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Nectar secretion dynamics and honey production potentials of some major honey plants in Saudi Arabia

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Abstract The contribution of a bee plant species to honey production depends on the plant's nectar secretion quality and quantity, which is mainly governed by biotic and abiotic factors. The aim of the current study, was to investigate the nectar secretion dynamics and honey production potential of 14 major bee plant species of the target area. We examined the quantity and dynamics of nectar sugar per flower five times a day using a nectar sugar washing technique and direct measuring of nectar with calibrated capillary tubes. The average nectar sugar amount of the species varied from 0.41 mg/flower to 7.7 mg/flower ($P < 0.0001$). The honey sugar per flower was used to extrapolate the honey production potential per plant and per hectare of land. Accordingly the honey production potential of the species observed to vary from 14 kg/hectare in *Otostegia fruticosa* to 829 kg/hectare in *Ziziphus spina-christi*. The nectar secretion dynamics of the species generally showed an increasing trend early in the morning, peaking toward midday, followed by a decline but different species observed to have different peak nectar secretion times. Generally, the tree species secreted more nectar sugar/flower than the herbs. The nectar secretion amount of the species was positively correlated with the ambient temperature, indicating the adaptation of the species to hot climatic conditions. However, different species were observed to have a different optimum temperature for peak nectar secretion. Despite the limited rainfall and high temperature of the area, many plants were found to have good potential for honey production. The monetary value of honey

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per hectare of the studied honeybee plant species can be of equal or greater than the per-hectare monetary value of some cultivated crops that require numerous inputs. In addition, the information generated is believed to be useful in apiary site selection and to estimate the honey bee colony carrying capacity of an area.

1. Introduction

Honey bee plants are those plant species that provide bees with food sources in the form of nectar and/or pollen. According to Crane (1990), only 16% of the world's flowering plant species contribute to honey bees as food sources. Moreover, not all bee plants are equally important to bees and honey production. Indeed, only 1.6% of the world's honey bee plants are the sources of most of the world's honey (Crane, 1990). This indicates that for every geographical region there are very few important honey source plants and it is of paramount importance to characterize them according to their degree of importance in honey production. Several studies have been performed on different plant species to quantify nectar secretion and to explore its dynamics, mainly in relation to pollination biology, floral phenology and biophysical environmental factors (e.g., Petanidou and Smets, 1996; Castellanos et al., 2002; Galetto and Bernardello, 2004). Moreover, quantitative studies on the nectar secretion of various melliferous plants have been conducted (Pesti, 1976; Mohr and Jay, 1990; Nepi et al., 2001; Farkas and Orosz-Kovács, 2003; Horváth and Orosz-Kovács, 2004; Zajácz et al., 2006). In addition, based on thorough studies of dynamics of nectar secretion and total soluble solids (TSS) concentration, it has been possible to estimate the honey production potentials of some major honey source plants such as *Trifolium pratense* L. (red clover) (883 kg of honey/ha/flowering season; Szabo and Najda, 1985); *Asclepias syriaca* L. (milkweed) (500–600 kg honey/ha/flowering season; Zsidei, 1993) and *Phacelia tanacetifolia* Benth (60–360 kg honey/ha/flowering season; Nagy, 2002). In addition, Crane et al. (1984) reported that the honey production potential of different *Tilia* (lime) species ranged from 90 to 1200 kg honey/ha. Moreover, Kim et al. (2011) estimated the amount of nectar secreted per flower and per tree for *Crataegus pinnatifida* Bunge (Chinese hawthorn).

Nonetheless, most of the studies have focused on melliferous plant species of temperate and subtemperate regions. Many important honey source plants of the tropics, subtropics and arid climatic zones, their nectar secretion potentials and their significance for honey production have not yet been well studied and documented. In Saudi Arabia, approximately 2200 flowering plants are reported to exist (Collenette, 1999; Chaudhary, 1999). The families *Fabaceae*, *Lamiaceae* and *Rhamnaceae*, which account for a significant share of the flowering plants of the country, are generally known as good sources of nectar for honey bees. Among these, some species from the genus *Acacia*, *Lamaceae* (*lavandula*), *Ziziphus* and others are known for being very good sources of honey. However, detailed characterization of the species, particularly the amount and dynamics of their nectar secretion are lacking.

The genus *Acacia* comprises more than 1200 species that are distributed in tropical and subtropical parts of the world, extending into the deserts of Africa and the Middle East and into large areas of the Arabian Peninsula (Wickens, 1995; Tandon and Shivanna, 2001; UNESCO, 1977; Walter and Breckle, 1986). The species are drought-tolerant and endures in the rainfall belts of 50–400 mm/annum (Wickens, 1995; Le-Houérou, 2012). Moreover, these species have multipurpose uses as important sources of firewood, timber, forage, gum, tannins, fiber, folk medicine, and food, and they are also useful for environmental protection and soil and water conservation (Boulos, 1983; Wickens, 1995; Midgely and Turnbul, 2003). They also contribute to the conservation of large numbers of herbivorous vertebrates and invertebrates (Krüger and McGavin, 1998) as well as many species of nectarivorous insects. Different species of *Acacia* have been reported as important honey bee forages in many semiarid regions of the tropics (Wickens, 1995; Stone et al., 1996, 1998). About 10 *Acacia* species, such as: *Acacia origena* Hunde, *Acacia johnwoodii* Boulos, *Acacia tortilis* Forssk., *Acacia asak* (Forssk.) Willd., *Acacia ehrenbergiana* Hayne, *Acacia etbaica* Schweinf., *Acacia oerfota* (Forssk.) Schweinf., *Acacia gerrardii* Benth. and others, have been reported to exist in Saudi Arabia, but their roles in honey production have not been quantified and documented.

