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Is the Nectar Sugar Content the Key to Improving Onion and Bunching Onion Seed Yield?

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Abstract: Bunching onion as well as onion show great variability in seed yield among cultivars. Understanding the role of floral rewards and attractants to pollinator species is crucial to improving crop seed yield. Nectar sugar concentration is one of the most important factors affecting bee-flower interaction. The objective of this work was to determine the differences in nectar sugar composition between onion and bunching onion lines grown in the same location during two consecutive cultivation cycles and in two different productive areas under open field conditions, and the relationship of these sugars with seed yield. The results obtained showed that, regardless of the season and the location, bunching onion produced higher seed yields than onion, and the sugar content was always higher than in onion. Fructose represented on average 56% of the total sugars, glucose 34% and, sucrose 9% of the total amount of sugars in nectar. There were differences between the two locations studied. Fructose content had a significant correlation with seed yield. The amount of sugars in bunching onion could be the reason why this species does not have pollination problems in contrast to onion plants. In addition, the differences found in seed yield between locations could provide options for seed companies to make production decisions.

Keywords: environmental conditions; fructose; Welsh onion



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1. Introduction

About 1250 species of perennial bulbous plants belong to the *Allium* genus [1]. Bunching onion (*Allium fistulosum* L.), also known as Welsh onion, spring onion, or scallion, belongs to section *cepa* of this genus, and is an important vegetable crop in East Asian countries, especially Japan, China, and Republic of Korea [2–4]. On the other hand, onion (*Allium cepa* L.) is among the world's oldest cultivated plants, and is one of the most important vegetable crops grown worldwide and (along with leek) are the most popular edible Alliums in most regions of the world [4,5].

Bunching onion was traditionally grown in Japan using seeds from the local producers. Therefore, there was considerable genetic variation within populations. Thus, breeding work to improve cultivar performance and homogeneity was needed. The main production areas are distributed in the southern part of Japan, Republic of Korea, and China. In South America, Colombia has a considerable production of bunching onion for domestic consumption [2,6]. Otherwise, onion cultivation is spread around the world, with cultivars with great diversity in shape, color, flavor, quality, and breeding with a focus on adaptations to new climates. However, the isolation of male sterility in cv. 'Italian Red' was the most

important event in the history of onion crop breeding, having a great impact on later onion breeding and bringing about the development of onion hybrid cultivars [5].

Nectar is an important reward for pollinators and its production increases the reproduction of many plants [7]. Sugars are the main compounds in nectar. Fructose, glucose, and sucrose differ greatly through the different species [8], and they are considered to have a direct impact on pollinator visitation and fruit yield [1,7,9–11]. The bunching onion umbels are smaller than onion umbels, but their flowers are larger. In both species, honeybees (*Apis mellifera* L.) are the most efficient and practical pollinator of these crops owing to their great affinity for nectar and ability to transfer pollen efficiently [12]. Nectar sugar concentration is one of the most important factors affecting bee–flower interaction. The foraging activity of honeybees on the inflorescences is highly dependent on the interactions of several factors such as nectar quality, sugar quantity, and environmental conditions, among others [1]. Seeds are formed as a result of cross pollination by insects. In consequence, any loss of attractiveness in these flowers usually results in reduced pollinator visitation, reduced pollen transportation, and reduced seed yields. Hence, increasing seed yield depends on increasing bee activity, which in turn depends on floral rewards, especially sugars [13,14].

Onion hybrids offer greater agronomic performance (increased yield and uniformity) and the possibility of intellectual property protection to seed companies. The production of hybrid onion seed is based on systems of cytoplasmic-genic male sterility [15]. The lead of hybrids over open-pollinated (OP) varieties has been reported by several researchers [5]. Nowadays, the market is mostly dominated by seed companies that produce most of the seeds in defined areas with specific climatic conditions, and nearly two-thirds of the cultivars in their catalogs are hybrids [16]. However, reports from these companies and several studies have revealed that hybrid seed yield is erratic and considerably lower compared to OP varieties [12,17]. In addition, seed companies have reported that bunching onion seed yield can also be irregular. All the cultivars available on the market in the 1980s were OP, and considering that the bunching onion is a typical allogamous crop that arose through protandry, with a high outcrossing rate, these old cultivars were characterized by a high level of heterogeneity [18]. However, it is not clear if the poor seed yield is due to the reduced vigor of inbred lines or if the pollinating bees do not visit certain lines [19]. This is the reason why companies nowadays mostly work with interspecific hybrids of *Allium fistulosum* × *Allium cepa* in order to obtain better yields. Examples of differential intervarietal pollinator attractiveness include such species as alfalfa, carrot, sunflower, and soybean [20], and we have reported differences among onion cultivars in previous works [14,21,22].

