CHAPTER 4

Dilute nectar of *Aloe greatheadii* var *davyana* as a resource for honeybees, *Apis mellifera scutellata,* during dry South African winters

H. Human and S.W. Nicolson

Department of Zoology and Entomology, University of Pretoria, Pretoria 0002, South Africa.

Abstract

The winter flowering *Aloe greatheadii* var *davyana* is a major indigenous bee plant; with a widespread distribution across the northern summer rainfall areas of South Africa. Its highly nutritious pollen is utilised by migratory beekeepers for colony buildup and the strong nectar flow for honey production. We looked at variation in nectar (volume and concentration) on various levels in an assessment of this nectar resource. There were no significant differences in nectar volume and concentration between the bulb and the floral tube, only between flower stages. Nectar was continuously available, with both volume and concentration remaining relatively constant throughout the day. The average volumes and concentrations of nectar in screened flowers (30.7 µl, 23.5% w/w) were significantly higher than those in unscreened flowers (14.7 µl, 18.6%). Nectar volume was observed to be lowest and nectar concentration highest late in the flowering season. The volumes and concentrations of nectar measured across the distribution range of *A. greatheadii* var *davyana* were significantly lower at Marble Hall in the east compared to Roodeplaat (middle of the range) and Zeerust in the west. *Aloe greatheadii* var *davyana* nectar, although dilute from a bee perspective, is more concentrated than that of other *Aloe* species, and is an ideal source of energy and water for honeybees.

Introduction

An important winter pollen and nectar source for South African beekeepers in the northern summer rainfall regions of the country is the indigenous *Aloe greatheadii* var *davyana.* Beekeepers move their hives over hundreds of kilometers to the "aloe fields" north of Pretoria where the highly nutritious pollen of this aloe (Chapter 1) promotes colony growth and the copious nectar contributes substantially to the honey crop (Williams, 2002). *Aloe greatheadii* var *davyana* flowers prolifically in mid-winter (end June - mid August), when few other nectar sources are available. These aloes occupy rocky areas in grassland and thrive in disturbed areas (Glen & Hardy, 2000; Van Wyk & Smith, 1996). They grow equally well in full sun and in shade beneath trees.

Aloe species are known for their copious dilute nectar; an example is the nectar of *A. ferox* with an average volume and concentration of 180 µl and 12.5% respectively (Hoffman, 1988). Hoffman (1988) found that nectar and pollen were the chief floral rewards for birds and honeybees respectively. Tubular flowers with low nectar concentrations are associated with bird pollination, while bee-pollinated flowers have higher nectar concentrations (>35%, Pyke & Waser, 1981). However, honeybees are known to collect nectar with concentrations ranging from 15 to 65% (Visscher & Seeley, 1982), and when they need to cool the hive by evaporation they will collect water or dilute nectar (Eisikowitch & Masad, 1982).

Nectar concentrations vary widely (7-70%), not only between but also within species (Nicolson, 1998). For example, the low end of the range is *Eucalyptus incrassata* (Myrtaceae) with extremely dilute nectar (7%) and at the high end is *Carum carvi* (Apiaceae) producing nectar with an average concentration of 66.5% (Bond & Brown, 1979; Langenberger & Davis, 2002). Variation within a species is illustrated by the range of 2 to 62% observed in *Echium plantagineum* (Boraginaceae) and 4 to 72% in *Clintonia borealis* (Liliaceae) (Corbet & Delfosse 1984; Plowright, 1981). The volume and concentration of nectar are influenced by factors such as nectary activity, flower age, temperature and relative humidity, water availability and animal visitors.

Nicolson and Nepi (2005) investigated nectar production during the dry winter in open, campanulate flowers of *Aloe castanea*. The nectar of these flowers is more exposed than

that of aloes with tubular flowers. The authors observed variation in nectar concentrations of 8 to10% between individual plants of *A. castanea*. We hypothesised that the tubular structure of *A. greatheadii* var *davyana* flowers would prevent evaporation of nectar. We looked at variation in nectar volume and concentration on various levels, from within individual flowers to across the summer rainfall area of South Africa, in order to assess the nectar resource being used by beekeepers. We compared nectar (volume and concentration) in the bulb and the tube, between different flower stages, in screened and unscreened flowers, and in flowers in the sun and shade. We sampled nectar over the flowering season as well as across the distribution range of *A. greatheadii* var *davyana*.

Methods

Nectar production in *A. greatheadii* var *davyana* was studied at Roodeplaat Nature Reserve (795 ha) (28º 39'E, 25º 66'S), at Rust de Winter (28º 23'E, 25º 12'S), Zeerust (26º 02'E, 25º 36'S) and Marble Hall (29º 17'E, 24º 59'S) during the winter months (June and July) of 2003-2005 (see Fig. 2B, Introduction). All areas have dense populations of *A. greatheadii* var *davyana,* especially Rust de Winter.

Nectar was collected in disposable haematocrit tubes (length 75 mm/75 µl). Volumes of nectar were determined from column length in haematocrit tubes and the concentrations measured as % w/w sucrose equivalents with a pocket refractometer (0-50%, Bellingham & Stanley Ltd, Tunbridge Wells, UK). Temperature and relative humidity were measured at flower height with either a hand-held thermohygrometer (Model TES 1365, TES Electrical Corp., Taiwan) or HOBO dataloggers (Onset Computer Corporation, Pocasset, MA, USA). The operating ranges of these loggers are -20ºC to 70ºC and 25 to 90 % for temperature and RH respectively.