The other important honey source plant family is *Lamiaceae*, which encompasses approximately 7200 species. This family is one of the most cosmopolitan in distribution, covering large areas in the world (Martin et al., 2013). According to recent studies, the *Lamiaceae* family is represented by 76 species in Saudi Arabia, most of which are useful for their medicinal values and antimicrobial properties (Abbasi et al., 2010; Dulger and Dulger, 2012; Raja, 2012; Venkateshappa and Sreenath, 2013; Saqib et al., 2014). Within *Lamiaceae*, the genus *Lavandula* is particularly important because it is naturally occurring and extensively cultivated in many parts of the world (Chu and Kemper, 2001; Boning, 2010; Lalande, 1984). The species grows well in arid and semiarid parts of the world and even in areas vulnerable to desertification (Azcón and Barea, 1997). Some of the species in genus *Lavendula* are used in cosmetics, food processing and aromatherapy (Welsh, 1995; Chu and Kemper, 2001; Lis-Balchin, 2003). Many species from *Lamiaceae* are known as good sources of high quality monofloral honey with a characteristic aroma and flavor (Tsigouri and Passaloglou-Katrali, 2000; Nicoleta, 2008; Nicoleta and Ion, 2007; Forler, 2013). Monofloral honeys from *Lavandula* sp. fetch premium prices ($50/kg) in specialty food stores (Forler, 2013).

Five *Lavandula* species (*Lavandula atriplicifolia* Benth, *Lavandula citriodora*, *Lavandula coronopifolia* Poir, *Lavandula stricta* Del., *Lavandula dentata* L. and *Lavandula pubescens*, Decne) grow naturally in Saudi Arabia (El-Karemy and Zayed, 1992; Rahman et al., 2003). The country is known as one of the main geographical area of *Lavandula* species diversity and endemism and has been suggested to be the center of origin of the genus (Miller, 1985). *Lavandula* species such as *L. dentata* and *L. pubescens* grow naturally and extensively in the southwestern mountain regions of Taif, Albaha and Asir and serve as a source of high quality *Lavandula* honeys, known locally as "Seyfi honey" and fetch premium prices of $50–120/kg. Most of the studies on *Lavandula* species generally have been limited to cultivated and commercial varieties in temperate regions. Despite the natural occurrence of different lavender species in the Arabian Peninsula, the nectar secretion dynamics and honey production potentials of these species in their natural habitats have not been studied.

Moreover, other plant species from the family *Lamiaceae*, such as *Otostegia fruticosa* (Forssk.) Schweinf. ex Penzig and *Nepeta deflersiana* Schweinf. ex Hedge, in addition to being used by humans for their medicinal properties (Aboutabl et al., 1995; Mothana, 2012), are frequently visited by honey bees for nectar collection.

The other important honey bee plant group belongs to the genus *Ziziphus* (family: *Rhamnaceae*) and consists of approximately 100 species that are distributed in the tropical and subtropical regions of the world (Cherry, 1985; Abalaka et al., 2010). Most of the species in this genus are drought and heat-tolerant and adapted to low rainfall conditions (Orwa et al., 2009). Some of the species, such as *Ziziphus spina-christi* (L.) Desf., grow in a wide range of habitats covering vast land areas of Africa, the Eastern Mediterranean, the Arabian Peninsula, and in the Tropical Asia (Scholte et al., 1991; Orwa et al., 2009). Some of the *Ziziphus* species produce a range of products that includes food, fodder, fuel, drink, timber, and medicine. Four *Ziziphus* species (*Ziziphus glabrata* Heyne, *Ziziphus mucronata* Willd., *Ziziphus nummularia* (Burm. f.) Wight & Arn., *Z. spina-Christi* var. *divaricata* Forssk., *Z. spina-christi* var. *inermis* Boiss., and *Z. spina-christi* var. *spina-christi* (L.) Willd.) are found in Saudi Arabia. Honey from *Ziziphus* trees is the most common and the most expensive honey in the region, selling for up to $60–100/kg (Nuru et al., 2014).

The contribution of a bee plant species to honey production not only relies on its flowering phenology and abundance but also on its nectar quality and quantity. Nectar is mainly produced by plants as a reward to flower visitors. Its production is a complex physiological process significantly influenced by flower species-specific characteristics (shape, size, and position) and is governed to a large extent by abiotic environmental conditions and the phenology of the flower (Mačukanović-Jocic et al., 2004). Nectar is the major raw material for honey production. However, not all flowering species produce nectar, and not all nectar produced by flowers is accessible to honey bees (Bastiaan, 1984). Even if accessible, the amount and concentration of nectar varies from plant to plant and over time (Roubik, 1991; Chalcoff et al., 2006).

The energy value of nectar in relation to its TSS concentration varies markedly among the different plant taxa and ranges from 10% to 80%. A wide range of nectar TSS concentrations from 12% (*Rhodophiala mendocina*) to 51.7% (*Escallonia rubra*) (Chalcoff et al., 2006) has been reported. The variation in concentration is not only due to plant species but also to the different times of the day (Roubik, 1991). Therefore, it is important to determine the value of bee plants in relation to the volume, dynamics and concentration of nectar secreted by the plant. In this regard, no adequate information exists on the apicultural values of major honey source plants of the country. The aim of the present study is to evaluate the nectar secretion dynamics and honey yield potential of some major honey bee plant species under Saudi Arabian environmental conditions. Accordingly, we investigated the nectar secretion dynamics of species and the amount of nectar TSS secreted per flower for major honey source plant species. We also extrapolated the honey production potential per tree and per hectare of land occupied with studied plant species.