A suitable area for seed production of both species must have low winter temperatures, cold enough to induce premature flowering or bolting, and dry weather between blooming and seed ripening [23]. In the last few years, bunching onion has become an important alternative for growers. However, the cultivated areas as well as yields are still limited. Seed yield is a major trait that has received little research attention in bunching onion. Since the funding of research schemes and overall agricultural research vision have almost exclusively been organized by seed companies, little data is available about bunching onion seed production and none related to the nectar composition of this species. Research related to the characteristics that define the potentialities of the clones and/or varieties of bunching onion that are commercially exploited is almost non-existent [24]. In addition, it seems that there is a certain variability among bunching onion lines attracting pollinators, but no research has documented a genetic basis [19]. Nonetheless, seed companies report that pollination problems are not recorded in this species, as occur in onion hybrids. Although it is to be expected that seed yield depends on the heterotic value of the cross between lines, there are male sterile lines that, regardless of the fertile line used, always give poor seed yield. Therefore, there are factors in these lines that would be related to their low attractiveness to bees beyond genetic compatibility. Bearing in mind the above-mentioned facts and that nectar sugars play an essential role in plant fitness, thus, the objective

of this work was to determine the differences in nectar sugar composition and sugar concentration between onion and bunching onion lines, and the relationship of these sugars with seed yield.

2. Materials and Methods

2.1. Plant Material

The bunching onion material used was an interspecific hybrid line (*Allium fistulosum* × *Allium cepa*) (F × C) and for onion was a male sterile line (MSL), obtained from Bayer. Assays were carried out in two commercial fields: Location A: Lujan de Cuyo, Mendoza, Argentina (33°06'42" S, 68°52'59" W) and Location B: San Juan, Argentina (31°46'16" S, 68°32'16" W), during 2018 and 2019 with a random plot design. Location A had a sandy loam soil and location B a loam soil. Bunching onion plants were cultivated at a density of 20 bulbs/m in a double row planting system, while onion were planted at a density of 10 bulbs/m in single row, 1 m apart. The 4:1 ratio of sterile/fertile plants was used, which is typical in onion commercial seed production. This distribution is proved by the seed company before releasing the materials to the growers. The male line used always had the best compatibility with the female line and it depended on the genotype of the used material. Pesticides were not used during the experiment; plants were watered by level-basin irrigation system. The fertilization program included 160 kg N/ha, 80 kg P/ha, and 40 kg K/ha for both crops. Plants of both species flowered from the end of September to the end of October.

2.2. Environmental Factors

Air temperature (°C) and relative humidity (%), wind speed (m/s), and rain (mm) data were taken from weather stations in both locations during the flowering period. In addition, temperature range, i.e., the difference between the highest and lower temperature during the day, was taken into account (ΔT).

2.3. Nectar Extraction

At midday, 50 umbels per plot of each species were randomly chosen from umbels that were between 40 and 60% of flowering. Only one umbel per plant was chosen. The collection of nectar was achieved by removing anthers, filaments, and peduncles from freshly opened flowers. Following excision from umbel, flowers were centrifuged in a 1.5 mL microtube at 13,000 × g rpm, at 4 °C during 20 min, to extract the nectar. An average of 200 µL of nectar was extracted from all the opened flowers of 10 umbels per plot. Nectar was preserved at −80 °C until analysis.

2.4. Nectar Chemical Analysis

Nectar samples were filtered and diluted 1:10 (*v/v*). Sugar analysis was completed using a Shimadzu LC 20A chromatograph coupled to a diode array detector and a Rheodyne injector with 20 µL sample loop, using an alkylamine column (5 µm, 250 by 4.6 mm) water/acetone (80:20 *v/v*) as mobile phase, at 1 mL/min. Fructose, glucose, and sucrose were analyzed. All the nectar analyses were completed in triplicate. Concentration of sugars was expressed as grams per liter of nectar [25].

