

# Floral phenology, nectar secretion dynamics and honey production potentials of two lavender species (Lavendula dentata, and L. pubescens) in southwestern Saudi Arabia

#### Type:

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The aim of the current study was to determine the floral phenology, nectar secretion dynamics and honey production potentials of two naturally growing lavender species (L. dentata and L. pubescens), in southwestern Saudi Arabia. In both species, flowering is continuous; that is, when open flowers on a spike are shaded, new flowers emerge. Such flowering pattern might be advantageous to the plant to minimize competition for pollinators and promote efficient resource allocation. The flowering periods of the two species overlap. Both species secreted increasing amounts of nectar from early morning to late afternoon, with the mean maximum volumes of accumulated nectar from bagged flowers occurring at 1500h for L. pubescens ( $0.50 \pm 0.24$  µl/flower) and at 18:00 h for L. dentata ( $0.68 \pm 0.19$  µl/flower). The volume of the nectar that became available between two successive measurements (three-h intervals) varied from 0.04 µl/flower to 0.28 µl/flower for L. pubescens and from 0.04 µl/flower to 0.35 µl/flower for L. dentata, reflecting the variation in the dynamics of nectar secretion by these species and indicating the size of the nectar that may be available for flower visitors at given time intervals. The distribution of nectar secretions appears to be an adaptation of the species to reward pollinators for longer duration. Based on the mean amount of nectar sugar secreted by the plants, the honey production potentials of the species are estimated to be 4973.34 mg and 3463.41 mg honey/plant for L. dentata and L. pubescens, respectively.

#### **Keywords:**

lavendula, flower morphology, flowering period, nectar secretion, Saudi Arabia



Floral phenology, nectar secretion dynamics and honey production potentials of two
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Running head: Nuru et al. Honey production potentials of lavender species

# Nuru Adgaba<sup>1</sup>\*, Ahmad A. Al-Ghamdi<sup>1</sup>, Yilma Tadesse<sup>1</sup>, Awraris Getachew<sup>1</sup>, Mohammad J. Aansari<sup>1</sup>, Anwer Al-Maktary<sup>1</sup>,

\*Corresponding author: Nuru Adgaba, Email: <u>nuruadgaba@gmail.com</u>

<sup>1</sup>Eng. Abdullah Baqshan Chair for Bee Research, Department of Plant Protection, Faculty of

Food and Agricultural Science, King Saud University, KSA, P.O. Box 2460 Riyadh 11451

#### Abstract

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The aim of the current study was to determine the floral phenology, nectar secretion dynamics and honey production potentials of two naturally growing lavender species (L. dentata and L. pubescens), which are some of the major sources of honey in southwestern Saudi Arabia. In both species, each individual flower remains open for only one day. However, flowering is continuous; that is, when open flowers on a spike are shaded, new flowers emerge. Such flowering pattern might be advantageous to the plant to minimize competition for pollinators and promote efficient resource allocation. The flowering periods of the two species overlap. Both species secreted increasing amounts of nectar from early morning to late afternoon, with the mean maximum volumes of accumulated nectar from bagged flowers occurring at 1500h for L. pubescens (0.50  $\pm$  0.24 µl/flower) and at 18:00 h for L. dentata (0.68  $\pm$  0.19 µl/flower). The volume of the nectar that became available between two successive measurements (three-h intervals) varied from 0.04 µl/flower to 0.28 µl/flower for *L. pubescens* and from 0.04 µl/flower to 0.35 µl/flower for *L. dentata*, reflecting the variation in the dynamics of nectar secretion by these species and indicating the size of the nectar that may be available for flower visitors at given time intervals. The distribution of nectar secretions appears to be an adaptation of the species to reward pollinators for longer duration. Based on the mean amount of nectar sugar secreted by the plants, the honey production potentials of the species are estimated to be 4973.34 mg and 3463.41 mg honey/plant for *L. dentata* and *L. pubescens*, respectively.

<sup>28</sup> Key words: Lavendula, flower morphology, flowering period, nectar secretion, Saudi Arabia



#### 29 Introduction

The majority of lavender species are indigenous to the mountainous regions of the western Mediterranean countries, the islands of the Atlantic, Turkey, Pakistan and India (Chu and Kemper, 2001). Moreover, they are native to northern, eastern and southern Africa; the Arabian Peninsula; Bulgaria; and Russia (Boning, 2010).