2. Materials and methods

2.1. Studied species and sites

In this study, 14 important honey source plant species which are commonly visited by honey bees for nectar collection and also serve as source of honey in the region were considered. Eight of these belong to the genus *Acacia* (*Fabaceae*), four species belong to the family *Lamiacae*, and two species belong to the genus *Ziziphus* (*Rhamnaceae*). The species are widely grown and well adapted to the prevalent arid climatic conditions of Saudi Arabia and are frequently visited by honey bees for nectar and pollen collection. The list of species, their general features and distribution are indicated in Table. 1.

The study was carried out in five sites in two regions of Saudi Arabia. The first two sites (Rawdhat-Khoraim and the Educational Farm of King Saud University) are located in central Saudi Arabia in the heart of the Arabian desert at the southern edge of the Palearctic ecozone. The other three sites (Wadi-Alkhitan, Wadi-Berha and Baljurashi) are located in southwestern Saudi Arabia (Albaha), which belongs to the Asian division of the Afro-tropical ecosystem (Fig. 1). The studied species were investigated according to their spatiotemporal distribution (Table 2).

2.2. Flowering period distribution

The distribution of the flowering period for each species was determined through continuous monitoring and recording of the plants' flowering patterns, including the commencement, peak, and end of their flowering period. For each species, the peak flowering time was indicated when approximately 50% of the flower buds were in the blooming stages. In addition, species with wide ecological distribution (lowlands and midlands) and species with multiple flowering seasons were also considered and recorded.

2.3. Phenology

For flower phenology, observations were made on three individual plants per species, and from each plant, an average of five flower buds (total of 15/species) were labeled in late afternoon and monitored over the next few days. During marking, all previously opened flowers from the marked branch were removed to avoid confusion. On the next morning, the phenology of the flowers, including the time of flower opening, the wilting of the flower parts and the average duration of the flower remaining, was monitored and recorded through observations made on the flowers every two hours (from 0600 to 1800). For those flowers that remained for more than one day, the observations were continued until the flowers wilted.

Table 1 Some general features of the studied honey plant species.

Family	Nomenclature	Habit	Common names		Uses	Distribution
			English	Arabic		
Fabaceae	*Acacia asak*	Tree		Asak, Dhahia, Dhahian	LP, gum, FW	Af, Ar
	A. ehrenbergiana	Shrub	Salam	Salam, Hardha	LP, FW	Af, Ar
	A. etbaica	Tree	Savannah thorn	Arad, Qardh	LP, FW, TM, T	Af, Ar
	A. gerrardii	Tree	Red thorn, Gerrard's acacia	Talh, Shaba'an	LP, FW, TM, T	Af, ME
	A. johnwoodii	Tree				Ar
	A. oerfota	Shrub	Green-barked acacia	Orfut, What	LP	Af, Ar
	A. origena	Tree		Kanahbal, Kulhab		Af, Ar
	A. tortilis	Shrub	White thorn	Samar, Somra	LP, TM, FW	Af, Ar
Lamiaceae	*Lavandula dentate*	Herb	Fringed lavender	Dhorm	TM, O	Af, Me
	L. pubescens	Herb	French lavender	Thafra, Atan		Af, Me
	Nepeta deflersiana	Herb		Sheah	TM, O	Ar
	Otostegia fruticosa	Herb		Sharm	LP, TM, O	Af, Ar
Rhamnaceae	*Ziziphus nummularia*	Shrub	Wild jujube	Sidr	Fruit, LP, TM	Af, ME, SWA
	Ziziphus spina-christi	Tree	Christ's thorn jujube	Sidr	Fruit, TM, T	Af, SWA

*Uses: LP, Livestock pasture; TM, Traditional medicine; FW, Firewood; T, Timber; O, Ornamental.
**Distribution: Ar, Arabia; Af, Africa; ME, Middle East; Me, Mediterranean; SWA, Southern and Western Asia.

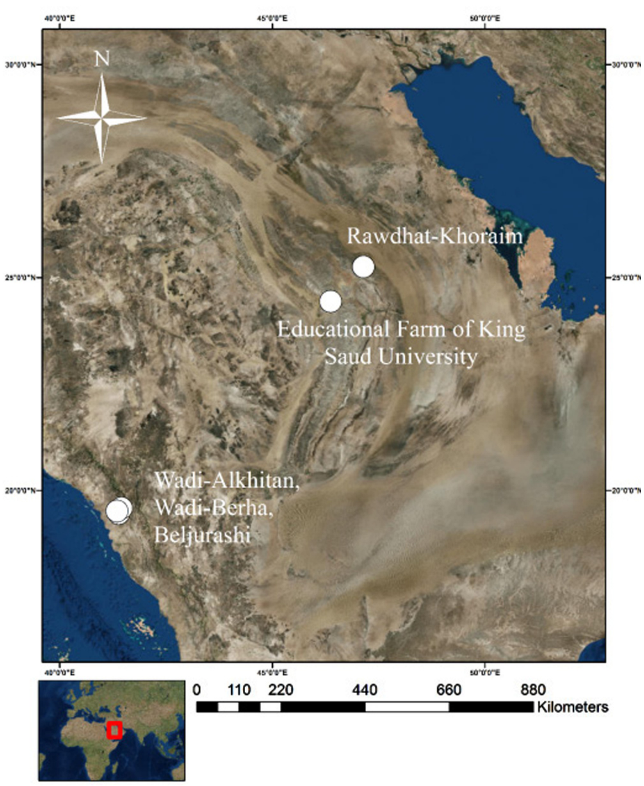

Figure 1 A physiographic map of Saudi Arabia with white points representing study sites.

