *Monarda* grown in Blairsville, GA, USA, in 2020. Different letters indicate significant differences (alpha = 0.05). Taxa: 1—*Monarda* 'Raspberry Wine', 2—*Monarda punctata* (Georgia provenance), 3—*Monarda didyma* 'Jacob Cline', 4—*Monarda* Sugar Buzz® Grape Gumball Bee Balm, 5—*Monarda punctata* (New Jersey provenance), 6—*Monarda didyma*, 7—*Monarda* × 'Judith's Fancy Fuchsia', 8—*Monarda fistulosa*, 9—*Monarda bradburiana*, and 10—*Monarda fistulosa* 'Claire Grace'.

Results and Discussion

We found sufficient evidence to support our hypotheses that floral morphology and nectar production vary among *Monarda*. The petal and corolla length and width, glomerule diameter, and total sugar content all displayed significant differences among taxa for both sites and years (Table 1). *Monarda* 'Raspberry Wine', *M. punctata* GA, *M. didyma* 'Jacob Cline', *M. punctata* NJ, *M. didyma*, and *M.* × 'Judith's Fancy Fuchsia' (Fig. 2A) had the largest corolla width ($F_{7,150}$ = 13.268); *M. didyma* 'Jacob Cline' (Fig. 2B) had the largest corolla length ($F_{7,150}$ = 536.794); *M. punctata* GA (Fig. 2C) had the greatest petal lobe width ($F_{7,150}$ = 20.148); and *M. didyma* 'Jacob Cline' and *M. didyma* (Fig. 2D) had the greatest petal lobe length ($F_{7,150}$ = 118.212) in Blairsville in 2020. *Monarda* 'Raspberry Wine', *M. didyma* 'Jacob Cline', *M. didyma*, *M.* × 'Judith's Fancy Fuchsia', and *M. fistulosa* 'Claire Grace' had the largest glomerule diameter ($F_{8,54}$ = 16.115) in Athens in 2021 (Fig. 3A). *Monarda* 'Raspberry Wine', *M. didyma* 'Jacob Cline', *M. didyma*, and *M.* × 'Judith's Fancy Fuchsia' (Fig. 3B) had the largest glomerule diameter ($F_{9,60}$ = 275.913) in Blairsville in 2021.

Monarda 'Raspberry Wine', *M. didyma* 'Jacob Cline', *M. didyma*, and *M.* × 'Judith's Fancy Fuschsia' (Fig. 4A) had the highest sugar content in Blairsville in 2020 ($F_{7,150}$ = 11.0326), in Athens (Fig. 4B) in 2021 ($F_{8,54}$ = 12.41377), and in Blairsville (Fig. 4C) in 2021 ($F_{9,60}$ = 38.8501).

The multivariate analysis from 2020 showed similar results as the linear modeling with *M.* 'Raspberry Wine', *M. didyma* 'Jacob Cline', *M. didyma*, and *M.* × 'Judith's Fancy Fuchsia' clustering along the same axis as petal lobe and corolla length as well as sucrose and nectar production (Fig. 5). Furthermore, petal and corolla length strongly correlated with sucrose and nectar production. Similar results were found in 2021 (Fig. 6), when glomerule diameter strongly correlated with sucrose and nectar production.

In Part I (Smith et al. 2024), we reported that *M. fistulosa* and *M. punctata* taxa had a greater number of flowers per plant compared with *M. didyma* and *M. didyma* cultivars, excluding *M.* Sugar Buzz® Grape Gumball. In this study (Part II), we found that *M. didyma* taxa had larger glomerules, longer corollas and petal lobes, and higher nectar volume and total sugar content per flower. *M. fistulosa* and *M. punctata* taxa had smaller glomerules, corolla and petal lobe lengths, and total sugar content per flower. There was some overlap between nectar volume in *M. punctata* taxa and *M. didyma* cultivars, and this could be due