2.5. Seed Yield

When seed development was completed, umbels were harvested and dried for 20 days. In location A, umbels were harvested during the last week of November and first week of December. In location B, umbels were harvested during the second and third week of November. The umbels were spread in a 20 cm thick layer and sundried. Umbels were turned regularly to achieve a uniform drying and to avoid rotting. Humidity was controlled every 2 days with a humidity sampler John Deer calibrated for onion and when the average humidity reached 14%, seed threshed was performed. Seeds were cleaned, collected in bags, and weighed to calculate seed yield and expressed as kilograms per hectare (kg/ha).

2.6. Statistical Analysis

Values were expressed as means \pm standard deviation. Data were analyzed by analysis of variance (ANOVA) to test the significant differences. All the analyses were completed in triplicate. Means were compared using Tukey's test. The results were considered significant at $p \leq 0.05$ unless specified otherwise. All analyses were performed using statistical package InfoStat2020 for Windows (Córdoba, Argentina).

3. Results

3.1. Seed Yield

Seed yield was always higher for bunching onion than onion in both seasons and both studied locations. In location A (Mendoza) yields were higher, around 15% more yielding than San Juan, location B (Figure 1). In addition, seed yield for the same line studied during two productive seasons showed marked differences, being the most yielding in the first season. Furthermore, there were interactions between year \times species, location \times species, location \times year, and location \times species \times year. However, 60% of the variability in seed yield was explained by the species (Table 1).

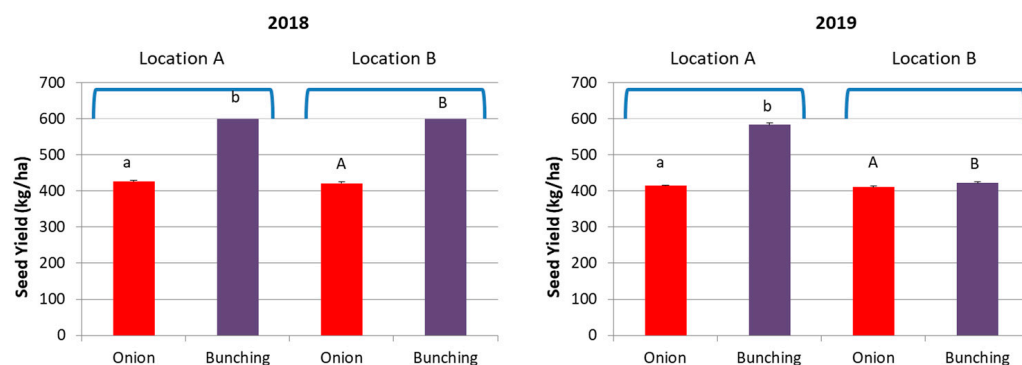


Figure 1. Bunching onion and onion seed yield in location A: Mendoza and location B: San Juan during 2018 and 2019. Seed yield is expressed as kilograms per hectare. Different letters present significant differences $p \leq 0.05$ for the species in the same location.

Table 1. ANOVA table of seed yield variation due to species, location, year, and their interaction.

Source	d.f	Sum of Square	F-Value	p-Value
SP	1	127,896 (60.22%)	10,621.12	<0.0001
Location	1	13,728.17 (6.46%)	1140.06	<0.0001
Year	1	26,533.5 (12.49%)	2203.47	<0.0001
SP \times Location	1	11,180.17 (5.26%)	928.46	<0.0001
SP \times Year	1	18,260.17 (8.59%)	1516.42	<0.0001
Location \times Year	1	7210.67 (3.39%)	598.81	<0.0001
SP \times Location \times Year	1	7350 (3.46%)	610.38	<0.0001
Error	16	192.67 (0.09%)		
Total	23	212,351.33	100	

SP: Species.

3.2. Environmental Factors

We observed significant differences between the environmental factors during the flowering period of both studied locations. Location A had lower temperatures than location B, with higher relative humidity and less wind. In addition, the range of temperature was wider in location A (Table 2). In both locations, it rained only one day through the flowering period. The rain was registered in the early days of flowering and in both locations and it was lower than 10 mm. During 2018, relative humidity was higher than 2019 and the maximum temperature was higher than the next year. The amplitude in temperature was lower than in 2019 (Table 2).