2.4. Determination of nectar secretion dynamics and amount

The amount and dynamics of nectar TSS production were determined from an average of three individual plants per species. For this, branches of a plant with mature flower buds were randomly selected, labeled and bagged one day before the flowers opened using bridal-veil netting (Wyatt et al., 1992). For nectar volume estimation and nectar TSS determination, direct nectar removal and nectar sugar washing techniques were applied depending on the nature of the flower morphology and the amount and concentration of the nectar.

2.4.1. Nectar TSS determination using washing techniques

In *Acacia* species with both spherical and elongated types of inflorescences, the individual florets are very small, and the nectar was too viscous (because of low humidity and high temperature of the study areas) to be easily measured using capillary tubes. Therefore, in this study, for all *Acacia* spp., the nectar TSS amount was determined following the flower nectar sugar washing techniques of Mallick (2000). In this procedure, one flower head was used only for one time measurement in that each flower head was removed and kept in a small, narrow plastic vial and washed with 1 ml of distilled water except for *A. tortilis* flowers which was enough to use 0.5 ml because of its smaller size. The flower heads were then left for 5 min until the sugar was completely dissolved. The nectar TSS was measured from five flowers per plant and for each sampling time (five times a day at 0600, 0900, 1200, 1500, and 1800 h) which equals to a total of 25 flower heads/day/plant. The measurements were repeated for three consecutive days, with TSS being measured for 225 flowers for each species.

For flowers with elongated inflorescence (*A. asak*) because all florets do not open simultaneously, 20 opened florets were taken at one time, and their nectar TSS amount was determined using the same above-described nectar sugar washing technique and extrapolated for the whole inflorescence. From the pooled clear nectar solution washed sugar; a drop of solution was taken using micropipettes, and the concentration of this solution was measured using an automatic temperature-compensated, digital, hand-held refractometer (Reichert, Catalog number 13950000, USA). The mass of the TSS in the nectar solution for each measurement was calculated from the volume and concentration of the solution that was measured. The sucrose concentration readings (mass/total mass, g of TSS/100 g of solution) were converted to sucrose mass/volume

Table 2 Study sites, species and years of investigation.

Regions	Study area and its description	Studied species	Year
	Wadi-Alkhitan: 1100 masl*, Wild forest	*A. tortilis*	2012
		A. ehrenbergiana	2012
		A. asak	2012
		A. johnwoodii	2014
		A. oerfota	2014
Al Baha-	Wadi-Berha: 1750 masl, Wild forest	*A. etbaica*	2013
	Beljurashi: 2200 masl, Wild forest	*A. origena*	2013
		L. dentate	2013
		L. pubescens	2013
		N. deflersiana	2013
		O. fruticosa	2013
Riyadh	Rawdhat-Khoraim: 570 masl, subtropical oasis	*A. gerrardii*	2012
	Educational Farm of KSU*: 650 masl, irrigated farm	*Z. nummularia*	2012
		Z. spina-christi	2011

* Masl refers to elevation in meters above sea level.
* KSU refers to King Saud University, Saudi Arabia.

using Weast's (1986) conversion table. For each species, the mean nectar TSS values were computed for each sampling time and per flower.

In *Ziziphus* flowers, because of the rapid crystallization of the nectar sugar on surface of the flowers, a similar washing technique was applied. However, in *Ziziphus*, because the flowers remain for two days, the nectar secretion dynamics was studied by measuring the same labeled flowers repeatedly at four hour intervals (at 0600, 1000, 1400 and 1800) during the day for two consecutive days. During each washing, 10 μl of distilled water was deposited onto the crystallized nectar sugar on the surface of each flower using a calibrated micropipette (Eppendorf Research®), and the water was allowed to remain for one minute to dissolve the sugar on the surface of the flowers. Because the TSS present were dissolved in the 10 μl of water that was added, the concentration of the recovered solution reflects that of the 10 μl 'pool' in the flower and was used to estimate the TSS present assuming a volume of pool solution is 10 μl. From this pool, a drop of solution was taken to measure the concentration using the same above mentioned hand-held refractometer. In this repeated measuring procedure, to avoid re-measuring of sugars that might remain from the earlier measurements, the flowers were rinsed/washed three times with 10 μl of distilled water after each measurement, which was sufficient to lower the refractometer reading to approximately 0 or $\leqslant 1\%$. The mean nectar TSS values were computed for each sampling time and flower.

2.4.2. Nectar volume and dynamics measurement through direct removal

For bee plants in the family *Lamiaceae* because their flower morphology is suitable to directly extract and measure the nectar volume; the volume of nectar was determined by directly removing the nectar from the flower using graduated capillary tubes. From each plant and for each sampling time, the nectar volume was measured from an average of 10 flowers, which was 50 flowers/day/plant. The nectar volume measurement was repeated for three consecutive days, totaling 450 flowers/species. The concentration of the nectar TSS was measured using the same device mentioned above, and the mass of TSS per volume was estimated following the above-described procedure. Then, the amount of nectar volume and nectar TSS concentration were computed per sampling time and flower and compared among plants, species and different hours.

2.5. Estimation of the honey production potentials of the species

The average amount of honey that can be obtained from a single plant was estimated from the average numbers of flowers per plant and the average mass of the nectar TSS per flower, following procedures similar to those of Masierowska (2003) and Kim et al. (2011).

The average number of flowers per tree was estimated by counting the number of flowers in three randomly sampled 1 m^2 areas or 1 m^3 volume per plant from three different plants. Surface area or volume was used depending on the distribution of flowers on the canopies of the studied species. The average number of flowers per tree was obtained by multiplying the average number of flower buds/m^2 or /m^3 by the average surface area or volume of the canopy of the species. The species canopy volume was calculated following Coder's (2010) plant crown shape formula (shape value $(0.375) \times$ (crown diameter)$^2 \times$ (crown height) $\times (0.2945)$ for fat cone canopies and (shape value $(0.667) \times$ (crown diameter)$^2 \times$ (crown height) $\times (0.5236)$ for spheroid canopies, depending on the crown shapes of the species). For each plant species, the canopy volume was determined by measuring 10–20 individual tree canopies.