Lavender species survive, and can thrive, in arid and semi-arid regions of the world, even in areas threatened by desertification (Azcón and Barea, 1997), and it is known as extremely drought resistant once established. Species of lavender prefer gravelly, slightly alkaline and limestone-based soils (Boning, 2010), and certain species (*Lavendula dentata* and *L. pubescens*) because of their thick branching from the base, are useful in soil erosion control.

Today, lavender species are extensively cultivated throughout the world, particularly in France, 39 Bulgaria, Russia, Italy, Spain, England, the USA, and Australia (Lalande, 1984; Boning, 2010). 40 They are grown commercially for the extraction of essential oils, which are used in perfumery, in 41 cosmetics, as ingredients in numerous cottage industry products, in food processing, as massage 42 products, as culinary herbs and as ornamental plants (Lis-Balchin, 2003). Certain types of 43 44 lavender oil have also been shown to have antimicrobial and antifungal properties (Chu and Kemper, 2001; Lis-Balchin, 2003), and the oils from the plants are also widely used in 45 aromatherapy (Welsh, 1995; Lis-Balchin, 2003). 46

Several species of lavender are visited frequently by honeybees, and where there is dense 47 growth, the plants serve as sources of premium mono-floral honeys with characteristic physical 48 49 properties such as a flowery, pleasant, very fine aroma and delicate floral scent with an evident of lavender component (Forler, 2013). Numerous countries, including France, Spain, Italy, 50 Bulgaria, England, the former members of USSR and Yugoslavia, Australia, the USA, Canada, 51 South Africa, and Tanzania are known for the production of lavender honeys (Forler, 2013). 52 Lavender honeys can command a premium price of approximately \$50/kg in specialty food 53 54 stores.

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In Saudi Arabia, there are five naturally growing lavender species: *L. atriplicifolia* Benth, *L. citriodora, L. coronopifolia* Poir., *L. stricta* Del., *L. dentata* L. and *L. pubescens* Decne (El-Karmy and Zayed, 1992; Rahman et al., 2003). The country is known as one of the main geographical areas of lavender species diversity and endemism, and it has been suggested as a center of origin for the genus (Miller, 1985). Uses of *L. dentata, L. coronopifolia, L. pubescens,* and *L. stricta* as medicinal plants in Saudi Arabia have been reported (Rahman et al., 2003). Within the country, *Lavandula* species such *L. dentata* and *L. pubescens* are widely distributed in the mountainous regions of Taif, Albaha and Asir and serve as sources of high-quality lavender honeys, locally known as "*Seyfi honey*," that sell for a premium price of \$50-120/kg.

The majority of the studies on lavender species have been limited to cultivated and commercial cultivars, whereas the growth and honey production of the species under their natural conditions, particularly in the semiarid areas of the Arabian Peninsula remain unaddressed. Despite the natural occurrence of multiple lavender species in the region and their remarkable ability to withstand extreme drought conditions, their ecological and socio-economic values, floral biology, nectar secretion dynamics and honey production potentials have not been documented.

70 Based on detailed studies on the dynamics of nectar secretion, including the amount and sugar concentration, it has been possible to estimate the honey production potentials of several 71 important honey source plants, e.g., Asclepias syriaca L. (500-600 kg honey/ha/flowering 72 season) (Zsidei, 1993), Trifolium pretense L. (883 kg of sugar/ha/flowering season) (Szabo and 73 Naida, 1985), and *Phacelia tanacetifolia* Benth (60-360 kg honey/ha/flowering season) (Nagy, 74 2002). Moreover, Crane et al. (1984) reported the honey production potential of different lime 75 species (Tilia spp.) range from 90 to 1200 kg honey/ha. Recently, Kim et al. (2011) quantified 76 the amount of nectar secreted per flower and per tree for Crataequs pinnatifida Bunge. 77 Moreover, the amount and dynamics of nectar secretion have been used to estimate the honey 78 production potential of Ziziphus spina-christi (Nuru et al., 2012). In this general context, the aim 79 of the current study was to determine the floral phenology, nectar secretion dynamics and honey 80 production potentials of the two major naturally growing Lavandula species (L. dentata, and L. 81 pubescens) which are used as important sources of honey in regions of southwestern Saudi 82 Arabia. 83



