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Evaluation of Native and Nonnative Ornamentals as Pollinator Plants in Florida: II. Floral Resource Value

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Abstract. **Consumer demand for novel, visually attractive ornamentals has often overshadowed the functional value plants may provide for flower-visiting insects. As native and nonnative species are hybridized for form, color, flowering, and disease resistance, it is important to assess whether some of these alterations influence plant nutrient quality for foraging insect pollinators. A study was conducted to ascertain the resource value of ornamental cultivars compared with their native congeners. The nectar volume and pollen quantity, viability, and protein content of 10 species of popular herbaceous flowering plants, commonly advertised as pollinator-friendly, were evaluated in northcentral Florida. Each genus encompassed a native and nonnative species, apart from pentas. Native species included blanket flower (*Gaillardia pulchella*), lanceleaf coreopsis (*Coreopsis lanceolata*), pineland lantana (*Lantana depressa*), and scarlet sage (*Salvia coccinea*). Nonnative species included Barbican™ yellow-red ring blanket flower (*Gaillardia aristata* 'Gaiz005'), Bloomify™ rose lantana (*Lantana camara* 'UF-1011-2'), mysty salvia (*Salvia longispicata* × *farinacea* 'Balsalmysty'), Lucky Star® dark red pentas (*Pentas lanceolata* 'PAS1231189'), ruby glow pentas (*Pentas lanceolata* 'Ruby glow') and UpTick™ Gold & Bronze coreopsis (*Coreopsis* × 'Baluptgonz'). Floral rewards differed significantly across species. The native scarlet sage exhibited the largest nectar volume per flower in the summer (2.13 ± 0.17 μL), followed by the nonnative mysty salvia (1.26 ± 0.17 μL). In the fall, ruby glow pentas exhibited the largest nectar volume per flower (1.09 ± 0.17 μL) compared with all other ornamentals. The composite flowers of the native and nonnative blanket flower and coreopsis species had the lowest nectar volume per flower regardless of sampling date. Likewise, ruby glow pentas displayed the highest quantity of pollen grains (96.29 ± 0.12) per sample, followed by Lucky star pentas (52.33 ± 0.12), and Barbican blanket flower (50.98 ± 0.12). Pollen viability was similarly high (92% to 98%) among all species, apart from Bloomify rose lantana (20%) and pineland lantana (48%). Pollen protein content was highest in Uptick coreopsis (11.378 ± 1.860 μg/mg dry weight) and Lucky star pentas (10.656 ± 3.726 μg/mg dry weight), followed by lanceleaf coreopsis (7.918 ± 1.793 μg/mg dry weight). These results largely showed that the nonnative ornamentals selected provided resource-rich floral rewards, comparable to native congeners. Still, care should be taken in making similar assessments of other modern floral types.**

Changes in land use patterns, resulting in overall reductions in natural habitat and nutrient-rich floral resources, have resulted in the decline of some wild and domesticated pollinator populations (Foley et al., 2005; Potts et al., 2010; Steffan-Dewenter and Westphal, 2008). To mitigate these effects, public interest in cultivating pollinator-friendly gardens in residential and commercial areas has risen (Campbell et al., 2017; Wignall et al., 2019). As this concern for pollinator health and well-being continues to grow, managed landscapes have become largely overshadowed by nonnative ornamentals (Hoyle et al., 2017; Thompson et al., 2003). Cultivation by breeders of modern ornamentals has led to selection for a series of traits such as improved disease resistance, prolonged floral phenology, noninvasiveness through reduced pollen production, and novel colors and forms broadly deemed attractive to the human eye (Horn, 2002; Mol et al., 1995; Noda et al., 1994). However, widely understudied is the resource value many of these modern floral forms offer to different pollinating insect communities, particularly compared with native, noncultivated plant species.

To ensure reproductive success, many native plants have solidified mutualistic relationships with flower-visiting insects over time. Traditionally, morphological and chemical traits such as distinct colors, shapes, sizes, and olfactory cues have conveyed honest information to pollinators that a nutrient reward in the form of nectar or pollen lay within (Bauer et al., 2017; Gumbert, 2000; Southwick and Southwick, 1983; Wright and Schiestl, 2009). Specifically, plant species reliant on animal-mediated pollination generate nectar solely as a floral reward: an incentive to transport pollen from male to female reproductive structures. Nectar comprises carbohydrates in fluctuating concentrations and serves as the primary energy source for many adult pollinating insects (Hill et al., 2001; Whitham, 1977). Some pollinators (e.g., bumblebees and butterflies) have shown distinct preferences for nectar-rich flowers, exhibiting the ability to distinguish even small variations in nectar concentrations among neighboring plants (Cnaani et al., 2006; May 1988). Further, bee pollinators amass the bulk of their protein content from pollen, which is required for proper larval development and adult reproduction (Brodschneider and Crailsheim, 2010; Michener, 2007).