For perennial shrubs, (such as in *Lavandula*) the number of flowers per plant was determined by counting the average number of branches or flower spikes per plant and then multiplying by the average number of flowers per spike or branches through counting 10–20 individual plants per species. Then the honey production potential of the plants was estimated by multiplying the average number of flowers per plant by the average mass of the TSS per flower. The number of plants per hectare was estimated based on the average canopy area of each species plus the space required between plants. These data have been used to estimate the possible amount of honey that can be obtained per hectare of land occupied by the species.

2.6. Weather data

Along with the nectar secretion amount and dynamics studies, weather (temperature and humidity) data of the study area were also recorded and correlated with the nectar secretion amount and dynamics of the species.

2.7. Statistical analysis

An analysis of variance (ANOVA) was used to compare the mean amount of nectar TSS that was secreted per flower head per 3 h (and per 4 h for *Ziziphus*) period from the different trees within species and also among the different species. A pair wise correlation analysis was performed between the environmental factors (temperature and relative humidity of the area) and the amount of nectar TSS secreted per flower or inflorescence. The analysis was performed using JMP-5 statistical software (SAS, 2002).

3. Results

3.1. Flowering period distribution

The flowering period distributions of the honey source plants varied from one species to another (Table 3). The majority of the species in this study flowered during spring with little extension into early summer. The remaining species flowered mostly in autumn. Generally, the species were characterized by a short flowering time, except for *A. ehrenbergiana* and *A. asak*, which have relatively longer flowering periods. Some species such as *Ziziphus* spp. and *A. etbaica* have multiple flowering periods, whereas *A. asak* and *A. johnwoodii* were observed to have intermittent flowering patterns. Moreover, species such as *Z. spina-christi*, *A. tortilis*, and *A. ehernbergiana* have a wide range of ecological distribution which varies from 200 to 1750 meters above sea level. Hence, their flowering periods varied accordingly within the same season. Moreover, species such as *A. tortilis* and *A. ehernbergiana* were observed to flower in the dry season during the leafless stage, but if rain occurred, the plants were observed to abort their flower buds and initiate new leaves.

3.2. Flower phenology

In this study, all *Acacia* spp. with spheroidal inflorescences; the flower heads commonly opened early in the morning at approximately 0500 h and stay for only a day, wilting at approximately 1500–1800 h. However, in *A. oerefata*, the opening of the flower heads was not restricted to a certain time of a day and observed to occur continuously throughout the day. In *A. asak*, which has an elongated inflorescence, half of the florets opened in one day, whereas the remaining half opened on the next day. In the genus *Lavandula* (*L. dentata* L. and *L. pubescens* Decne), the individual flowers from a spike were observed to open in a sequential manner during the day, and each flower lasted for an average of 12 h. In these species, when the flowers that had opened earlier were about to wilt, new flowers started to open so that flowering was continuous with some degree of overlap in the opening times of individual flowers. However, in *O. fruticosa* and *Ziziphus* species, the flowers opened early, between 0500 h and 0600 h, and stayed open for about two days.

3.3. Nectar secretion amount and dynamics

Within the genus *Acacia*, the highest average nectar TSS (7.7 ± 3.2 mg/inflorescence) was recorded for *A. oerfata*, whereas the lowest average of 1.6 ± 0.5 mg/inflorescence was recorded for *A. etbaica* ($P < 0.0001$; Table 4). In the case of species in the family *Lamiaceae*, the highest average nectar TSS (0.52 ± 0.22/flower) was recorded for *L. dentata*, whereas the lowest (0.41 ± 0.13 mg/flower) was recorded for *L. pubescens* and the variation was significant ($P < 0.000$) (Table 5). In the genus *Ziziphus*, a higher nectar TSS of 0.79 ± 0.10 mg/flower was recorded for *Z. spina-christi* compared to the 0.64 ± 0.04 mg/flower recorded for *Z. nummularia* ($P < 0.000$; Table 6).

The nectar TSS secretion dynamics of the studied species showed an increasing trend early in the morning, peaking toward midday, followed by a decline (Fig. 2A–C). However, different species were observed to have different peak nectar secretion times. Moreover, species such as *A. ehrenbergiana*

Table 3 Flowering periods distribution of the studied honey plant species. Bars with different colors indicate the lengths of the flowering duration of each species.

Species	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Acacia asak								x	x	x	x	
Acacia ehrenbergiana		x	x	x	x							
Acacia etbaica					x	x		x	x	x		
Acacia johnwoodii										x	x	
Acacia oerfota			x	x								
Acacia origena					x	x						
Acacia tortilis			x	x	x							
Acacia gerrardii						x	x	x				
Ziziphus spina-christi					x	x		x	x	x		
Z. nummularia						x	x		x	x		
Lavandula dentata			x	x	x							
L. pubescens			x	x	x							
Nepeta deflersiana			x	x	x							
Otostegia fruticosa				x	x	x						

Table 4 Comparison of the mean nectar TSS (mg)/inflorescence of eight Acacia species growing in Saudi Arabia at different local times of the day.