#### 84 Materials and methods

#### 85 Study site and species description

The study was conducted in the area of Baljurashi, Al-Baha region, Saudi Arabia, at 86 19°52'06.819" N and 41°36'48.218" E, at 2050 meter above sea level. The study area is 87 88 categorized under the highland physiographic and climatic conditions. The humidity ranges from 52%-67%, and the rainfall ranges from 229-581 mm/annum with a mean temperature of 22.9°C 89 (Al-Baha Meteorological Station, 2012). The studied species are mainly growing on gentle to 90 steeply sloping lands in shallow, rocky, limestone-based soil types (Fig. 1 A & B). The plants, in 91 some locations, occur as dominant vegetation type while in other sites grow in association with 92 various species such as Olea chrysophylla Lam., Juniperus procera Hochst., Psiadia punculata 93 (DC.) Vatke., Dodonaea angustifolia L.f., Maytenus spp. and Acacia origena Asfaw. Both L. 94 pubescens and L. dentata grow naturally with almost overlapping distributions under the same 95 environmental conditions. L. dentata is much branched, bushy shrub type up to 75 cm tall. 96 Leaves are aromatic, sessile, linear, up to 35 mm long 3 mm wide with strongly revolute-97 margined. Inflorescences are dense with terminal spike, up to 7 cm long. L. pubescence is also 98 densely spreading perennial herb, up to a meter tall, branches glandular-pubescent. Leaves 99 petiolate, deeply dissected into short, oblong-linear lobules. Inflorescences are dense, with 100 branched or unbranched terminal spikes. Both species are characterized by their remarkable 101 102 adaptation to long dry periods via the suppression of their physiological activity during this period both the leaves and spikes look like completely dry however, when there is sufficient 103 moisture, they rapidly resume their growth and produce numerous new young shoots and 104 105 flowering buds.

#### <sup>106</sup> Floral and plant morphological features

The morphological features of the flowers, such as the shape of flower and their arrangements
 were observed and described. Moreover, the number of flower lobs and the depth of the corolla
 tubes were characterized by measuring 10 flowers per plant and 50 flowers/species.





The mean length and number of spike per plant was determined by counting all spikes from 20 110 (L. pubescens) and 10 (L. dentata) plants. The mean number of flowers per plant was obtained 111 by counting the mean number of spikes per plant and multiplying by the mean number of 112 flowers/spike.The mean number of flowers/spike was obtained by counting the number of 113 flowers per spike (N = 51 for *L*. *dentata* and N = 76 for *L*. *pubescence*). In addition to the floral 114 features, the plant morphological features such as: plant height, crown height and crown 115 diameter were determined by measuring 63 and 47 individuals of *L. dentata* and *L. pubescens*, 116 respectively. 117

#### <sup>118</sup> Flower phenology and flowering period distribution

To determine the phenology of flowers, three individual plants per species were labeled. From each plant, eight mature flower buds/day were marked in late afternoon to be monitored the following day. When marking, all of the previously opened flowers from the spike were carefully removed to prevent confusion. On the next morning, development of flower buds was monitored every 2 h from 06:00 to 18:00. The observations were replicated for three consecutive days (a total of 72 flowers/species). The time of flower opening and flower abscission, and the life span of a single flowering were recorded.

The flowering period patterns (commencement, peak, and end) and total duration of flowering 126 127 were determined by monitoring and recording the flowering periods for each species. For this purpose, a proportional sampling was performed; 20 and 10 individual plants of *L. pubescens* 128 129 and L. dentata, respectively, were selected and labeled before the commencement of flowering. During selection, an effort was made to choose plants representative of differing land gradations 130 131 (flat, gently sloped and steeply sloped lands), ages and branching conditions. For each labeled plant, the number of shoots (spikes) that initiated flowering was recorded every week from the 132 commencement of flowering until the end of flowering. The peak flowering was considered as 133 the time at which more than 50% of the potential flower buds were in the stage of blooming. 134

#### 135 Amount and dynamics of nectar secretion

<sup>136</sup> The amount of nectar secreted per flower and its dynamics were determined for a total of six <sup>137</sup> individual plants (three plants/species). The amount of nectar was estimated five times per day at





138 06:00, 09:00, 12:00, 15:00 and 18:00. The flower buds were bagged a day before opening using
bridal-veil netting (Wyatt et al., 1992). From each plant and at each sampling time, the amount of
nectar was measured in ten flowers (a total of 50 flowers/day/plant). The nectar volume
measurement was repeated for three consecutive days (total of 450 flowers/species). Each flower
was measured only once. The volume of nectar contained in the flower was determined by
directly removing the nectar using 1 µl capillary tubes (Drummond Scientific Company, USA).
Then the volumes of nectar were compared between the species.

