

NECTAR PRODUCTION DYNAMICS IN TWO MELLIFEROUS PLANT SPECIES

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Summary: Nectar production of two melliferous plant species in response to climatic factors was assessed. The nectar volume and sugar concentration of 100 flowers (50 per plant species) were measured at hourly intervals. Microclimatic parameters in the vicinity of the two plant species, and honeybee visits to their flowers were recorded. The volume of nectar in both melliferous plant species was high in the early hours of the day. Total mean volumes in *Antigonon leptopus* and *Thevetia peruviana* were 14.86 ml and 16.58 ml, respectively. Sugar concentration in *A. leptopus* increased from 11 % at 0.6:00 h to 30% in the afternoon; but in *T. peruviana* it increased gently after 07:00 h and peaked at 17:00 h. Significant differences occurred in the concentration of nectar sampled during the day ($n=50$, $F_{2,35}$ df = 49, $P = 0.56$). The sugar concentration of nectar produced in both plant species was inversely proportional to the volume of nectar produced. Positive correlation existed between sugar concentration and temperature in *A. leptopus* ($r = 0.59$, $P = 0.05$), and *T. peruviana* ($r = 0.32$, $P = 0.05$). Temperature had greater influence on nectar production ($F = 0.211$). The results indicated that temperature had overall influence on the nectar flow and sugar concentration, and this determined the foraging and pollinating activities of the honeybee.

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Keywords: *Antigonon leptopus*; melliferous plants; nectar production; *Thevetia peruviana*; temperature; sugar concentration.

INTRODUCTION

Nectar is a floral resource commonly sought after by plant visitors such as insects, birds and small mammals, because of its nutritional importance

(Baker and Baker, 1973; Kevan and Baker, 1983; Philips et al 2010; Bobrowiec and Oliveira, 2012). It therefore plays a critical role in attracting

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potential pollinators, and in determining the reproductive success of plants (Leiss et al 2004; Kudo and Harder, 2005). On the hand, nectar is the main raw material for honey. The healing properties of honey depend largely on the floral source with which honeybees are nourished. Recent research in nectar chemistry shows that nectar is more than water and sugars. The biochemical functions and different substances of nectar act as protection against microbial infestation through a novel biochemical pathway called the “Nectar Redox Cycle” (Feás et al 2013). Understandably, studying the nectar production in melliferous (bee-loving) plant species in relation to temporal changes and the influence of environmental factors could improve honey production, as well as increase understanding of pollinator energetics and behavior (Kearns and Inouye, 1993; Williams, 1997; Silva et al, 2004).

Nectar production, however, is believed to be part of an evolutionary development (Wesselingh and Arnold, 2000; Hopper, 1992). It involves some intricate biological processes determined by plant characteristics in response to the prevailing environmental conditions (Shuel, 1992; Macukanovic- Jovic, and Djurdjevic, 2005). This implies that studies of nectar production must be plant-specific, taking cognizance of the effects of environmental factors operating in plant's location. Studies have shown that nectar production in plants is controlled by various factors. These include environmental factors (Yeboah – Gyan and Woodell, 1987; Jakobsen and Kristjansson, 1994); location of flowers on the plant (Yeboah – Gyan and Woodell, 1987); the number

of newly open flowers per plant (Cawoy et al., 2008); and foraging activities of pollinators (Jakobsen and Kristjansson, 1994; Keasar et al., 2008). Physiological factors involved are re-absorption of the nectar (Davis, 1997; Langenberger and Davis, 2002); and age of the flowers (Galletto, 1994; Navarro, 2001). According to Nepi and Stpiczynska (2008) the volume, concentration, and viscosity of nectar do “change dynamically in time”. Other authors (Cruden et al., 1983; Pacini and Nepi, 2007; Galletto and Bernardello, 2004) have also indicated that nectar secretion rate, sugar concentration and energy content are determinants of the plant/pollinator relationship. Considerable energy is expended by plants in nectar production (Southwick, 1984; Galen et al., 1999), yet in comparison to other floral rewards such as pollen and oils it is a major attractant to flower visitors (Simpson and Neff, 1983). Galletto and Bernardello (2004) have also noted that nectar secretion follows particular rhythms throughout the lifespan of a flower, and this determines the nectar production dynamics of a species.