Table 2. Environmental factors, maximum (Tmax) and minimum (Tmin) temperatures (°C), temperature range (ΔT), maximum (RHmax) and minimum (RHmin) relative humidity (%), wind speed (m/s) during crop season for the different locations and productive seasons.

Location	Year	Tmax	Tmin	RHmax	RHmin	Wind	ΔT
A	2018	21.79 \pm 0.35 a A	8.85 \pm 0.28 a A	93.23 \pm 0.76 b B	37.24 \pm 3.31 b B	5.07 \pm 2.01 a B	17.34 \pm 2.20 b B
B		26.56 \pm 1.50 b A	14.26 \pm 0.30 b B	69.66 \pm 5.06 a A	26.1 \pm 6.97 a B	10.46 \pm 0.75 b B	12.8 \pm 1.25 a A
A	2019	25.02 \pm 0.71 a A	6.32 \pm 0.80 a A	75.33 \pm 1.02 b A	23.23 \pm 2.73 b A	3.33 \pm 0.07 a A	18.70 \pm 0.88 b B
B		28.5 \pm 0.70 b B	14.75 \pm 0.40 b B	72.08 \pm 2.23 a A	19.49 \pm 2.11 a A	7.41 \pm 0.01 b A	13.74 \pm 0.32 a A

Location A: Mendoza; location B: San Juan, Argentina. Values represent mean \pm SD of data between 10 and 90% of flowering. Values in the same column with different letters present significant differences $p \leq 0.05$. Lower cases denote differences between locations in the same year; upper cases denote differences between years for the same location.

3.3. Nectar Composition

Fructose was in higher concentration, representing around 50–65% of the total sugars, followed by glucose (20–43%) and much lower levels of sucrose (2–14%) in both species. Bunching onion always showed higher levels of sugars, with an average of 15% more sugars than onion. In addition, sugars were higher in location A, with around a 25% higher concentration than in location B (Figure 2). Levels of sucrose were always higher in location B for the same species. In addition, sucrose showed differences between both seasons, while the hexoses did not show differences between the different years of study. Glucose did not have differences between both species, whilst the other sugars showed marked differences between species ($p \leq 0.05$). The ANOVA revealed significant interactions between species and location, and the greatest variability was given by the different species for fructose and location for glucose and sucrose.

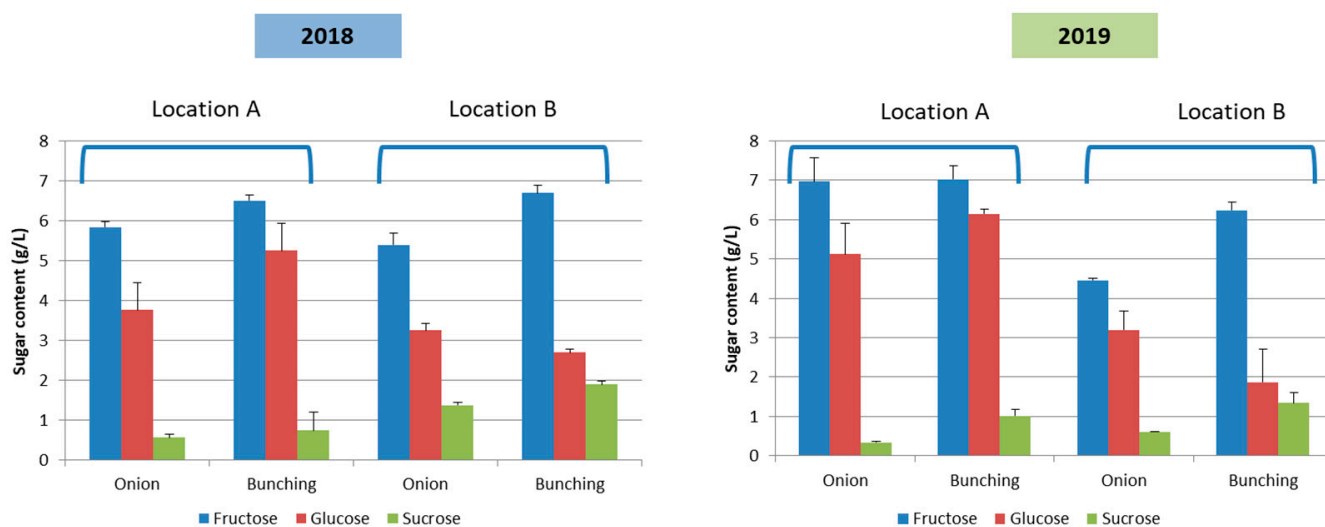


Figure 2. Sugar concentration for the onion and bunching onion lines in location A: Mendoza and location B: San Juan during 2018 and 2019. Sugar content is expressed as grams per liter of nectar.