#### 145Honey production potential

The honey production potential was estimated by multiplying the mean number of flowers/plant 146 by the mean amount of nectar sugar/flower. The mean mass of sugar in the secreted nectar was 147 calculated from the volume and concentration of the solution measured using a pocket 148 refractometer (ATAGO, No. 3840, Japan). The honey production potential per plant was 149 calculated by multiplying the mean number of spikes per plant by the mean number of 150 flowers/spike and then multiplying by mean nectar sugar/flower following the method described 151 152 by Kim et al. (2011). These data were used to estimate the honey production potential/plant and to further extrapolate the honey production potential/ha for each species. The estimation of the 153 number of plants per hectare was based on considering the maximum number of plants that can 154 be found in densely grown natural fields or commercially cultivated fields. The estimation was 155 156 also based on the mean canopy diameter of each species and the space required between plants. For the determination of the mean canopy diameter; 63 and 47 individual plant crown 157 dimensions were measured for *L*. *dentata* and *L*. *pubescens*, respectively. 158

- <sup>159</sup> Weather data
- In addition to the above-described observations, weather data such as the temperature, and
   relative humidity (RH) of the area were recorded at each sampling time using an Environment
   Meter (N09AQ, UK).
- <sup>163</sup> Statistical analyses

<sup>164</sup> One-way ANOVA t-test and f-test results were computed to compare means between the species <sup>165</sup> and among the times of day, respectively; Two-way ANOVA was employed to determine the





effect of the interaction between the time of day and species. Correlation and regression analyses
 were performed to explore the relationship of nectar secretion with the morphological and
 weather condition parameters. The JMP-5 statistical software (SAS, 2002) was employed for the
 analyses.



#### 170 **Results**

#### <sup>171</sup> Flower morphology and arrangement

The flowers of *L. pubescens* arise from an elongated spike that varies from 4.6 to 18.0 cm in length, with a mean length of 9.7 cm (Fig. 2). Some of the spikes are branched and a single spike contains, on average, 64.0 flowers. The corolla are deep blue and are bilabiate, with upper lip 2lobed and the lower 3-lobed. The total length of the corolla varies from 10.0 to 15.0 mm, with a mean of 12.6 mm, of which, approximately 8 - 10 mm forms the corolla tube. Pistil bicarpellate, style branches flat. Stamens 4, concealed in the corolla tube, didynamous, the anterior pair longer. The anthers are located 2-3 mm below the mouth of the corolla tube.

The inflorescence in *L. dentata* (Fig. 3) is dense with terminal spike. The length of the spike ranges between 3.5 and 6.2 cm (mean of 4.5 cm). A single spike contains, on average, 91.0 small flowers. Corolla bilabiate, with 5-lobed limb. The corolla tube is about 4-5 mm in depth. The total length of the corolla varies between 6 and 9 mm (mean of 7.6 mm). Stamens 4, and are concealed in the corolla tube, didynamous, the anterior pair longer. Pistil bicarpellate, style branches flat.

#### <sup>185</sup> Flower phenology and Flowering period (season) distribution

186 From the 72 total flower buds marked per species, 63 and 59 were observed to open in the morning (06:00) for *L. pubescens* and *L. dentata*, respectively indicating in both species the peak 187 opening time is morning. All of the remaining flowers from both species opened by 10:00. From 188 16:00 to 18:00, 65 of the L. pubescens and 57 of L. dentata labeled flowers wilted and dropped 189 their petals, and the remaining few flowers lasted up to 18:00, indicating that a single flower 190 191 generally stays for less than one day. Between 12:00 and 18:00, a number of new flowers were observed to open from buds other than the labeled ones, indicating that, in both species, the 192 opening of flowers is continuous, that is when 5-7 previously opened flowers/spike shade off, 193 about the same number of new flowers/spike sequentially open with a certain degree of overlaps 194 195 among individual flowers opening times; hence, the time of flower opening is not restricted 196 within a day.