Modern cultivars and native plant species have been appraised by some for their nutrient value to pollinating insects. Selection of modern floral traits by plant breeders such as larger flowers (Bauer et al., 2017), increased nectar rewards (Harder and Cruzan, 1990), or prolonged bloom periods (Stelzer et al., 2010) have had some positive effects on foraging insects. Conversely, features such as doubled ray florets, the omission of nectar-bearing floral spurs, and elongated corolla tubes have resulted in the inability of many pollinators to use flowers (Comba et al., 1999; Portlas et al., 2018). Adverse consequences like nonintuitive color preferences resulting from altered color and pigment accumulation, have also been reported in horticulturally modified ornamentals (Erickson et al., 2020; Noda et al., 1994).

Native plants aid in supporting biodiverse landscapes, alongside serving as refuge and food sources for pollinators and other wildlife (Burghardt et al., 2008; Diekelmann and Schuster, 2002; Ikin et al., 2013). Studies have indicated that customers are even willing to pay higher prices for native plants compared with their nonnative counterparts

(Helfand et al., 2006; Yue et al., 2012; Zadegan et al., 2008). Still, a major challenge to scaling up the use of native species in landscaping is the availability of native ornamental plants that are attractive, ecologically functional, and economically viable (Wilde et al., 2015). Consequently, the demand for native species must be matched by nursery production, which is a current limitation (White et al., 2018).

Although some have sought to compare the relative nutrient value and attraction of nonnative cultivars and native plants for pollinators (Native Plant Partnership, 2014; Seitz et al., 2020; Tew et al., 2021; Williams et al., 2011), research is largely site- and species-specific, leaving much opportunity for evaluating not only pollinator use of popular ornamentals but nectar and pollen attributes as well. Kalaman et al. (2021) investigated ornamentals commonly advertised as "pollinator-friendly" in provisional garden plots in Florida, finding few significant differences between native and nonnative plants in their ability to attract different generalist pollinator types. This study was conducted to determine the actual floral rewards that these plant species offered to visiting insect pollinators. Specific objectives were to compare the nectar quantity and the quantity, viability, and protein content of pollen in both native and nonnative ornamentals commonly advertised as pollinator-friendly.

Materials and Methods

Plant material and field conditions. Ten ornamental plant species were selected for use in this study, displaying a range of flower types, colors, textures, and growth habits as described by Kalaman et al. (2021). Native species included blanket flower (*Gaillardia pulchella* Foug.), lanceleaf coreopsis (*Coreopsis lanceolata* L.), pineland lantana (*Lantana depressa* Small var. *depressa*), and scarlet sage (*Salvia coccinea* Buc'hoz ex Etl.). Nonnative species included Barbican yellow-red ring blanket flower (*Gaillardia aristata* 'Gaiz005'), Bloomify rose lantana (*Lantana camara* 'UF-1011-2'), mysty salvia (*Salvia longispicata* ×*farinacea* 'Balsalmysty'), Lucky star dark red pentas (*Pentas lanceolata* 'PAS1231189'), ruby glow pentas (*Pentas lanceolata* 'Ruby glow'), and Uptick gold and bronze coreopsis (*Coreopsis* × 'Baluptgonz').

On 30 Apr. 2019, plants were installed at field plots located at the University of Florida Plant Science Research and Education Unit located in Citra, FL (Fig. 1). Specific experimental conditions were previously reported (Kalaman et al., 2021). Briefly, five white polyethylene raised bed rows were prepared with each bed containing 10 plots, each plot 3 m in length by 0.9 m in width, with 0.9 m of spacing between each row. Each plot contained a single species, with species arranged in a Latin Square design with split-plot restrictions, with five replicated plots per species. Depending on predicted size at maturity, two or three plants of each species were assigned to each plot. Each plant received 28.4 g of 15N–3.9P–10K of 8- to 9-month controlled-release fertilizer (Osmocote Plus; Scotts, Maryville, OH) upon planting. Plants were maintained with appropriate irrigation and fertigation as scheduled events throughout the 6-month study.