3.4. Relation between Sugar Nectar Composition, Environmental Conditions, and Seed Yield

In both locations, we found that fructose content was related to seed yield (Table 3); $r = 0.49$ for onion and $r = 0.60$ for bunching onion. Sugar profiles and levels were affected by the environment. Fructose was related to the minimum temperature in both species as well the temperature range, but negatively for ΔT , whilst sucrose was negatively related to the maximum of relative humidity in bunching onion and positively correlated in onion.

Table 3. Correlation between onion and bunching onion nectar sugars, climatic conditions, and seed yield.

Species	Sugar	Tmax	Tmin	RHmax	RHmin	Wind	ΔT	Seed Yield
Onion	Fructose	0.37 ^{ns}	0.69 ^{**}	0.02 ^{ns}	−0.08 ^{ns}	0.32 ^{ns}	−0.52 [*]	0.49 [*]
	Glucose	0.33 ^{ns}	0.45 ^{ns}	0.01 ^{ns}	−0.21 ^{ns}	0.10 ^{ns}	−0.31 ^{ns}	0.32 ^{ns}
	Sucrose	0.05 ^{ns}	0.28 ^{ns}	−0.35 ^{ns}	0.10 ^{ns}	0.65 ^{**}	0.37 ^{ns}	0.19 ^{ns}
Bunching onion	Fructose	0.55 ^{ns}	0.79 ^{**}	−0.27 ^{ns}	−0.23 ^{ns}	0.56 ^{ns}	−0.58 [*]	0.60 [*]
	Glucose	0.05 ^{ns}	0.42 ^{ns}	0.35 ^{ns}	0.12 ^{ns}	0.09 ^{ns}	−0.25 ^{ns}	0.54 ^{ns}
	Sucrose	0.40 ^{ns}	0.31 ^{ns}	−0.70 ^{**}	−0.31 ^{ns}	0.57 ^{ns}	−0.37 ^{ns}	0.30 ^{ns}

^{*}, ^{**} Significant at $p \leq 0.05$ and 0.01 , respectively, ^{ns}: non-significant. Maximum (Tmax) and minimum (Tmin) temperatures, temperature range (ΔT), maximum (RHmax) and minimum (RHmin) relative humidity, and wind speed during crop season for the different locations and seasons.

4. Discussion

This research was carried out in commercial fields in different locations and during different productive seasons. Our results showed that, regardless of the season and the location, bunching onion produced higher seed yields than onion. This species had more sugars, which was highly correlated with seed yield. In addition, location A, Mendoza, was better than location B for the production of bunching onion seeds. Plant breeding and seed companies have focused their breeding programs on different traits better fitting the actual growing market and producers' needs, including disease resistance, late bolting, and yield [18]. To the best of our knowledge, there are no data available on bunching onion seed production and its relationship with sugar nectar composition. Alternatively, there are a few reports about the preferences of pollinators to produce onion seeds. Hagler [26] and Silva and Dean [27] reported significant differences between onion cultivars for sugar content in nectar and seed yield. Our previous studies were in agreement with these works. Moreover, we have reported that in onion nectar most of the compounds showed an interaction with the location, and onion seed yield was mostly dependent on the genotype and not on environmental conditions [14,21,22].