Species	0600 h	0900 h	1200 h	1500 h	1800 h	Mean
A. asak	1.3 ± 2.3^{c}	3.0 ± 2.8^{bc}	4.7 ± 2.2^{ab}	5.0 ± 4.2^{a}	5.0 ± 3.5^{a}	3.8 ± 1.6
A. ehrenbergiana	4.2 ± 2.4^{c}	4.8 ± 2.7^{c}	5.6 ± 2.8^{c}	7.3 ± 2.6^{b}	9.0 ± 2.3^{a}	6.2 ± 2.0
A. ethbaica	0.8 ± 0.9^{b}	1.8 ± 2.0^{a}	1.4 ± 1.3^{ab}	2.2 ± 1.7^{a}	1.7 ± 1.5^{a}	1.6 ± 0.5
A. gerrardii	5.4 ± 1.7^{a}	5.4 ± 2.3^{a}	7.0 ± 4.7^{a}	5.6 ± 3.9^{a}	3.2 ± 1.1^{b}	5.3 ± 1.4
A. johnwoody	1.5 ± 1.3^{b}	2.0 ± 1.6^{b}	4.0 ± 1.9^{a}	3.4 ± 2.1^{a}	2.2 ± 1.2^{b}	2.6 ± 1.0
A. oerfata	2.8 ± 1.6^{d}	6.2 ± 2.6^{c}	8.6 ± 2.7^{b}	10.6 ± 3.7^{a}	10.0 ± 4.0^{ab}	7.7 ± 3.2
A. origena	3.0 ± 2.0^{a}	2.6 ± 2.2^{a}	3.2 ± 2.6^{a}	3.3 ± 2.3^{a}	1.4 ± 0.9^{b}	2.7 ± 0.8
A. tortilis	1.0 ± 0.6^{c}	1.5 ± 1.0^{bc}	2.3 ± 1.8^{ab}	3.0 ± 2.4^{a}	2.4 ± 2.0^{ab}	2.0 ± 0.8

Values in the same row which are not connected by same letter are significantly ($P < 0.0001$) different; One inflorescence is used for one time measurement only; For each species: $DF = 4$, $P < 0.0001$, $N = 45$ (Except *A. gerrardii* $N = 55$).

Table 5 The mean ± SD nectar volume amount secreted/flower in μl at different local times of the day for *Lavandula* (*L.*), *Nepeta* sp. (*N.*), and *Otostegia* sp. (*O.*) growing in Saudi Arabia.

Species	0600 h	0900 h	1200 h	1500 h	1800 h	Mean
L. dentata	0.35 ± 0.15^{a}	0.40 ± 0.14^{a}	0.53 ± 0.19^{b}	0.64 ± 0.20^{c}	0.68 ± 0.19^{c}	0.52 ± 0.22
L. pubescens	0.28 ± 0.19^{a}	0.41 ± 0.25^{ab}	0.46 ± 0.23^{b}	0.50 ± 0.24^{b}	0.41 ± 0.21^{c}	0.41 ± 0.24
N. deflersiana	0.31 ± 0.10^{c}	0.44 ± 0.13^{a}	0.47 ± 0.13^{a}	0.43 ± 0.15^{ab}	0.39 ± 0.13^{b}	0.41 ± 0.13
O. fruticosa	0.37 ± 0.20^{c}	0.59 ± 0.21^{a}	0.51 ± 0.21^{ab}	0.45 ± 0.24^{bc}	0.40 ± 0.20^{c}	0.47 ± 0.21

Values in the same row which are not connected by the same letter are significantly ($P < 0.0001$) different; One flower is used for one time measurement only. For each species: $N = 90$, $DF = 4$, $P < 0.0001$.

and *Lavandula dentata* were observed to continue their nectar secretion even until late afternoon (1800 h).

3.4. Honey production potentials

Nectar TSS and honey production potentials of the studied plants varied significantly at $P < 0.000$ among species (Table 7). Based on the number of flowers per unit area or volume and the amount of nectar TSS per flower or inflorescence, a minimum amount of nectar TSS of 0.0012 kg/plant was recorded for *Nepeta deflersiana*, whereas a maximum of 4.33 kg/plant was recorded for *Z. spina-christi*. Moreover, depending on the estimated number of plants per hectare of land, and also assuming that 18% of honey is water, a minimum of 14.49 kg and a maximum of 829 kg honey/hectare were estimated to be obtained from *O. fruticosa* and *Z. spina-christi*, respectively (Table 7). Within the genus *Acacia*, a maximum of 2.60 kg nectar TSS/tree was recorded for *A. gerrardii*, whereas a minimum of 0.15 kg nectar TSS/tree was recorded for *A. etbaica*. With the optimal plant densities of the *Acacia* species, the expected amount of honey per hectare of *Acacia* forestland was estimated at a maximum of 624.5 kg for *A. johnwoodi* and a minimum of 51.1 kg for *A. etbaica* (Table 7).

3.5. The effects of weather conditions on nectar TSS secretion

The average temperatures and RH recorded during the study period varied from 25–45 °C and 20–40% respectively. Generally, in all species, the amount of nectar TSS secreted has significant positive correlation with the ambient temperature and negatively correlated with RH, except in *L. dentata*, which was significantly positively correlated. However, the optimum temperatures and humidity recorded for peak nectar TSS secretion times differed among species. For example, the highest nectar TSS was recorded at an average temperature of 35.7 °C and 28.7% RH for *L. pubescens* and at 28.3 °C and 37.7% RH for *L. dentata*. However, in *Z. spina-christi* the peak nectar TSS was recorded at 45 °C.

4. Discussion

4.1. Flowering period distribution

The differences in the flowering periods of the species could be attributed to the variations in their ecological distribution and the climatic factors (temperature, rainfall and photoperiod). In this regard the effects of rainfall on the onset of green-up and growth and in defining flowering durations in some desert plants have been well reported (Fox, 1990; Borchert, 1994; Abd El-Ghani, 1997; Peñuelas et al., 2002). Moreover, photoperiod and temperatures have been stated as being the main factors in governing the flowering seasons of different plant species (Ausín et al., 2005). The variations in flowering periods within related and sympatric species (such as different *Acacia* species) could be considered as a mechanism to minimize competition for pollination. The temporal separation of flowering periods of sympatric species has been interpreted as their adaptation to avoid competition for pollination (Pleasants, 1983; Rathcke, 1983; Stone et al., 1998, 2003).