Nectar sampling protocol. Available floral nectar resources were quantified in terms of total nectar per flower per sampling period following protocols described by Hicks et al. (2016). The nectar production rate was evaluated by enclosing flowers of each ornamental species in mesh exclusionary bags for a period of 24 h before extraction sampling. This protocol allows for the quantity of nectar present in floral nectaries to be determined, less the rate of removal from foraging insect pollinators (Corbet, 2003). Bridal veil exclusionary bags (Carolina Biological Supply Company, Burlington, NC) were deployed as they are least likely to have microclimatic effects as compared with pellon, plastic, or paper bags, with limited impact on temperature and humidity (Wyatt et al., 1992). Each 14.0 × 10.4 cm bag was fully enclosed around an individual flower or inflorescence and secured with a string.

Regardless of flower morphology, 10 flowers were bagged for each ornamental species in each of three separate rows for a total of 30 samples per species. To address the variation in flower type among composite and non-composite flowers, sampling protocols were designated based on similar definitions made by Hicks et al., (2016). Entire composite flowers were defined as a single flower and are henceforth referred to as "flower" for simplicity. Individual florets of all noncomposite flowers were defined as a flower. For noncomposite species (Bloomify rose lantana, pineland lantana, scarlet sage, mysty salvia, Lucky star pentas, and ruby glow pentas), we sampled five flowers per plant on two plants per plot, totaling 10 flowers per species plot. For composite species (blanket flower, Barbican blanket flower, lanceleaf coreopsis, and Uptick coreopsis), we sampled five capitulate flowers on separate plants within each plot to allow similar sampling of five flowers per plant and 10 flowers per species plot.

After a period of 24 h, nectar sampling was conducted using 0.5-, 1.0-, and 5.0-µL glass microcapillary tubes (Drummond Scientific, Broomall, PA), dependent on the nectar volume present. For each of the 10 flowers sampled, floral nectaries were probed using as many microcapillary tubes as necessary until no nectar could be further extracted. Field sampling took place twice, first in the summer season (3 July 2019) and then in the fall season (2 Oct. 2019). Total nectar volume was calculated as the total measured nectar column length (millimeters), divided by the total length of the microcapillary tube (32 mm), multiplied by the microcapillary unit volume (0.5, 1.0, or 5.0 µL).

Pollen sampling and storage protocol. To examine floral rewards in terms of pollen, flowers of all ornamental species were collected preanthesis when buds were near opening. Ten flowers were collected from each species plot in three rows, totaling 30 samples per species (as in the nectar sampling previously described). As often as possible, 10

Fig. 1. Depiction of field site and ornamental species located at the Plant Science Research and Education Unit (PSREU) in Citra, FL. Photo courtesy of Heather Kalaman.

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flowers were sampled from at least two individual plants within each species plot as described earlier. When overall floral availability was low and samples could not be collected from separate plants or blocks, as many flowers as possible were collected across the site to allow for a uniform quantity of 30 samples per species. While collecting, the peduncle of each flower was cut close to the stem, placed upright in plastic vials containing water, and allowed to open in a laboratory under natural light conditions. For composite species with very small flowers (blanket flower, Barbican blanket coreopsis, lanceleaf coreopsis, and Uptick coreopsis), each of the 30 samples contained five individual disk florets collected from a single composite head as flowers opened before dehiscing any pollen. For inflorescences with larger individual flowers (Bloomify rose lantana, pineland lantana, Lucky star pentas, scarlet sage, and mysty sage), each of the 30 samples consisted of one flower collected before opening and dehiscing pollen. Flowers were immediately placed in 1.5-mL microcentrifuge tubes (Fisherbrand, Waltham, MA) with 1000 µL of 70% ethanol and stored at 4 °C until further analyses to prevent germination or pollen tube growth (Mesnoua et al., 2018). All additional samples collected for future protein analysis were stored similarly in 1.5-mL microcentrifuge tubes with 1000 µL of 70% ethanol at –80 °C (Mesnoua et al., 2018).