Nectarivorous insects can readily evaluate the sugar concentration of nectar, and respond to the modest differences in nectar accumulation (Waddington, 1985; Cane and Schiffhauer, 1997). Therefore, the secretion of nectar is essential to plants dependent on insect pollination for reproduction (Shuel, 1992; Philips et al., 2010). An accurate prediction of the pollinator guild of plants could be made from a thorough examination of nectar and its production. Notwithstanding the contribution of nectar to plant pollination and fitness their biological process in

tropical plants is woefully understudied (Shuel, 1992). This study is an attempt to appraise the diurnal pattern, volume and sugar concentration of the nectar in two melliferous plant species commonly found in the West African sub-region with emphasis on the influence of climatic factors on nectar production under tropical conditions.

MATERIALS AND METHODS

The Biophysical characteristics of the study area

The study was carried out at the Kwame Nkrumah University of Science and Technology (KNUST) of the Kumasi metropolis, Ghana. Kumasi is located between latitudes 7°00' and 6°30' N and longitudes 2°00 and 1°30'E. It is in the humid region of the tropics having moist, semi-deciduous forest. The mean monthly rainfall ranges between 19.1-235.1mm, with a peak in June. The area experiences a bimodal rainfall pattern of a major rainy season which starts in March and peaks in June, and a minor rainy season between August and November. A dry and dusty West African trade wind also known as Harmattan sets in from December

to February. Temperature is relatively constant ranging from 22.2°C to 35.1°C. The study sites were characterized by patches of natural habitats suitable for wild honeybees.

Study plant species

Natural populations of two melliferous plant species, *Antigonon leptopus* (Hook. and Arn.) (Fig.1 and 3A, B), and *Thevetia peruviana* (Pers.) K. Schum (Fig. 2 and 4A, B), both of which are common in West Africa were used in the study. *Antigonon leptopus*, commonly known as coral vine, is a climbing vine with slender stem belonging to the family Polygonaceae. It is one of the known plant species assessed as having good potential for supplying nectar during dearth flowering periods (Abrol, 2003). *A. leptopus* flowers are edible (Charmaine, 1998) and the whole plant has medicinal properties (Chistokhodova, 2002; (Mitchell and Ahmad, 2006; Lans, 2006). For example, a hot tea made from the ariel parts is used to relieve symptoms of cold and flu; an extract of its leaves and flowers inhibits lipid peroxidation. It has antioxidant, anti-inflammatory and analgesic properties. Flowers are fertile



Figure 1. Flowers of *Antigonon leptopus*.



Figure 2. *Thevetia peruviana* with flowers.

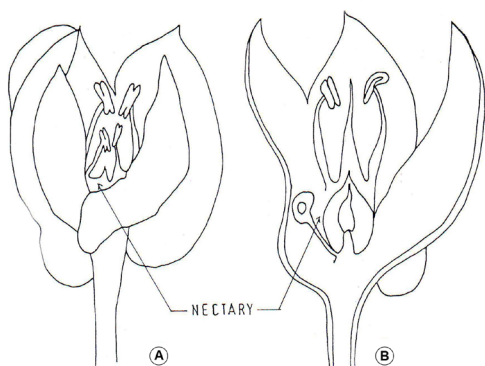


Figure 3. Diagram of A) full and B) half flower of *A. leptopus* showing exposed nectary.

hermaphrodites and together constitute an inflorescence. They are deep pink and small to medium-sized (up to 2 cm long), with 5-parted and persistent perianth. Each flower has unilocular ovary which has an open architecture (i.e. exposed nectary) as they are wide open, and could be visited by insects such as flies, beetles, and the honeybee *Apis mellifera adansonii* during the nectar flow (Raju et al., 2001; Adjaloo and Yeboah-Gyan, 2003).

Thevetia peruviana or milk bush belongs to the family Apocynaceae. It bears large yellow flowers. Its stem is green turning silver/gray as it ages. Flowers are reported to possess good medicinal value in traditional system of medicine (Kumar et al., 2012). The flowers are arranged in terminal cymes, with 2-loculed ovaries. The corolla is funnel-shaped with throat hairy scales resulting in concealed nectaries (Kareru et al., 2010). Although *Thevetia peruviana* plants are toxic to most vertebrates as they contain cardiac glycosides called digitoxigenin (Usman et al., 1997), they are visited by insects such as bees, moths and undergo entomophilous pollination.

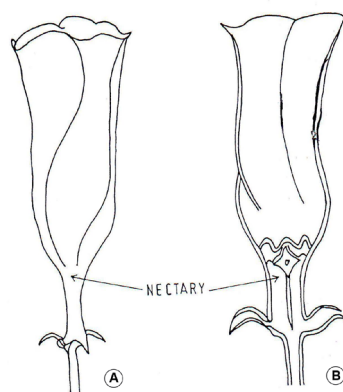


Figure 4. Diagram of A) full and B) half flower of *Thevetia peruviana* showing concealed nectary.