Generally, sugars are the compounds with predominance in nectar; in both species fructose was found in major proportion. In both species there were no significant differences ($p \leq 0.05$) between the studied seasons and locations for this compound. However, climatic conditions did affected onion fructose nectar content, but this was not the case for bunching onion. In addition, fructose had a strong relationship with seed yield in both species. In concordance with these data, our group has reported that in onion nectar sugars had analogous behavior among different lines and sites, and did not vary as much as other secondary compounds. Additionally, a strong influence of sugars, especially fructose, was observed on bee visits and seed yield [22]. On the other hand, sucrose was always in lower concentration than hexoses and there were significant differences between the two species. These results are in agreement with our previous studies in onion nectar [14,21,22], and the results reported by Hagler [26] and Silva and Dean [27], who showed that the concentration of sucrose was always lower than fructose. However, higher levels of this sugar were found in bunching onion nectar than in onion nectar. Furthermore, Silva and Dean [25] reported that a certain amount of variability is expected to be found among the different seasons of study for onion nectar, which is what we observed in the onion samples; fructose and glucose did not show differences through the different years of study, whereas sucrose did. Comparing the two locations where seeds were produced, we found that, in spite of hexoses being in higher concentrations in location A than in location B, conversely, sucrose was in lower concentration in location A. Chalcoff et al. [28] reported a significant association between the climatic zone of occurrence for angiosperms and nectar sucrose proportion. In places with low temperatures, low sucrose content was observed, so that sucrose-poor nectar was associated with higher latitudes and lower temperatures; our results showed this effect in location A. Thus, both intrinsic (e.g., plant physiology) and extrinsic (e.g., pollinator preferences associated with climatic conditions)

factors may explain this pattern and are related to plant fitness [28]. Pollination problems have not been reported in bunching onion by seed companies, in contrast to onion flowers, which have serious problems of seed yield due to lack of pollination. Our results showed that sugars, especially fructose, are clearly related to seed yield, and that sugars were higher in bunching onion than onion, which has higher yields. Besides sugar content, other factors such as flower morphology can affect the attraction of pollinators. Flower traits could be affecting bee pollination behavior, as was observed for onion flowers [14]. Moreover, nectar production may depend on the position of a particular flower within an inflorescence, the location of nectaries within a flower, or even on subsequent phases of floral development [11], which has not been studied in this species yet.

Bunching onion seed production offers several advantages in comparison to onion seed production. Among them, we can quote: the flowering cycle of bunching onion is about 20 days earlier than onion, which means that it requires less vernalization for flowering. The root system is very strong and in some cases tolerant to soil fungi (e.g., *Fusarium* or *Sclerotium*) and grows well in soils where onions could not be planted, since they are sensitive to these fungi [23]. In addition, this species can be planted in one year and it can be maintained for up to 3 harvest cycles, while onions need to be replanted every year. On the other hand, the optimal moment for seed harvest is when 5–10% of capsules are open, and seeds are black and hard. In a typical production year, bunching onion seeds are about half the size of an *A. cepa* seed [18]. Among the disadvantages, the mature fruit opens easily and seed companies report that uneven flowering is the main problem, which means the harvest has to be carried out at least three times to obtain a normal seed germination (between 85 to 90%). This leads to seed losses by the simple rubbing of the harvest labor, when the exposed seed is thrown from the umbel to the ground. Another drawback is the umbel dehiscence which is much more explosive than in onions; in 2 days an umbel could go from showing 5% to 70%, so a light breeze could throw seeds to the ground. These voluntary and involuntary falls mean that a good portion of seed yield is lost. In order to reduce further production costs and allow the bunching onion products to enter the market at more competitive prices, cultivars more suitable for mechanized production and harvest should be developed, thus, hybrid breeding will become an increasingly important issue in order to achieve cultivars with high quality [18]. In addition, knowing the relationship of the nectar sugars with the seed yield is an important tool that could help decision making in order to obtain cultivars with higher yields.

5. Conclusions

Research related to bunching onion seed up to the present was almost non-existent. This is the first report describing bunching onion nectar and its relationship with seed production, and it has been compared to onion nectar, which has until now been studied to a greater extent. We found that fructose has a strong relationship with plant fitness. Hexoses were found in higher concentrations, and fructose and glucose remained constant through the different seasons. The correlation found between sugars and seed yield could be a great contribution for breeders to select lines with promising traits and, in consequence, better seed yields. In addition, the differences between locations could provide options for seed companies in their production decision-making. Furthermore, the amount of sugars in bunching onion could be the reason why this species does not have pollination problems in contrast to onion plants. The use in this study of genotypes that are released by the seed companies and available for producers makes our research more relevant. However, nectar traits could not explain the total variability in the performance of the different studied species, and further studies in bunching onion are required concerning floral traits with regard to their relationship to bee attraction.

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