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Although the two species grow under the same ecological conditions, there was a slight difference in the timing of flowering. Plants of *L. pubescens* started to flower slightly earlier than those of *L. dentata* (Fig. 4). *Lavendula pubescens* commenced flowering in winter in mid-December. The species continued to flower throughout January and March, with peak flowering occurring in February, and flowering ended after the first week of March lasting for about 80 days.

Lavendula dentata commenced and finished flowering relatively later in the season than L. 203 pubescens, starting flowering in the first week of January and attaining its peak between the 204 second week of February and the first week of March. The plants continued flowering until the 205 third week of March, and flowering ended at the end of March, indicating that L. dentata exhibits 206 an extended flowering period lasting for about 90 days. The peak flowering periods of the two 207 species were observed to overlap. In both species when there is moisture stress, the buds on the 208 spike stop growing and flowering, but when there is sufficient rainfall, the buds resume growth 209 and flowering. 210

#### 211 Morphomet

#### Morphometric values of the two species

The study results show the presence of significant differences in morphological measures (Table 212 1) between studied species. On average, the plant heights and crown dimensions of L. pubescens 213 214 were 38% and 33% lower, respectively, than those of L. dentata. However, L. pubescens was significantly (P < 0.003) wider in terms of crown diameter than L. dentata. The number of 215 flowers on L. dentata was significantly (P < 0.001) greater than those on L. pubescens. The mean 216 numbers of flower buds per plant were slightly greater on *L. dentata* than on *L. pubescens*. 217 218 Moreover, the results revealed the presence of a significant (P < 0.001) positive correlation (r >0.61) between the number of flowers and other morphological features, such as plant height, 219 crown height, crown diameter, and crown volume. 220

#### 221 Nectar secretion dynamics and amount.

The study results indicate the presence of significant variation (P < 0.001) in the mean amount of nectar secreted/flower over the course of the day in both species (Table 2). Moreover, the total

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amount of nectar secreted by *L*. *dentata* was significantly higher (P < 0.001) than *L*. *pubescence* , and the interaction between the time of day and species was significant (P < 0.001).

In both species, the period of nectar secretion started in the early morning (06:00) and extended into the late afternoon, with maximum accumulated volumes of nectar of  $0.50 \pm 0.24 \mu$ l/flower and  $0.68 \pm 0.19 \mu$ l/flower recorded at 15:00 and 18:00 for *L. pubescens* and *L. dentata*, respectively. Regarding the trends in the amount of nectar secreted, the accumulated volume increased until 18:00 in the case of *L. dentata*. A similar trend was noted until 15:00 for *L. pubescens*, but there was a decreasing trend between 15:00 and 18:00 (Table 2).

Generally, the mean secreted nectar volume/flower and the mean maximum accumulated nectar volume/ flower at the end of the day were greater in *L. dentata* than *L. pubescence* (Table 2).

The amount of nectar calculated as the difference between two successive measurements (3 h intervals) varied from 0.04 µl/flower to 0.28 µl/flower for *L. pubescens* and from 0.04 µl/flower to 0.35 µl/flower for *L. dentata*. These values indicate the variation in nectar secretion of studied species and their nectar volume that might be available for flower visitors at given time intervals (Table 2).

#### <sup>239</sup> Nectar dynamics in relation to weather conditions

240 For both *L. pubescens* and *L. dentata*, the nectar amount per flower significantly increased with an increase in temperature (P < 0.001; Table 3). Moreover, the nectar amount in L. dentata 241 242 tended to increase (P < 0.004) with an increase in relative humidity. However, in the case of L. *pubescens*, though not statistically significant (P > 0.05), the nectar volume tended to decrease 243 with an increase in relative humidity. The highest nectar volumes were recorded at a mean 244 temperature of 35.7°C and 28.7% RH for L. pubescens and at 28.3°C and 37.7% RH for L. 245 246 dentata. This finding indicates that the two species may have different optimum weather conditions for peak nectar secretion. 247

#### 248 Honey production potentials of the species

The mean maximum volumes of accumulated nectar/flower recorded were  $0.68 \pm 0.19 \mu$ l at 18:00 for *L. dentata* and  $0.50 \pm 0.24 \mu$ l at 15:00 for *L. pubescens*. Considering the mean maximum nectar volumes and their respective nectar sugar concentrations; 0.22 mg and 0.16 mg of nectar sugar/flower were recorded for *L. dentata* and *L. pubescens*, respectively.