Experimental procedure

The diurnal dynamics of nectar secretion and sugar concentration of two melliferous plant species were studied for 20 days during their flowering period from February to March, and October to November in 2011. Flowering of the plant species was generally sparse at the peak of rainy season so data were not taken. Five plants of each plant species were randomly selected in one location; hence they were under the same climatic conditions. Ten fully opened flowers marked at random from the selected plant species were bagged in gauze. Thus, a total of 100 flowers (50 per plant species) were involved in the entire study.

By non-destructive method hourly nectar sampling of the marked flowers was carried out concurrently between 06:00h and 19:00h each day, using fine microcapillary tubes (1-ml, Camlab, Cambridge). Hourly record of microclimatic parameters i.e. air temperature (°C) and relative humidity (%) in the vicinity of the studied plants was taken using a thermohygrograph with an eight-day chart. The data gathered was

used to determine the temporal changes in nectar production during the day, and to correlate nectar production with the environmental factors (Castellanos et al., 2002).

The sugar concentration i.e. the amount of sugar per unit volume of nectar (Deppe et al., 2000) was obtained by measuring the refractive index of the nectar with a pocket refractometer for small volumes (Bellingham and Stanley Limited, Tunbridge Wells, U.K.) requiring volume less than 0.5 ml. Honeybee visits to the flowers of the plants were observed 10 min after the data collection.

Statistical Analysis

The experimental design was the Completely Randomised Design (CRD) with five replications. Data collected from each plant species were pooled together for detailed analysis, and no transformation of the raw data was required. Following Macukanovic- Jovic, and Djurdjevic (2005) the volume per flow was determined from the column length in the collecting pipette after it was measured with a millimeter paper immediately in the field, and the results were presented as the mean value using the formula:

$$V \text{ (mean value)} = \frac{\Sigma(r^2\pi \times H)}{\text{flower number}} \\ \pm \text{SD (ml per flower)}$$

r – Radius of the capillary glass (mm)

H – Nectar height in the tube (mm)

The nectar volume was divided by time to obtain hourly nectar production rates per-flower. Nectar production rate per plant species was also calculated by multiplying the mean per-flower

production rate by the mean number of flowers per plant as earlier suggested by Keasar et al (2008).

Nectar sugar concentrations were obtained as percentage (%) reading from the pocket refractometer. The hourly values per plant were then calculated by averaging the amount per hour produced by individual flowers over the 20-day period. Analyses of variance were performed with the general linear method procedures. Means were given \pm SE separated by Duncan's test. Pearson's correlation was carried out to show the relationship between nectar volume and sugar concentration produced by individual flowers of the melliferous plants species, and their micro-climatic factors (temperature and relative humidity). General Linear Model's stepwise regression was performed at F-value of 0.05 to determine which of the environmental factors greatly influenced nectar production. Therefore, any variable with F-value greater than $\alpha = 0.05$ was considered not significant. All analyses were performed with the Statistical Package for the Social Sciences (SPSS version 17) and were considered at an overall significance level of $P = 0.05$.

RESULTS

Nectar production trends in the two study plant species are illustrated in Fig. (5A, B). There was a general increase ($P=0.28$) in nectar volume in both plant species in the early hours of the day. Within each plant species the individual flowers differed considerably in the volume of nectar as demonstrated by the SE bars.