Pollen quantification. Anthers were slightly crushed to ensure the dislodging of all pollen grains into the solution within each microcentrifuge tube. To attain a measurable quantity of pollen, samples were vortexed for a minimum of 15 s, and counts were performed on a standardized volume aliquot of 20 µL. The specified aliquot was pipetted onto a hemocytometer (Daigger Scientific, Buffalo Grove, IL) and enclosed with a glass cover slide (Begcy et al., 2018). Mature pollen grains of all 10 species were observed under a microscope (Zeiss Axio Imager Z1, Oberkochen, Germany) equipped with a monochromatic camera (Begcy et al., 2018). To quantify pollen, three samples were selected at random for each ornamental species across three plots. Pollen counts were replicated four times from the same sample, totaling 36 individual counts for each ornamental species across nine independent samples per species. Each microcentrifuge tube sample was then stored for future viability analysis.

Pollen viability staining. To evaluate pollen viability of each ornamental species, pollen staining was carried out on a standardized volume aliquot of 100 µL. These samples were taken directly from the same 1000-µL microcentrifuge tubes used for pollen counts. Each sample was vortexed for 15 s and a 100-µL aliquot was extracted and pipetted into a separate 2.0-mL microcentrifuge tube (Seal-Rite Ocala, FL) with 10 µL of staining solution (3.33 g/L iodine and 6.66 g/L potassium iodide) as determined to be suitable by Begcy et al. (2018). Samples were centrifuged for a period of 15 s, and 20-µL aliquots were analyzed on a hemocytometer (Daigger Scientific, Buffalo Grove, IL). Pollen that was stained dark blue in color was considered viable. These counts were made four times for each of the three species plots sampled, totaling 36 individual viability counts per species.

Pollen protein analysis. Floral tissues were harvested from each of the 10 ornamental plant species and ground in liquid nitrogen. Three samples were analyzed per species, each consisting of a standardized weight of ground floral tissue. Crude extracts were prepared using urea buffer [8 M Urea, 10 mM Tris-HCl (pH 6.8), 10% (v/v) glycerol, 1% (w/v) SDS, 5 mM DTT, and 1% (v/v) protease inhibitor cocktail (for plant cell and tissue extracts; Sigma-Aldrich, St. Louis, MO)]. Total protein was determined using a colorimetric assay (Bio-Rad Protein Assay Kit II, Bio-Rad Laboratories, Hercules, CA). Nine dilutions of a protein standard containing 0 to 20 µg/mL protein were used. A standard curve was prepared each time the assay was performed. The absorbance at 595 nm (A_{595nm}) was then measured with a microplate spectrophotometer (Epoch Microplate Spectrophotometer; BioTek, Winooski, VT) and the normalized absorbance values were plotted vs. the mass concentration (µg/mg).

Statistical analysis. Response data were analyzed using generalized linear mixed model procedures as implemented in SAS PROC GLIMMIX (SAS/STAT 15.1; SAS Institute, Cary, NC). Random effects were based on the underlying Latin Square Design with a split-plot restriction on randomization. The assumptions for linear models with respect to residuals were evaluated graphically by inspecting the residual plots as suggested by Kozak and Piepho (2018). Nectar volume was analyzed using a normal distribution function. Species, sampling date (in the case of nectar), and their two-way interaction (for nectar) were considered fixed effects. Nectar sampling for each experimental unit across two sampling dates required R-side modeling. The unstructured (UN) model was the best fit based on the AICc criterion (small-sample Akaike information criterion). Least squares interaction means were calculated using the "bottoms-up approach," i.e., a significant two-way interaction determined the least squares means to be calculated. Species were compared by sampling date (for nectar) using the SLICEDIFF option of the LSMEANS statement in the aforementioned procedure means without correction for multiple comparisons as suggested by Milliken and Johnson (2009) and Saville (2015). Pollen counts were analyzed using a negative binomial distribution because of overdispersion issues indicated by the ratio χ^2/df greatly exceeding unity, and pollen viability was analyzed using a binomial distribution function. Pollen protein content among the 10 plant species was analyzed using one-way analysis of variance ($P = 7.27e^{-07}$). Statistical differences among species were determined using Duncan's multiple range test at the significance level of 0.05.