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Moreover, the mean numbers of spikes/plant.were 204 for *L. dentata* and 277 for *L. pubescens*. 253 and the mean numbers of flowers per spike, were 90.87 and 64.08 for L. dentata and L. 254 pubescens respectively. Hence the mean numbers of flowers/plant were estimated to be 18,537 255 for L. dentata and 17,750 for L. pubescens. Based on the mean numbers of flowers/plant; the 256 estimated amounts of nectar sugar per plant were then calculated to be 4078.14 mg and 2840 mg 257 for L. dentata and L. pubescens, respectively. Assuming 18% of a honey is water; from the 258 average amount of nectar sugar recorded by the individual plants; L. dentata and L. pubescens 259 can produce 4973.34 mg and 3463.41 mg honey/plant. 260

Based on the mean canopy diameter of each species (Table 1) and the space required between plants; the numbers of plants estimated to grow per hectare of land were 10249.8 and 6936.6 for *L.dentata* and *L.pubescense* respectively. According to the above-described computations, the expected nectar sugar for *L. dentata* and *L. pubescens*, were 41.8 kg/ha and 19.7 kg/ha respectively. Consequently, *L. dentata* and *L. pubescens* can yield an estimated 51.0 kg honey/ha and 24.1 kg honey/ha respectively. Thus, the expected honey production potential of *L. dentata* is twice that of *L. pubescens*.

#### 268 Discussion

## 269 Floral morphology and phenology

The floral morphologies of the two lavender species appear suitable to the body size of small 270 271 insects such as honeybees to easily alight on flowers and collect nectar. The corolla tube of L. dentata is relatively short (4 -5 mm); hence, the smallest indigenous honeybee (Apis mellifera 272 273 *jemenitica*), with a proboscis length of  $5.277 \pm 0.210$  mm (Ruttner, 1988), can easily access the nectar. Though the corolla tube of *L. pubescens* is relatively longer than the proboscis lengths of 274 275 indigenous honeybees, however, the bees observed to collect nectar which might be with the help of the capillary action of the style. Similarly, despite their short proboscis lengths, honeybees 276 managed to draw nectar as far as 11.65 mm by taking advantage of the capillary action of the 277 style to access the corolla tube of cardamom (Venkateshalu and Vivek, 1997). However, honey 278 bees prefer to collect nectar (greater frequency) from L. dentata than L. pubescens flowers 279 (personal observation), possibly because the corolla tube length matches well with their 280 proboscis length. The location of nectar and the proboscis length are known to be important 281 factors in determining the associations between flowers and flower-visiting insects (Martina et 282



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- al., 2009). In general, the pollen grains of the two species are not easily dislodged and are not
  thus dusted onto the bodies of honeybees to be packed into their pollen baskets. Nevertheless, the
  visiting of honeybees may provide a sufficient level of pollination via mechanical dislodging and
  the movement of the proboscis through the corolla tubes.
- In terms of flower phenology, interestingly, only a few (5-7) flowers open at a time per spike, 287 and when these flowers are near wilting, other new flower buds prepare to open. This sequential 288 opening of a few flowers at a time might be an adaptation of the species for the economic 289 allocation of sufficient synthesized energy (in the form of nectar) to attract flower visitors and 290 might also act to minimize competition among flowers for pollinators. The display of only a few 291 flowers at a time by plants has been reported to impart an advantage in terms of maximizing 292 pollen export (Klinkhamer et al., 1994), whereas plants that display greater numbers of flowers 293 at a time may attract a greater number pollinators but are reported to experience substantial 294 pollen transport losses (Biernaskie and Cartar, 2004). In this context, both species might be well 295 adapted for efficient pollen transfer. 296
- The individual flowers of each species are present for a considerable length of time (9 h and 12 h in *L. pubescens* and *L. dentata*, respectively). Moreover, their nectar secretion dynamics follow the life span of the flower. Floral longevity has been reported to play an important role in reproductive ecology, influencing the total number of visits by pollinators and the amount and diversity of pollen received (Ashman and Schoen, 1996).