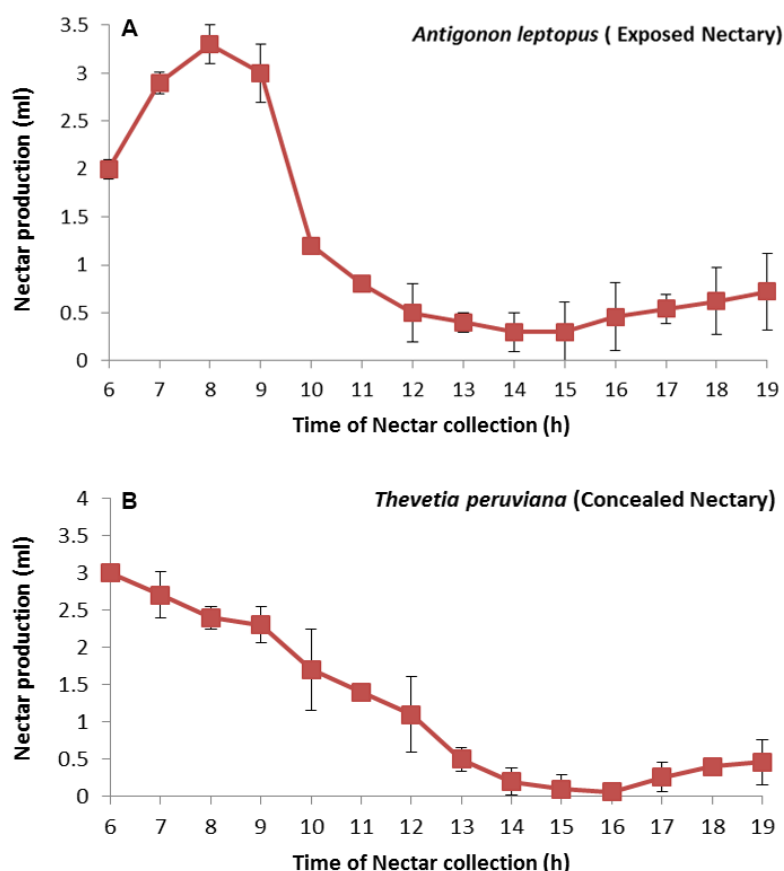


Figure 5. Diurnal dynamics of nectar production of (A) *A. leptopus* and (B) *T. peruviana* flowers. Data shown are means \pm SE of hourly nectar production from 50 flowers per plant species during the 20-day period.

Nectar production in *Antigonon leptopus* increased in volume from 06:00 h and peaked at 08:00 h with a mean volume of 3.3 ml ($n = 50$, $F_{2, 12} = 23.6$, $P = 0.05$). However, there was a sharp decline in volume after 09:00h. The nectar volume increased again from 15:00h. Total mean (\pm SE) volume of nectar sampled during the study amounted to 14.86 ml. It was observed that *A. leptopus* flowers were visited by honeybees in the morning from 8:00h and afternoon usually after 14:00h (Table 1; $P = 0.05$).

Nectar volume in *T. peruviana* reached its peak of 3 ± 1.1 ml ($n = 50$,

$F_{2, 12} = 6.4$, $P = 0.05$) and this occurred at 06:15h (Fig. 5b). There was a consistent drop in nectar volume till 16:00h, after which it increased again. Total mean volume of nectar collected from the flowers was 16.58 ± 1.18 ml but this was not significantly different ($P = 0.58$) from that of *A. leptopus*. Flowers of *T. peruviana* received high honeybee patronage of 20, as early as 05:15h till 07:00h and ceased temporarily (ref. Table 1). Bee visits resumed after 15:00h each day.

The mean sugar concentration in *A. leptopus* increased steadily from $11 \pm 0.05\%$ at 06:00h to $30 \pm 1.2\%$

Table 1. Daily visits of *Apis mellifera adansonii* on melliferous plant species. Bee visits were monitored from 06:00h till 19:00h GMT.

Plant species	Max/h	Min/h	Mean \pm SE	<i>F</i>	<i>P</i> > <i>F</i>
<i>A.leptopus</i>	15	5	9.3 \pm 2.4	14.3	0.05
<i>T. peruviana</i>	20	7	5.2 \pm 3.6	8.24	0.05

ANOVA was carried out and the means separated by Duncan's test for pairwise comparison at $\alpha = 0.05$ level.

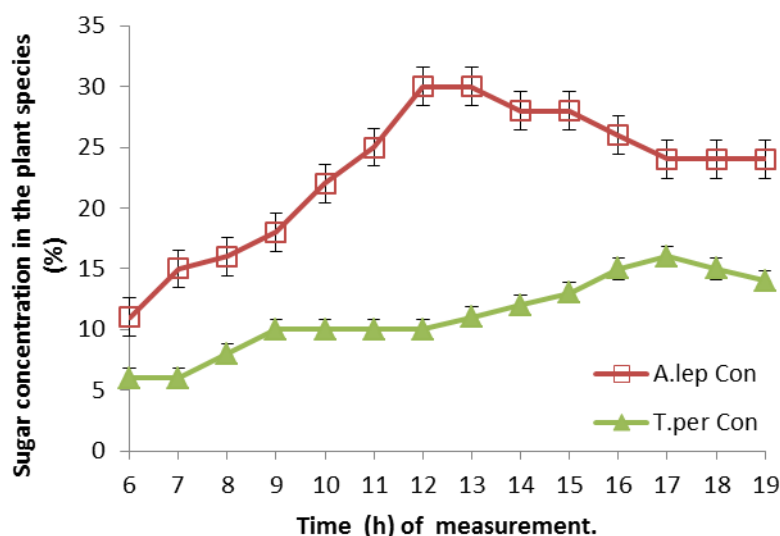


Figure 6. Pattern of sugar concentration in the nectar of *A. leptopus* and *T. peruviana*. Results are presented as mean values \pm SE of hourly sugar concentration of 50 flowers per plant species during the 20-day period.