Results

Nectar quantity. Overall, there was no significant difference between native and nonnative plant species in their measured nectar volume per flower. Rather, nectar quantity significantly varied by plant species ($P = 0.0001$) and sampling date ($P = 0.0020$), revealing a significant two-way interaction ($P = 0.0001$) between plant species and sampling date (Fig. 2). On the first sampling date (3 July 2019), nectar volume per flower ranged from 0.09 to 2.11 µL. The native scarlet sage had the largest nectar volume (2.11 ± 0.13 µL), followed by the nonnative mysty salvia (1.26 ± 0.13 µL) and Lucky star pentas (0.64 ± 0.11 µL). Notably, the native scarlet sage had 1.7 times more nectar than the nonnative mysty salvia. There were no significant differences of nectar volume between the native and nonnative blanket flower, coreopsis, and lantana. On the second sampling date (2 Oct. 2019), nectar volume per flower ranged from 0.02 to 0.88 µL (Fig. 2). Ruby glow pentas exhibited the largest nectar volume per flower (0.88 ± 0.18 µL) compared with all other ornamental species evaluated. Specifically, ruby glow pentas produced two times more nectar per flower than Lucky star pentas. There were no significant differences of nectar volume between the native and nonnative blanket flower, coreopsis, lantana, and salvia.

Pollen quantity. Pollen rewards—expressed as the average quantity of pollen grains per 20-µL sample—varied significantly among ornamental species evaluated ($P = 0.0001$; Table 1). Specifically, ruby glow pentas had significantly more pollen grains per sample (96.29 ± 0.12) than all other ornamentals. The second largest pollen producers were Lucky star pentas (52.33 ± 0.12), Barbican blanket flower (50.98 ± 0.12), Bloomify rose lantana (40.49 ± 0.11), and lanceleaf coreopsis (39.01 ± 0.11). Finally, scarlet sage had the lowest number of pollen grains (4.02 ± 0.19) compared with all other species. Differences in pollen grain numbers were also observed when comparing native and nonnative species within each genus. For example, the native lanceleaf coreopsis produced 1.5 times more pollen than the nonnative Uptick coreopsis. The native blanket flower, pineland lantana, and scarlet sage had 1.8, 1.6, and 7.5 times less measured pollen compared with their respective nonnative cultivated forms.

Pollen viability. Pollen viability, expressed as the total proportion of viable pollen grains per 20-µL aliquot sample, was significantly different across plant species ($P = 0.0001$; Table 1). Total proportion of pollen viability per 20-µL sample was similarly high (92% to 98%) among all species except Bloomify rose lantana (20%) and pineland lantana (48%). Specifically, the female-sterile, nonnative Bloomify rose lantana had the lowest pollen viability, 2.4 times lower than the native pineland lantana and up to 4.9 times lower than all other species evaluated.

Pollen protein. Plant provenance (native or nonnative plant status) had no significant