# 302 Blooming season distribution

303 The flowering of the two species is very long and lasts for approximately two to three months while the spikes continue to grow and a few flowers open at a time. This flowering strategy is 304 advantageous to the plant for resource distribution and for effective pollination. Moreover, the 305 elongated flowering period is useful in relation to beekeeping in that the bees have considerable 306 307 time to collect and store nectar. The contribution of a longer flowering period to increased honey production has been well documented (Burge et al., 2006). The overlap in the flowering duration 308 and the periods of peak flowering of the two species might be attributed to their similar 309 physiological responses to environmental stimuli. 310



#### 311 Morphometric values

Despite sharing similar habitats, the morphometric values of plant height: crown height and 312 canopy volume, which are measures of biomass, were generally greater for *L*. dentata compared 313 to *L. pubescens*. The higher number of flowers per spike in *L. dentata* than in *L. pubescens* may 314 be associated with the higher biomass of the former species. Furthermore, the current study 315 revealed a strong positive correlation between the evaluated morphological parameters and the 316 number of flowers, which is in agreement with Zhang et al. (2013), who reported a significant 317 positive correlation between the number of flowers and the aboveground biomass in 318 Stellera chamaejasme. The higher biomass of L. dentata is expected to supply greater nectar and 319 pollen resources and, thus, attract a greater number of flower visitors. 320

#### 321 Amount and dynamics of nectar secretion and effect of weather conditions

Even though a single flower was used for one time measurement, from the mean accumulated 322 amounts of nectar recorded for different flowers at different times of day, it was clear that both 323 species continue to secrete nectar throughout the day, for approximately 9 h and 12 h for L. 324 pubescens and L. dentata, respectively. Under natural conditions, while the flowers remain open, 325 it is expected that flower visitors can consume the nectar. Thus, for each species, the increases in 326 327 the amounts of nectar recorded over time in caged flowers (Table 2) indicates the additional amount of nectar secreted by the flowers during the interval between two consecutive 328 329 measurement times. Generally the mean amount of nectar secreted per flower of L. dentata was significantly (P < 0.0001) higher than the amount of nectar secreted per flower of *L. pubescence*. 330 Moreover at the end of the flower stage *L*. *dentata* had more accumulated nectar amount than *L*. 331 pubescence (Table 2). 332

In addition, the maximum nectar secretion attainment time varied between the two species (Table 2) which may be related to the variation in life span of their flowers. The decline in the amount of nectar in bagged *L. pubescens* flowers after 15:00 (Table 2) might be attributable to the reabsorption of secreted nectar by the plants. The reabsorption and modification of unconsumed nectar is considered a strategy for the partial recovery of the energy cost invested in nectar production for numerous species (Nepi and Stpiczyńska, 2008; Nepi et al., 2011).



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The mean temperature (35.7°C for *L. pubescens* and 28.3°C for *L. dentata*) and relative humidity 339 (28.7% for *L. pubescens* and 37.7% for *L. dentata*) at which the highest nectar volumes were 340 recorded might be considered the optimal weather conditions for maximum nectar secretion and 341 effective pollination for each species. Although the two species have overlapping flowering 342 periods, they have different optimum humidity and temperature levels for the secretion of 343 maximum nectar, which may be an adaptation of the two co-existing and co-flowering species to 344 minimize competition for pollinators. The temporal partitioning of floral resources as a 345 mechanism of minimizing competition for pollinators has been well documented for several 346 sympatric and co-flowering plant species (Ollerton and Lack, 1992; Stone et al., 1998). 347

The positive correlations between the amount of nectar and the air temperature of the area might indicate the adaptation of these species to warm climatic conditions. Similarly, positive correlations between ambient temperature and nectar secretion amount have been recorded for numerous nectar-secreting species *Trifolium repens*, (Jakobsen and Kristjansson, 1994), *Thymus capitatus*, (Petanidou and Smets, 1996), and *Ziziphus spina-christi*, (Nuru et al., 2012).

## 353 Honey production potential

In general, under natural conditions, the amounts of honey obtained per ha of land (51.0 kg/ha from *L. dentata* and 24.1 kg/ha from *L. pubescens*) are relatively greater than the honey production values of 20.14 kg/ha and 23.02 kg/ha recorded for *Nepeta deflersiana* and *Otostegia fruticosa*, respectively (Al-Ghamdi et al, 2015 unpublished).