in the afternoon between 12:00h and 13:00h (Fig. 6). There were significant differences in the concentration of nectar sampled during the day ($n = 50$, $F_{2, 35} = 2.5$, $df = 49$, $P = 0.46$). Sugar concentration of nectar in *T. peruviana* at 06:00h was $6 \pm 0.04\%$ followed by a gentle increase after 07:00h. It peaked at 17:00h with $16 \pm 0.1\%$ (Fig. 6). As a whole the sugar concentration in *A. leptopus* was significantly higher than that in *T. peruviana* ($n = 50$, $P = 0.04$).

Sugar concentration of nectar produced in *A. leptopus* was inversely proportional to the volume produced

between 06:00h to about 12:00h ($r = -0.34$, $n = 50$, $P = 0.73$). Similarly, the sugar concentration in the nectar in *T. peruviana* was inversely proportional to the volume of production, and this was more pronounced during latter part of the day ($r = -0.45$, $n = 50$, $P = 0.54$).

Environmental factors and nectar production

The mean ambient temperature in the study area was $33.92 \pm 4.37^\circ\text{C}$ (range: $28\text{--}42^\circ\text{C}$), while the mean relative humidity was 43.14% (range: $33\text{--}73\%$). The daily temperature around *A. leptopus* plants

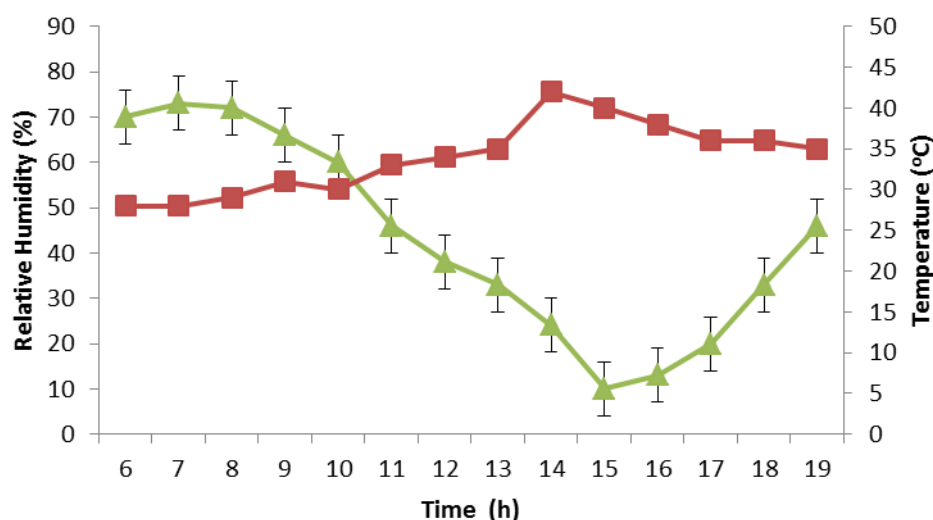


Figure 7. Daily mean temperature (°C) and relative humidity (%) in the vicinity of *A. leptopus*.

increased gradually from 06:00h and peaked at 14:00h after which it dropped (Fig. 7). Relative humidity was high in the early hours of the day (06:00 - 08:00h).

The highest temperature 25°C in the vicinity of *T. peruviana* was recorded between 13:00h and 14:00h. Relative humidity peaked at 07:00h and steeply declined to the lowest at 14:00h (Fig.

8). The peak of temperature therefore coincided with the lowest relative humidity, indicating an inverse relationship between the two environmental parameters ($r = -0.79$, $n = 50$, $P = 0.54$).

The results indicated that temperature correlated positively with sugar concentration of the two plant species (Fig. 9 A, B): sugar concentration in *A. leptopus*