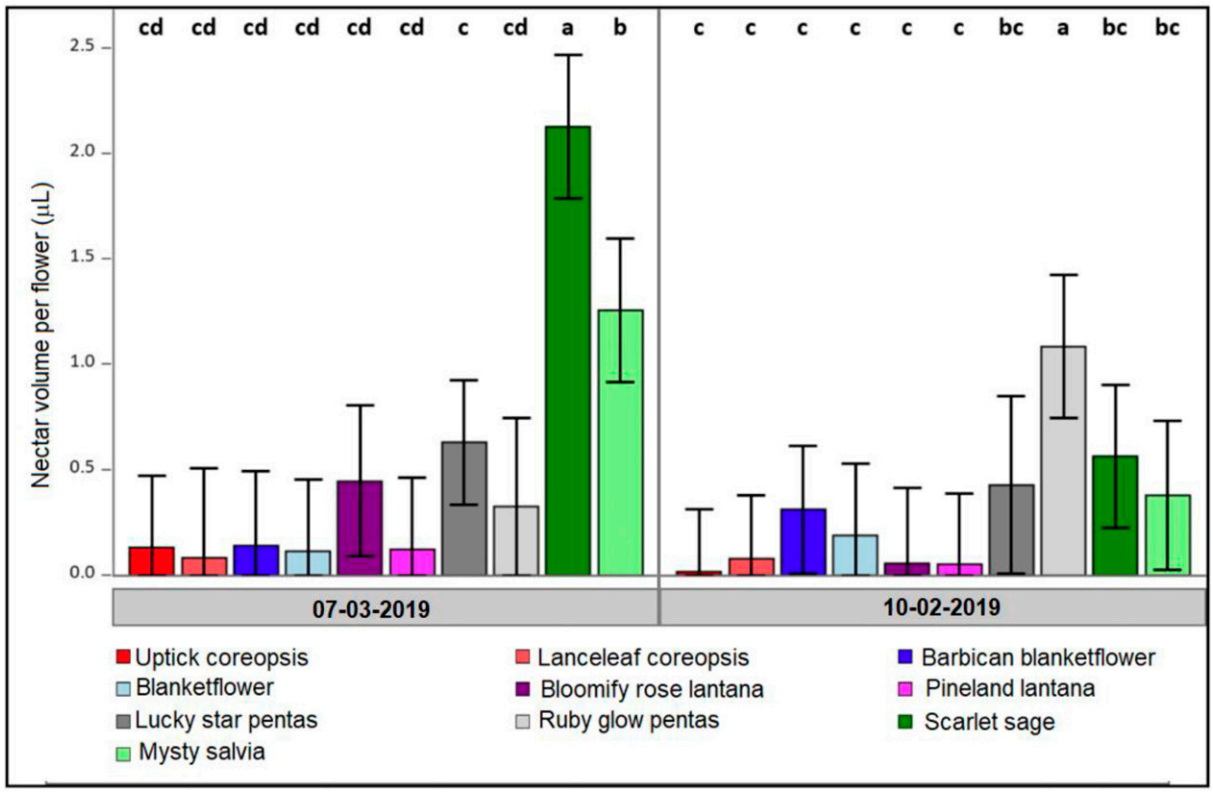

Fig. 2. Least square (species and sample time) interaction means for average nectar volume per flower (in microliters) sampled on two dates (3 July 2019 and 2 Oct. 2019) for each of the 10 ornamental species evaluated. Ten flowers were bagged for each ornamental species in each of three separate rows for a total of 30 samples per species. Total nectar volume was calculated as the total measured nectar column length (mm), divided by the total length of the microcapillary tube (32 mm), multiplied by the microcapillary unit volume (0.5, 1.0, or 5.0 µL). Means ± 95% confidence limits are presented. Means within sample time sharing letters are not significantly different at $P \leq 0.05$.

effect on overall measured pollen protein. The pollen protein content of plant species ranged from 2.28 to 11.38 µg/mg dry weight. The nonnative Uptick coreopsis (11.38 ± 1.86 µg/mg dry weight) and Lucky star pentas (10.66 ± 3.73 µg/mg dry weight) had greater protein content than all other ornamental species evaluated. The native lanceleaf coreopsis had the second greatest protein content (7.92 ± 1.79 µg/mg dry weight) followed by pineland lantana (5.73 ± 0.80 µg/mg dry weight). Within each genus, nonnative species had similar amounts of pollen protein as respective native species, with two exceptions. The nonnative Uptick coreopsis had 1.4 times greater protein content than the native lanceleaf coreopsis, whereas the modern hybrid Lucky star pentas had 4.7 times more protein than pollen from the traditional nonhybrid ruby glow pentas.

Discussion

Over time, as many urban landscapes have become aesthetically enriched by ornamentals, both native and horticulturally modified in type, there has been a continued need to assess their resource value for pollinating insect communities. Results from our study showed that these ornamental species differed in their nectar volume dependent on sampling date and floral morphology. Furthermore, pollen quantity, viability, and protein content varied significantly among the ornamental plants evaluated. However, there were no consistent differences between native and nonnative plants in their measured floral rewards.

Floral morphology is often associated with nectar volume, and flowering plants possessing deep corolla tubes have shown to be greater nectar producers than those with short or shallow corolla tubes (Dafni, 1991; Gomez et al., 2008; Harder and Cruzan, 1990). This difference is generally attributed to larger flowers secreting higher quantities of photosynthates, a capacity for deeper floral tubes to physically hold more nectar, and the ability to slow down nectar evaporation rates within

Table 1. Least square means for quantity, viability, and protein content of pollen grains collected from six nonnative and four native ornamental species grown in northcentral Florida for 6 months.