In addition, because lavender honey is a specialty item, its high market price as well as the 358 possibility of enhancing the vegetative performance of lavender species with improved 359 360 agronomic practices may indicate additional premium production potentials for these lavender species. In this regard, further research on the potential for the planting and adaptation of these 361 species to both degraded lands and backyards, with the integration of beekeeping, would be 362 useful for the assessments of its ecological and economic values. Moreover, in both species, 363 flowers were observed to open in succession (day and night) without having definite time of 364 opening. In this regard, further observations on the presence of nocturnal visitors (if any) might 365 be important. 366



#### 367 Conclusion

Based on the dynamics and the amounts of nectar secreted per flower and per plant, the two lavender species can be considered as potential honey source plants for the region. In general, the importance of the species is significant not only in terms of serving as sources of specialty honey but also in terms of their ecological values, attributed to their ability to thrive under low moisture and poor soil conditions and to contribute to ecosystem functioning and the maintenance of insect diversity under these conditions.

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Table 1: Plant and flower morphometric parameters of *Lavendula pubescens* and *Lavendula dentata* (mean values are given ± SD)

Species	Plant height	Crown height	Crown	Crown	No. of
	(cm)	(cm)	diameter	volume (m <sup>3</sup> )	flowers
			(cm)		/plant
L. dentata	85.7±17.5ª	$41.4 \pm 9.4^{a}$	74.7±28.5ª	$0.09 \pm 0.1^{a}$	18537
L. pubescens	53.0±20.8 <sup>b</sup>	27.6±10.0 <sup>b</sup>	97.4±23.8 <sup>b</sup>	$0.04 \pm 0.1^{b}$	17750
t-value	8.701	7.383	-3.324	3.975	-
P-value	0.000	0.000	0.003	0.000	-

Means followed by the same letter within columns are not significantly different at  $\alpha = 0.05$ N = 63 for *lavendula dentata* & N = 47 for *L. pubescence* 





5	5		1			1				
			Mean nectar							
			volume (µl)							
			accumulated							
			in a flower at							
			different							
			times of the							
			day (local							
			time =							
			GMT+3 h)	F-value			P-value			
			06:00	09:00	12:00	15:00	18:00			
	Ν		(a)	(b)	(C)	(d)	(e)			
L. pubescens	90		$0.28 \pm 0.19^{a}$	$0.41 \pm 0.25^{ab}$	$0.46 \pm 0.23^{b}$	$0.50 \pm 0.24^{b}$	0.41±0.21 <sup>c</sup>	12.597	< 0.0	001
Ratgpefcies	-		a = 0.28	b-a = 0.13	c-b = 0.05	d-c = 0.04	e -d = -0.09			
secretion *	00			0 40 1 0 1 48						001
L. aentata	90		$0.35\pm0.15^{\circ}$	$0.40\pm0.14^{\circ}$	0.53±0.19°	$0.64\pm0.20^{\circ}$	$0.68\pm0.19^{\circ}$	62.645	< 0.0	001
Rate of			a = 0.35	b-a = 0.05	c-b = 0.13	d-c = 0.11	e -d = 0.04			
secretion *										
			Mean for							
			species							
		Ν	L. pubescens	L. dentata				t-value		P-value
Nectar volume	e per	450	$0.41 \pm 0.24^{a}$	$0.52 \pm 0.22^{b}$					-6.99	< 0.0001
flower (µl)								1		
	11 .	1	1		o o <b>-</b>					

Table 2: Daily dynamics of nectar production in flowers of the two lavender species

Means followed by the same letter are not significantly different at  $\alpha = 0.05$ 





\* Rate of nectar secretion is the average volume of nectar secreted during 3 hours which is calculated as the difference between the two consecutive measurements.





Table 3: Correlation of temperature and relative humidity with nectar volume measurements for the two lavender species

	Correlation		P-value	
Variable By variable Count	L.	L. dentata	<i>L</i> .	L. dentata
	pubescens		pubescens	
Temperature (°C) Nectar in µl 450	0.2360	0.2796	0.0001	< 0.0001
Relative humidity Nectar in µl 450	-0.0826	0.1373	= 0.080	= 0.004





Fig. 1. A.



Fig. 1 B.







Fig. 2: Floral morphology of spike (left) and corolla (right) of *L. pubescens* 







Fig. 3: Floral morphology of spike (left) and corolla (right) of *L. dentata* 





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