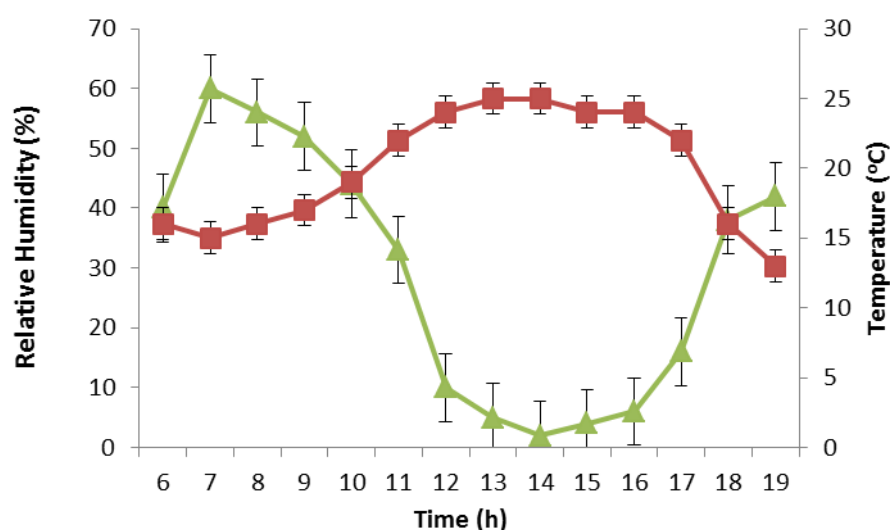


Figure 8. Daily mean temperature (°C) and relative humidity (%) in the vicinity of *T. peruviana*.

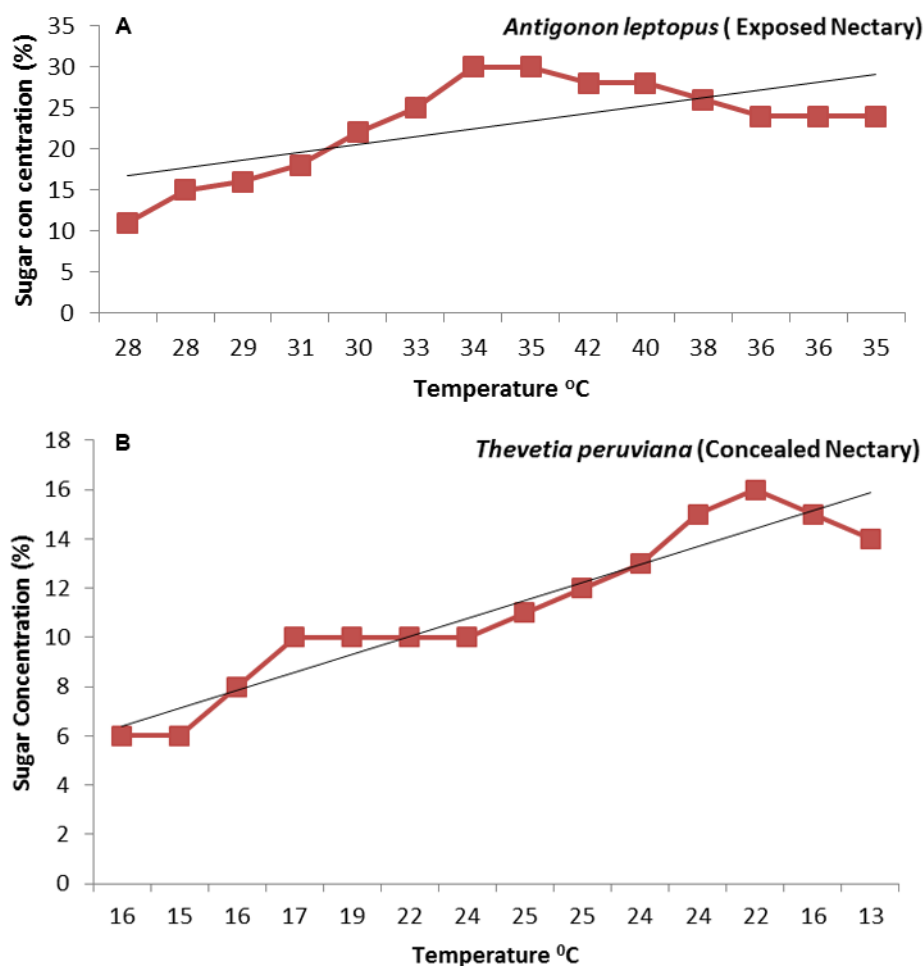


Figure 9. Relationship between sugar concentration in *A. leptopus* (A) and *T. peruviana* (B) and temperature in their vicinity.

correlated moderately with temperature ($r = 0.59$, $n=100$, $P = 0.05$), but in *T. peruviana* there was low correlation ($r = 0.32$, $n=100$, $P = 0.05$) between sugar concentration and temperature.

The volume of nectar produced in the melliferous plant species, however, correlated negatively with temperature ($r = -0.45$, $n=100$, $P = 0.05$). In both plant species relative humidity correlated positively with volume ($r = 0.68$, $n=100$, $P = 0.05$), but negatively with sugar concentration ($r = -0.49$, $n=100$, $P = 0.05$).