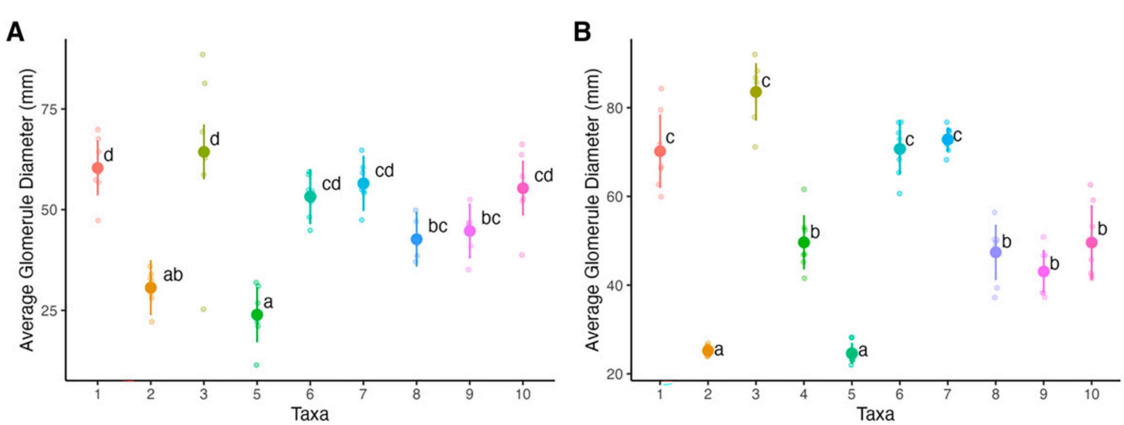

Fig. 3. Average glomerule diameter grown in Athens (**A**) and Blairsville (**B**), GA, USA, in 2021. Different letters indicate significant differences (alpha = 0.05). Taxa: 1—*Monarda* 'Raspberry Wine', 2—*Monarda punctata* (Georgia provenance), 3—*Monarda didyma* 'Jacob Cline', 4—*Monarda* Sugar Buzz® Grape Gumball Bee Balm, 5—*Monarda punctata* (New Jersey provenance), 6—*Monarda didyma*, 7—*Monarda* × 'Judith's Fancy Fuchsia', 8—*Monarda fistulosa*, 9—*Monarda bradburiana*, and 10—*Monarda fistulosa* 'Claire Grace'.

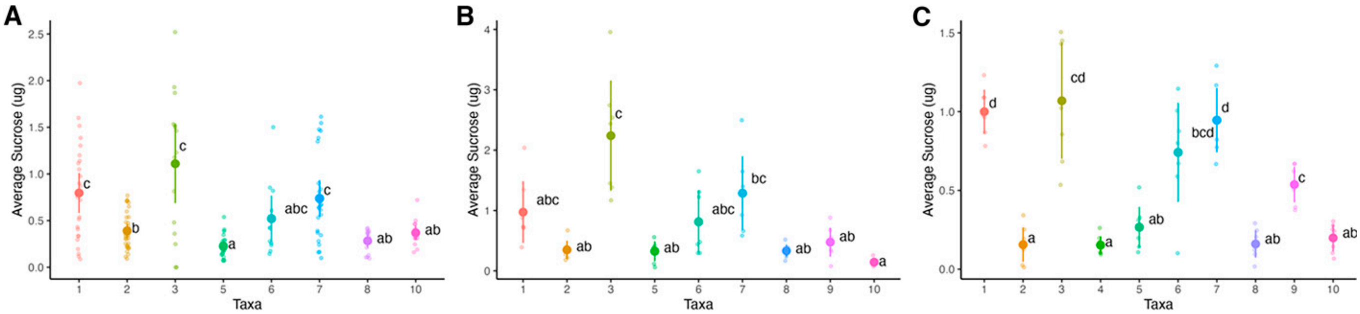

Fig. 4. Total sugar content (nectar volume × concentration × nectar density), for *Monarda* grown in Blairsville, GA, USA, in 2020 (**A**), Athens, GA, USA, in 2021 (**B**), and Blairsville in 2021 (**c**). Different letters indicate significant differences (alpha = 0.05). Taxa: 1—*Monarda* 'Raspberry Wine', 2—*Monarda punctata* (Georgia provenance), 3—*Monarda didyma* 'Jacob Cline', 4—*Monarda* Sugar Buzz® Grape Gumball Bee Balm, 5—*Monarda punctata* (New Jersey provenance), 6—*Monarda didyma*, 7—*Monarda* × 'Judith's Fancy Fuchsia', 8—*Monarda fistulosa*, 9—*Monarda bradburiana*, and 10—*Monarda fistulosa* 'Claire Grace'.

to larger corolla and petal lobe width in *M. punctata* relative to *M. fistulosa* (data not shown).