Plant species	Pollen no.[z] (20 µL)	Pollen viability[z,y] (%)	Pollen protein[z] (µg/mg dry wt)	Native to United States
Uptick coreopsis	25.75 ± 0.16 e	97.9 ± 0.40 a	11.38 ± 1.07 a	No
Lanceleaf coreopsis	39.01 ± 0.11 bcd	97.0 ± 0.25 a	7.92 ± 1.04 b	Yes
Barbican blanket flower	50.98 ± 0.12 b	94.3 ± 0.27 ab	3.06 ± 0.21 cd	No
Blanket flower	28.72 ± 0.11 de	95.9 ± 0.26 ab	4.22 ± 0.19 cd	Yes
Bloomify rose lantana	40.49 ± 0.11 bc	20.5 ± 0.21 d	3.41 ± 0.52 cd	No
Pineland lantana	25.85 ± 0.13 e	48.2 ± 0.25 c	5.73 ± 0.46 bc	Yes
Lucky star pentas	52.33 ± 0.12 b	98.1 ± 0.27 a	10.66 ± 2.15 a	No
Ruby glow pentas	96.29 ± 0.10 a	96.3 ± 0.21 ab	2.28 ± 0.16 d	No
Scarlet sage	4.02 ± 0.19 f	92.2 ± 0.31 ab	2.76 ± 0.69 d	Yes
Mysty salvia	29.97 ± 0.11 cde	92.5 ± 0.23 ab	3.18 ± 0.31 cd	No

[z]Means ± SE are presented. Means with similar letters are not significantly different at $P \leq 0.05$.

[y]Pollen viability expressed as a proportion of total pollen grains per 20-µL aliquot sample. Means were compiled from 36 separate 20-µL aliquots for each of the 10 ornamental species.

deeper flower tubes (Ornela et al., 2007; Pleasants, 1983). Consistent with this theory, our results showed that salvias and pentas—both of which possess longer corolla tubes compared with other species evaluated—produced high quantities of nectar. Conversely, lower volumes of nectar per flower were typically observed for the Asteraceae species (blanket flower, Barbican blanket flower, lanceleaf coreopsis, Uptick coreopsis), regardless of sampling date. Still, the nature of composite disk flowers, each containing an immense quantity of very small florets, can present difficulty in nectar extraction and quantification and may have contributed to low recorded nectar levels. The resource value of many composite species is easily underestimated for this reason (Hicks et al., 2016). In fact, when the high flower density of ornamental asters is considered, smaller levels of nectar per floret or entire flower head could still collectively provide rich nectar resources (Solman Raju, 2004). In a previous study, native and nonnative composite species were highly attractive to several insect groups, specifically bee pollinators, although this finding may be attributed to pollen rather than nectar rewards (Kalaman et al., 2021).

As nectar volume can vary considerably based on the time of day (Galetto and Bernardello, 1992), floral age (Kato and Sakai, 2008), and season (Farkas et al., 2012), the importance of quantifying the available nectar content of flowering species at different times within an environment was further demonstrated in our study. Many flowering species secrete greater volumes of nectar earlier in their maturity to better attract foraging pollinator groups, thereby ensuring higher reproductive success rates through the transfer of pollen (Kato and Sakai, 2008). Likewise, the majority of the ornamental species evaluated showed higher concentrations of nectar per flower in July compared with October. However, some species (e.g., pentas) showed notably high nectar volume in the fall, possibly due to artificial selection for nectar production in these cultivated plants. In this study, plants were irrigated sufficiently to avoid drought stress. Under drought stress, the results may have been different because nectar production generally decreases during periods of drought, but the magnitude of this effect can vary across plant species (Carroll et al., 2001; Gallagher and Campbell 2021; Kuppler and Kotowska 2021; Rering et al., 2020). Our results further highlight the need to sample nectar across seasons as nectar production, and relative differences across taxa, can vary over time. Specifically, butterflies may be the most responsive to nectar quantity because they generally only forage for nectar (unlike bees, which forage for pollen as well). We thus expected their foraging preferences to strongly reflect nectar volume. Interestingly, although both salvia species produced the greatest nectar volumes per flower during the first sampling date, butterflies were still significantly more attracted to lantana species across all three seasons (May–June, July–August and September–October) (Kalaman et al., 2021). Further, Lepidoptera require a surface to land on before feeding, lacking the ability to hover-feed like other flower-visiting insects (Linton, 2007). The morphology of lantana inflorescences may have better provided a more suitable "landing pad" for these insects than the salvia ornamentals, which have horizontal-facing floral tubes that are generally only accessible to pollinators that can crawl inside, grasp onto floral tissue, or hover.