Stepwise regression analysis (Table 2) showed the influence of environmental

factors on nectar production in the two plant species. Temperature alone had a very significant ($F = 0.21$) role in the nectar production in *A. leptopus* during the study. However, a combination of temperature and relative humidity had a relatively lower impact on the volume of nectar produced ($F = 1.22$). Similarly, temperature alone exerted significant influence on nectar sugar concentration in *A. leptopus* ($F = 0.49$), but together with relative humidity had less significant impact ($F = 0.52$) on nectar production. The same trend was observed in the case of *T. peruviana*.

Table 2. Stepwise regression models of environmental variables on nectar production: general linear model (GLM).

Variables	Model	Regression Equation	R ²	F-value
<i>A. leptopus</i> (VOL, TEMP)	GLM	13.21+23.74 MTEMP	0.32	0.21**
(VOL, TEMP, RH)	GLM	19.32+30.75 MTEMP+161.61 RH	0.63	1.22
<i>A. leptopus</i> (SUG, TEMP)	GLM	15.58+0.96 MTEMP	0.46	0.46
(SUG, TEMP, RH)	GLM	29.21+33.25 MTEMP+20.61 RH	0.56	0.52
<i>T. peruviana</i> (VOL, TEMP)	GLM	11.84+28.91 MTEMP	0.76	0.25**
(VOL, TEMP, RH)	GLM	51.18+12.37 MTEMP+43.22 RH	0.59	0.38*
<i>T. peruviana</i> (SUG, TEMP)	GLM	23.57+15.42 MTEMP	0.10	0.15**
(SUG, TEMP, RH)	GLM	13.51+10.28 MTEMP+16.37 RH	0.29	0.65

MTEMP = Mean daily temperature (°C) *significant; ** very significant.

DISCUSSION

The results from this study demonstrated that nectar production in the two melliferous plant species was high in the early morning hours when temperature was low with high relative humidity. Similar observations were made in *Prunus spinosa* L. (Yeboah-Gyan and Woodel, 1987), *Trifolium repens* L. (Jakobsen and Kristjansson, 1994), and *Aloe castanea* (Nicolson and Nepi, 2005). For both species nectar volume picked up again in the late evening: after 16:00h for *A. leptopus* and 17:00h for *T. peruviana*. Some authors have noticed that the rate of moisture loss (via transpiration) from nectar is greatly reduced under conditions of high relative humidity (Barrera and Nobel, 2004; Nicolson and Thornburg, 2007). This could mean that under such conditions nectar retains more moisture and thus

maintains high volume. The observation in this study therefore corroborates the assertion.

The considerable differences in the volume of nectar and sugar concentration among individual flowers (Figs. 5 and 6) could be attributed to the random selection of flowers for the study. The sampling was done irrespective of age and position of flowers on the stem, factors which have profound impact on nectar production (Navarro, 2001; Yeboah-Gyan and Woodel, 1987; Proctor and Yeo, 1973). Lack (1982) has pointed out that such variations may be of selective importance.

The data also indicated that the volume of nectar in the two plant species decreased during the day. A similar phenomenon was observed in *Glechoma hirsuta* (Macukanovic-Joeic and Djurdjevic, 2005) and *Allium cepa* L. (Silva et al., 2004). In another

study, however, Proctor and Yeo (1973) observed an increase in nectar volume in species of Lamiaceae viz: *Lamium maculatum* and *Ajuga reptans* during the day. These contrary observations suggest that nectar volume in the plants might be controlled by many dynamics as indicated above. The volume decline in *T. peruviana* though gradual started earlier (after 06:00h) than that in *A. leptopus*. The decline may be attributed to the interplay of the micro-environmental factors as already discussed. An alternative explanation may be large energy expenditure involved in nectar production (Southwick, 1984; Galen et al., 1999). The plants may have conserved the excess nectar produced through reabsorption (Langenberger and Davis, 2002; Nepi and Stpiczynska, 2008).

The foraging activities of the honeybees as observed on both *T. peruviana* and *A. leptopus* during the day could be another critical factor. Nectar from these plants was a floral reward and hence an important attractant to honeybees (Adjaloo and Yeboah-Gyan, 2003). The drop in nectar volume might therefore be the result of nectar uptake by the honeybees as proposed by Seymour et al. (2003) and Galetto and Bernardello (2004). It was however, noted that honeybees visited *T. peruviana* earlier (from 5:15h) than *A. leptopus* (from 08:00h), and in greater numbers. Even though the study did not focus on the rate of nectar uptake it could be inferred that the visits of the honeybees might have accounted for the faster decline in the volume of nectar in *T. peruviana*.