Floral traits can be useful for breeders of ornamental plants, especially if they are paired with nectar data. The wider floral organs could be linked to a larger cavity for nectar (Erickson et al. 2022). Like conclusions in a study of ornamental asters, it is important to consider high flower density regarding nectar because the collective stand of flowers provides a rich nectar resource (Kalaman et al. 2022; Solman Raju 2004). As reported in Part I, most taxa had more inflorescences than *M. didyma* and *M. didyma* 'Jacob Cline', especially in the Athens study site. These factors could influence the foraging patterns and preferences of bee pollinators (Kalaman et al. 2022; Leonhardt and Blüthgen 2012). Our results are consistent with findings from a similar study on pollinator choice among *Salvia* species and cultivars (Braman et al. 2022). Such empirical evidence provides detailed resource value of *Monarda* species and cultivars, which allows considerations for wildlife when designing urban landscapes (Kalaman et al. 2022). As we increase the use of native ornamental plants in the landscape, we must also continue to assess the trade-offs among resource value and novel color, form, and disease tolerance (Wilde et al. 2015). Additionally, studies of insect visitations and detailed investigation of arthropod community on *Monarda* could provide a complete picture of the resource value of the taxon.

Conclusions

These studies were designed to inform breeders, the ornamental industry, landowners, park managers, civic entities, and consumers on the resource value of select *Monarda* species and cultivars and to assess the effect of differences in flower morphology. We documented significant differences in diameter of inflorescence, length and width of corolla and