The aborting of flowers and the initiating of new leaves following the onset of rain in some studied *Acacia* species could be due to a shift in the resource allocation of the species from reproductive functions to vegetative growth. Such resource

Table 6 The mean ± SD nectar TSS amount (mg/flower) measured at different local times of the day from a single flower of the two *Ziziphus* spp. growing in Saudi Arabia.

Species	*N*	1st day				2nd day				Total/flower
		0600 h	1000 h	1400 h	1800 h	0600 h	1000 h	1500 h	1800 h	
Z. nummularia	80	0.06 ± 0.02^{e}	0.21 ± 0.08^{a}	0.12 ± 0.08^{c}	0.15 ± 0.07^{b}	0.07 ± 0.04^{d}	0.02 ± 0.01^{f}	0.01 ± 0.01^{g}	0.01 ± 0.01^{h}	0.64 ± 0.04
Z. spina-christi	90	0.06 ± 0.01^{c}	0.13 ± 0.11^{b}	0.35 ± 0.32^{a}	0.16 ± 0.17^{b}	0.05 ± 0.07^{d}	0.02 ± 0.03^{e}	0.02 ± 0.04^{e}	0.01 ± 0.02^{f}	0.79 ± 0.10

Values in the same raw which are not connected by same letter are significantly ($P < 0.0001$) different; One flower was used for repeated measurement. For each species: $DF = 7$, $P < 0.0001$.

shifting patterns are known to be typical adaptations of plants to dry climatic conditions and considered as a strategy for partitioning of the use of resources between reproductive and vegetative purposes (Singh and Kushwaha, 2006). Moreover, general spatiotemporal phenological shifts in response to rainfall changes have been well documented (Peñuelas et al., 2004). With regard to this, some beekeepers have argued that when the rain occurs and the plants produce new green leaves while flowering, these plants will not be a good source of nectar (personal communication), which could indicate resource trade-offs by the species between vegetative and reproductive functions. The variation in the flowering periods among and within species allows beekeepers to harvest honey several times in a year by migrating their colonies to different localities (an average of 6 times/year) in search of better flowering plants (Nuru et al., 2013, 2014). Moreover, the flowering seasons of *Z. nummularia* and *A. gerrardii* in the extremely harsh summer in central Saudi Arabia reported to be valuable for bees and beekeeping (Alqarni, 2015).

4.2. Phenology

The variations in phenology of the different species in this study could be attributed to the adaptations made to ensure maximum pollination through the partitioning of pollinators and the efficient distribution of resources. Variations in phenology and the timing in the release of floral rewards among sympatric species have been reported to be a selective response to competition for pollination and mechanisms of partitioning pollinators (Pleasants, 1983; Rathcke, 1983; Stone et al., 1998).

4.3. Nectar TSS amount and dynamics

Significant variations in the amount and patterns of nectar secreted by the different honey source plants could be due to the variations in biotic and abiotic factors associated with the different plant species in their respective environments. Variations in nectar concentration and production patterns as a result of variations in pollinator guilds have also been well documented (Baker and Baker, 1975; Cruden et al., 1983; Galetto and Bernardello, 1992). Moreover, separations in peak floral reward release times among different species have been interpreted as a means of partitioning of pollinators (Stone et al., 1998). One possible reason for the continuous increase and eventual peak in nectar at approximately 1800 h for species such as *A. ehrenbergiana* and *L. dentata* (Fig. 2 A and B) could be the absence of re-absorption of the nectar by the flower. In addition, it could also be an adaptation by the species to nocturnal flower visitors. These possibilities require further investigation.

4.4. Nectar TSS secretion amount and dynamics and its association with weather conditions

The significant positive correlations between the nectar secretion and the ambient temperature in all the studied species may indicate the adaptations of the species to higher temperatures. Similarly, the presence of a positive correlation between nectar values (volume/flower, TSS content and concentration) and temperature was recorded in the Mediterranean species *Thymus capitatus* up to 38 °C (Petanidou and Smets, 1996)