The honeybees' visit and nectar intake may be explained in terms of energetics of

their foraging and pollinating activities. Price (1997) and Price et al. (2005) have observed that the cost of foraging is high in terms of calories used in flying, and therefore the reward must be higher to make a net energy gain while foraging. Bees have been found to usually change their resources, concentrating their activities on more rewarding flowers (Pyke, 1991; Morse, 1980). Hence, the volume of nectar could determine the cost-effectiveness of a visit to a plant, and periods of low standing nectar volume maybe interpreted by the bees as a poor food source (Silva et al., 2004). Nectar quantity during the day could therefore have implication on the honeybee activities on both plant species; however, further study may be needed to confirm this assertion.

The sugar concentration in *A. leptopus* nectar was significantly ($P < 0.45$) higher than that in *T. peruviana*. This could be attributed to the architecture of the nectary. The more exposed nectary of *A. leptopus* might have been greatly influenced by the prevailing micro environmental factors (temperature and relative humidity) than the concealed nectary of *T. peruviana* (Pacini and Nepi, 2007). Corbet (1978) observed that diluted nectar was not attractive to insects because it did not offer enough rewards in terms of energy; and also highly concentrated nectar cannot easily be sucked by bees (Corbet et al., 1979). It is proposed that bees prefer moderate sugar concentration range of 20% -50% (Corbet, 2003). The concentration recorded for the melliferous plant species in the present study fell within this range, suggesting an adaptive mechanism adopted by these plant species.

Effect of environmental factors on sugar concentration and nectar volume

The sugar concentration of nectar of both plant species also showed much variation with the prevailing temperature and humidity conditions. There was an increasing concentration during the day as temperature increased with corresponding decrease in relative humidity. The correlation between the environmental factors, on one hand, and the volume and sugar concentration in both plant species, on the other hand underscore some observations that the inter-play between temperature and relative humidity has impact on nectar production (Jakobsen and Kristjansson, 1994; Carroll et al., 2001). From the results (Table 2) temperature appears to have more influence on the volume and sugar concentration of the nectar produced by the two melliferous plants. This confirms earlier assertion that the periodicity of nectar secretion is temperature-dependent (Vogel, 1983). Our study indicated that nectar volume in the studied plants declined at higher temperatures during the day. Castellanos et al (2002) made similar observation in *Penstemon* flowers, and attributed it to an in-built homeostatic mechanism by which some plants maintain the concentration of sugar as the nectar loses water via transpiration.

The effect of high temperatures (mean range: 19.85-33.9°C) coupled with corresponding low relative humidity (mean range: 29.14 – 43.35%) in the sampling sites was noted when at mid-day nectar in flowers of *A. leptopus* became viscous. The observation seems to suggest that “higher temperatures could result in sudden cessation or

dwindling of nectar production” (Silva et al., 2004). The phenomenon may be attributed to reduced moisture in the nectar (Butler et al 1972). The positive correlation between sugar concentration of nectar and temperature as indicated by the data might have contributed to the bimodal pattern of foraging by *Apis mellifera adansonii* on the melliferous plant species (Castellanos et al., 2002). According to Faegri and van der Pijl (1980) nectar volume and sugar concentration are important factors in the attraction of pollinators to entomophilous plants.

Heinrich and Raven (1972) have observed that sugar concentration in nectar determines the pollinator type that visits a flower. Therefore, sugar concentration is likely to be an important factor determining the behavior of the insect visitor, and the breeding systems of plants (Waiselboim et al., 2003). The differences between the nectar produced by the melliferous plant species are likely to be detected by their insect visitors, and they may visit most frequently plant species with the right reward. Selection against such possible competition for pollinators may have been the mechanism partly responsible for temporal difference in the daily dynamics of nectar secretion and sugar concentration between the two melliferous plant species as shown in this study.

CONCLUSION

The present study revealed that there was great variability in the nectar production by the two plant species. The process of nectar production, however, is influenced by climatic factors of which

temperature has greater impact. It is evident that higher nectar production occurred at high humidity and low temperature.

Our study was limited to the effect of environmental factors on nectar production. However, the results indicate that there is need for further detailed research focusing on other physiological processes such as reabsorption of nectar, effect of plant and flower age, location of flowers on the plant, honeybee activities on the flowers including nectar removal and its effect on nectar production. Future work on the rate of nectar intake by the insect visitors will also be in the right direction.

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