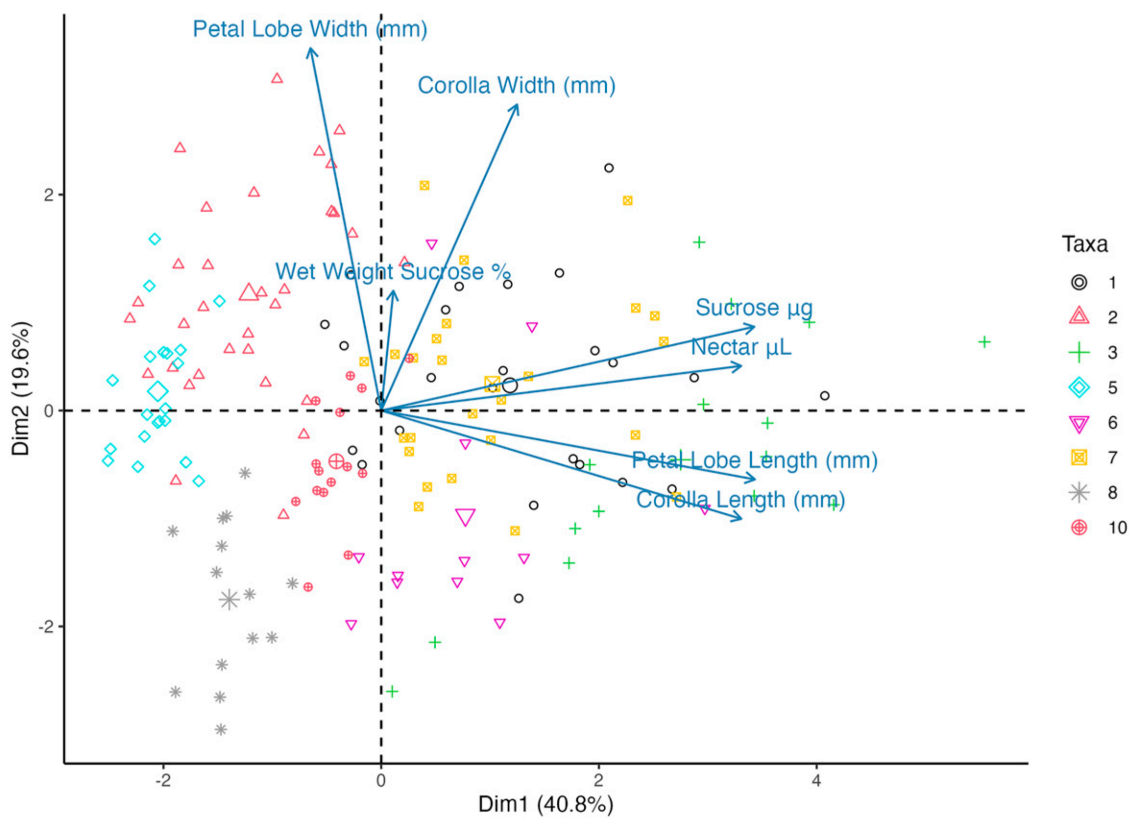

Fig. 5. The ordination results of the principal component analysis of the flower morphology and nectar production data among the *Monarda* tested in Blairsville, GA, USA, in 2020. The variables included are the width and length of the corolla and petal lobe (widthC, lengthC, widthPL, lengthPL, micrograms sucrose, microliters nectar, w/w sucrose). Taxa: 1—*Monarda* 'Raspberry Wine', 2—*Monarda punctata* (Georgia provenance), 3—*Monarda didyma* 'Jacob Cline', 4—*Monarda* Sugar Buzz® Grape Gumball Bee Balm, 5—*Monarda punctata* (New Jersey provenance), 6—*Monarda didyma*, 7—*Monarda* × 'Judith's Fancy Fuchsia', 8—*Monarda fistulosa*, 9—*Monarda bradburiana*, and 10—*Monarda fistulosa* 'Claire Grace'.

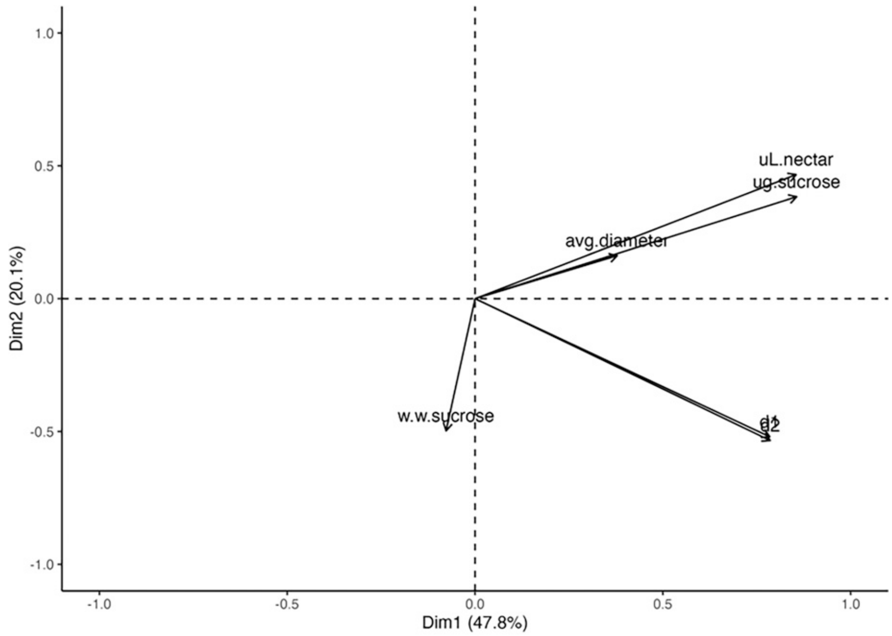

Fig. 6. Ordination results of the principal component analysis of the flower morphology and nectar production data among the *Monarda* tested in Athens and Blairsville, GA, USA, in 2021.

petal lobe, and nectar content among 10 *Monarda* taxa grown in montane and piedmont sites in Georgia.

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