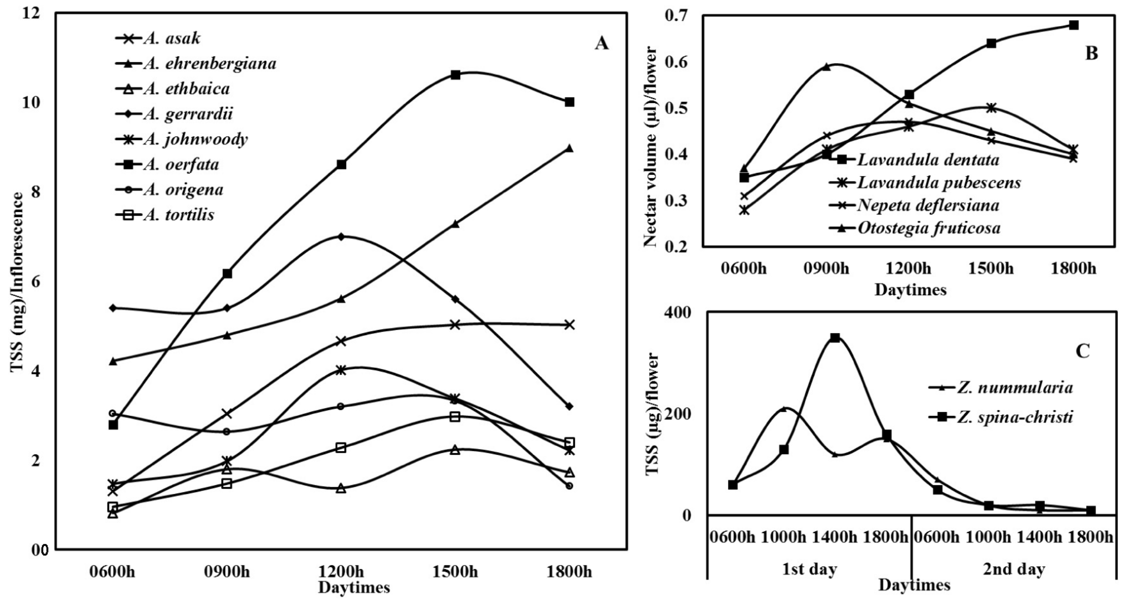

Figure 2 Nectar secretion dynamics of some honey plant species in Saudi Arabia at different times of a day (A = *Acacia*, B = *Lamiacae*, C = *Ziziphus*).

Table 7 The expected nectar TSS amount per flower and per tree and honey production potential per hectare of land covered with the studied honey plant species in Saudi Arabia.

Plant species	Max. average nectar TSS (mg)/flower	No. of flowers/m^3 or per plant	Nectar TSS (mg)/m^3	Crown volume in m^3	Nectar TSS (kg) plant	Estimated plants/hectare	Expected nectar TSS (kg)/hectare	Expected honey yield (kg)/hectare
Acacia asak	5.0	1954	9770	20.0	0.20	462	91	110
A. ehrenbergiana	9.0	2902	26,114	32.2	0.84	432	363	443
A. etbaica	1.8	2963	5333	27.6	0.15	284	42	51
A. gerrardii	7.0	4000	28,000	93.0	2.60	161	419	511
A. johnwoodii	4.0	11,560	46,240	46.3	2.14	239	512	625
A. oerfota	10.6	3000	31,800	1.9	0.06	1651	99	120
A. origena	3.3	4256	14,045	71.6	1.01	265	266	325
A. tortilis	3.0	6370	19,110	22.8	0.44	421	183	223
Lavandula dentata	0.2	18,537/plant	–	–	0.004	10,454	43	51
Lavandula pubescens	0.2	17,750/plant	–	–	0.003	6873	19	24
Nepeta deflersiana	0.3	56,099/plant	16,830	0.1	0.001	12,548	16	18
Otostegia fruticosa	0.4	27,939/plant	10,337	0.2	0.002	7708	12	14
Ziziphus nummularia	0.64	57,420	36,837	45	1.66	224	371	447
Ziziphus spina-christi	0.79	43,000	33,970	127.5	4.33	157	680	829

and in Saudi Arabia up to 45 °C for *Z. spina-christi* (Adgaba et al., 2012) and *Z. nummularia* (Alqarni, 2015). In contrast, the negative correlation between the nectar values and relative humidity was expected because at midday when the flowers attained peak nectar TSS secretion, the humidity was generally low in the area. The secretion of more nectar TSS at high temperature and low humidity may indicate how well the species adapted to the prevalent weather conditions. However, high temperature and low humidity cause rapid crystallization of nectar TSS on the open surface of *Ziziphus* flowers, which makes it difficult for the bees to properly utilize the nectar. Similarly, Corbet et al. (1979) reported that low relative humidity and exposed nectaries enhance water evaporation and the concentration of the nectar, which ultimately leads to its crystallization.

4.5. Honey production potentials

Despite the arid and semiarid climatic conditions of the region, some of the studied plant species were observed to have high potential for honey production (Table 7); these results are comparable to the reports made for different annual plants and trees such as *A. syriaca* L. (milkweed) (500–600 kg honey/ha; Zsidei, 1993); *T. pratense* L. (red clover) honey yield of 883 kg/ha/flowering period (Szabo and Najda, 1985; various *Tilia* (lime) species (90–1200 kg honey/ha; Crane et al., 1984); and *Brassica juncea* and *Sinapis alba* crops (65.5 kg and 71.2 kg/hectare, respectively; Masierowska, 2003). In general, trees were more productive in nectar secretion than herbs due to their larger biomass, dense flowers, deep roots and resistance to moisture stress.

Moreover, in most trees, the flowers are not colorful and are expected to secrete more nectar to strongly attract sufficient pollinators. However, herbaceous plants have conspicuous colors and may not need to produce large amount of nectar (Schemske and Bradshaw, 1999). In line with this, Alqarni et al. (in press) described the mass flowering behavior *A. gerrardi* as evolutionary adaptation of the species to withstand pre and post fruiting obstacles and this may have contributed to copious gross nectar per tree.

In some species, the amount of nectar TSS per flower was high, but the amount of honey per tree or hectare of land was low because honey production potential also depends on the number of flowers per unit area or volume and the canopy of the plant. The actual honey production of the species is expected to be lower than the honey production potential estimated in this study because a significant amount of the nectar is utilized by the honey bees for brood rearing and for the energy required for the collection and processing of nectar and pollen.

The study indicated that despite the limited rainfall and high temperature in the region; the studied species secrete a significant amount of nectar sugar and are very potential for beekeeping. The contributions of the studied species as honey source plants are relatively better than other agricultural activities, which require sufficient water. Based on the estimated amount of TSS, the monetary value of honey that can be obtained per hectare for the species in this study can be equal or greater than the per-hectare monetary value of some cultivated crops that require many inputs. Therefore, rehabilitation and conservation of such multipurpose plants seems worthwhile, both for economic reasons and their environmental value. In addition, the information generated in this study is believed to be useful in apiary site selection and to estimate the honey bee colony carrying capacity of an area.

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