Collectively, our results on pollen quantity, pollen viability, and pollen protein content are invaluable to gaining a better understanding of the nutrient value of modern hybrids for pollen-gathering insects. While viability is important to indicate species dispersal, fitness, and succession (Impe et al., 2020), actual protein content can further quantify its dietary value to pollinators (Roulston et al., 2000). Furthermore, previous research has positively correlated pollen viability to pollen protein content in some flowering species (Yeamans et al., 2014). In general, we did not find consistent differences in pollen quantity and quality between native and nonnative species; however, there were some differences within individual genera. To illustrate, while the native blanket flower produced less pollen than the nonnative Barbican blanket flower, they exhibited similar viability and protein content. Moreover, the native lanceleaf coreopsis produced more pollen with similar viability, but less protein than the nonnative Uptick coreopsis. In general, the compound flowers of many Asteraceae species are reported to have large quantities of pollen, lengthy bloom periods, and frequent pollinator visitation (Norcini and Aldrich, 2007; Rollings and Goulson, 2019). While these qualities suggest they may be ideal nutrient resources for a variety of bee pollinators, studies have indicated that the protein quality of Asteraceae species falls on the lower to intermediate end of the spectrum as compared with other plant families (Human et al., 2007; Nicolson and Human, 2013). However, we found that within Asteraceae, some species (Uptick and lanceleaf coreopsis) had notably high pollen protein content, comparable to non-Asteraceae ornamentals. These results illustrate the need for species-specific studies because cultivated plants in particular may not follow general trends at the family level. Furthermore, foraging patterns and preferential selection by bee pollinators is highly influenced by nutrient requirements determined by body size and maturity, as well as colony size for social species (Leonhardt and Blüthgen, 2012). Although evidence exists that bee pollinators, such as bumble bees, show preferences for high-quality pollen (Vaudo et al., 2015), honey bees do not seem to forage with a specific predilection for high-protein pollen (Pernal and Currie, 2001; Van der Moezel et al., 1986).

The quantity of pollen and its accessibility—highly influenced by floral morphology—undeniably has an impact on the decisions made by foraging insects (Roulston et al., 2000). Notably, Lucky star pentas had one of the highest pollen protein contents and the third highest nectar content across all ornamentals evaluated. Yet visitations to this ornamental were largely made by wasp pollinators in the previous study (Kalaman et al., 2021). Although there are some wasp species in the family Vespidae that are known to consume pollen (Gess, 1996; Hunt et al., 1991), the majority of both social and solitary species feed on nectar, extrafloral nectar, and honeydew as adults (Wackers, 1999). It is likely that nectar or pollen chemistry and floral scent are largely influencing a distinct preference by wasps and not bees for the pentas cultivars evaluated in our study (Shuttleworth and Johnson, 2009).

This study is the first report to compare the floral rewards between the native pineland lantana and the nonnative, female-sterile Bloomify rose lantana. As a product of a planned breeding program aimed to produce highly infertile lantana, nonfruiting Bloomify rose lantana is triploid in nature with pollen stainability reduced by 99% compared with the wildtype invasive form (Deng et al., 2017). Using a fluorescein diacetate staining solution, Deng et al. (2017) reported average pollen stainability of Bloomify rose lantana to be 9.7%. Although this percentage is lower than the 20% pollen stainability reported in our study (we used an iodine and potassium iodide staining solution), it supports our findings that overall, Bloomify rose lantana has very low pollen viability. Still, its combined quantity of flowers and quality of nectar and pollen were sufficient in attracting both lepidopteran and bee pollinators (Kalaman et al., 2021).

Conclusions

This study showed that the majority of nonnative ornamental cultivars evaluated provided nutritional floral resources in similar ways as native species. Although results from our study showed that these newer, horticulturally modified ornamentals were relatively resource rich, it also demonstrates the critical need to evaluate cultivated floral types individually because this finding may not hold true for other modern ornamentals. Additionally, because specialist pollinators and other native fauna possess tightly woven relationships with native plant species, nonnative ornamentals will not satisfy the explicit ecological needs of many insect communities across a landscape gradient. Therefore, we suggest that the nonnative ornamentals evaluated in this study be incorporated, if at all, into modified landscapes as an accompaniment to native plants, increasing floral diversity rather than replacing native plant species. Furthermore, the data presented herein are a first report of both pollen and nectar content for many of these ornamental species and may be foundational to future pollinator-plant studies with similar objectives. Assessing the resource value of both native and nonnative ornamentals for cultivated gardens should be a goal of future research seeking to support our pollinating insect communities.

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