Flower development and effect of flower age on nectar production

Twelve flower buds that were about to open (three each on four different plants) were tagged and flower development followed. During observations the duration of events such as filament and style elongation, anther dehiscence and the presence of nectar as well as floral characteristics were recorded. Observations were made every 30 min from 09.00 until 16.00 h on the first day, and again at 09.00 h on subsequent days.

The effect of flower age on nectar production (volume and concentration) was then determined by marking just opening flowers on five plants prior to nectar collection. Racemes with marked flowers were covered with gauze (2 mm mesh size) to exclude pollinators. This allowed for nectar sampling from five flowers of each stage (Fig. 1) from each of the five plants between 10.00 and 12.00 h on the following day.

All remaining measurements of nectar volume and concentration were made on stage 3 flowers (Fig. 1D) which showed the highest nectar production; see Results. Each flower was sampled only once.

Nectar in the bulb and floral tube

A characteristic feature of the family Pictae (spotted aloes), to which *A. greatheadii* var *davyana* belongs, is the distinct basal swelling (bulb) at the bottom of the tubular flowers (see Fig. 1). Five flowers from ten plants each were measured for bulb depth and length and total length of flower. Thereafter four flowers (stage 3) were picked from five plants each on three consecutive sampling days (11, 12 and 13 August 2004) at Roodeplaat Nature Reserve and at Rust de Winter, and the volume and concentration were measured separately for nectar in the bulb and in the floral tube. Two of these sampling days were at Roodeplaat Nature Reserve; one was a warm day and the other a cool, cloudy day. At Rust de Winter the weather was similar to the warm day at Roodeplaat. All other measurements were made on bulb and floral tube combined.

Screened and unscreened flowers

Nectar present in unscreened flowers (standing crop) represents the nectar encountered by floral visitors. Twenty plants were randomly marked and the inflorescences from 10 plants were covered in gauze (2 mm mesh size) while the remainder were left open. Nectar volumes and concentrations were measured hourly from 08.00 to 16.00 h in three flowers (stage 3) from each plant; gauze covers were replaced after each collection. Two HOBO dataloggers on one plant were used to measure temperature and humidity for the duration of the experiment: one was attached to an open raceme and the other to a raceme covered with gauze.

Plants in the sun and shade

Differences between nectar volume and concentration in plants growing in the sun and in the shade were also recorded. The volume and concentration of nectar from three unscreened flowers on six plants in the sun and six plants in the shade were recorded hourly from 08.00 until 17.00 h. Ambient temperature and humidity were also recorded hourly in dappled shade.

Nectar production during a flowering season

To determine whether nectar production varied during the flowering season, full day measurements of nectar volume and concentration were made at Roodeplaat Nature Reserve on 5 July, 26 July and 15 August 2003. On each date we sampled three unscreened flowers on each of 10 plants from 08.00 until 17.00 h.

Nectar production across the distribution range

In order to evaluate nectar production across the distribution range of *A. greatheadii* var *davyana*, full day nectar measurements were made (hourly from 08.00 until 17.00 h) of nectar volume and concentration early in the flowering season (on 5, 10 and 13 July respectively) at Zeerust, Roodeplaat and Marble Hall. Zeerust is at the western end of the distribution range of *A. greatheadii* var *davyana* and Marble Hall at the eastern end, with Roodeplaat being more central (see map on page 4 of Introduction). All flowers were sampled once.

Statistical analysis

The effects of flower age on nectar volume and concentration were compared within and between plants by multivariate ANOVA. The data met the assumptions for parametric statistics after the nectar volumes were $\log_{10}$ transformed. Post hoc comparisons of nectar production between different flower stages were performed by Tukey tests (Zar, 1984).

Data for nectar measured in the bulb and floral tube met the assumptions for parametric statistics, therefore paired Student's t-tests were used to compare variation in nectar volume and concentration.

All other nectar data did not meet the assumptions for normality; variances were not homogeneous and data did not conform to a normal distribution. The effect of treatment (screened and unscreened flowers, plants in the sun or shade) and time on nectar volume and concentration as well as variation in nectar volume and concentration through the flowering season and across the distribution range were therefore assessed with Kruskal-Wallis ANOVA. Mann-Whitney U-tests were used for comparisons of the mean volumes and concentrations throughout the day.

Analyses were performed with the program Statistica 6.0 (1984-2004). The level of statistical significance for all analyses was $P = 0.05$. Values are given throughout as means ± SD.

Results

Effect of flower age on nectar production

Flower stages for *A. greatheadii* var *davyana* are illustrated in Figure 1. Flowers opened throughout the day and had an average lifespan of four days. Nectar was collected from flowers of different stages between 10.00 and 12.00 h on a warm day and volumes are combined values for nectar available in the bulb and floral tube. The temperature increased from 19.4°C to 21.7°C and RH decreased from 41 to 29% during this time. Nectar was already present in stage 1 flowers (just opening), and remained present until the flowers wilted. The mean nectar volume increased to a maximum of 33.5 µl in stage 3 flowers, and then decreased in wilted flowers (Fig. 2). The average concentration of nectar varied much less with flower age, with a maximum of 21.4% in stage 3. There were no significant differences in nectar volume and concentration between ($F = 1.767$, $df = 8$, $P = 0.08$) or within plants ($F = 0.934$, $df = 10$, $P = 0.503$), only between flower stages ($F = 41.943$, $df = 6$, $P < 0.001$). The results of Tukey tests for comparisons between stages are indicated in Figure 2. Nectar volume varied significantly between all flower stages while nectar concentration remained relatively stable across flower stages, but was significantly lower in stages 1 and 4 than stages 2 and 3 (Fig. 2).

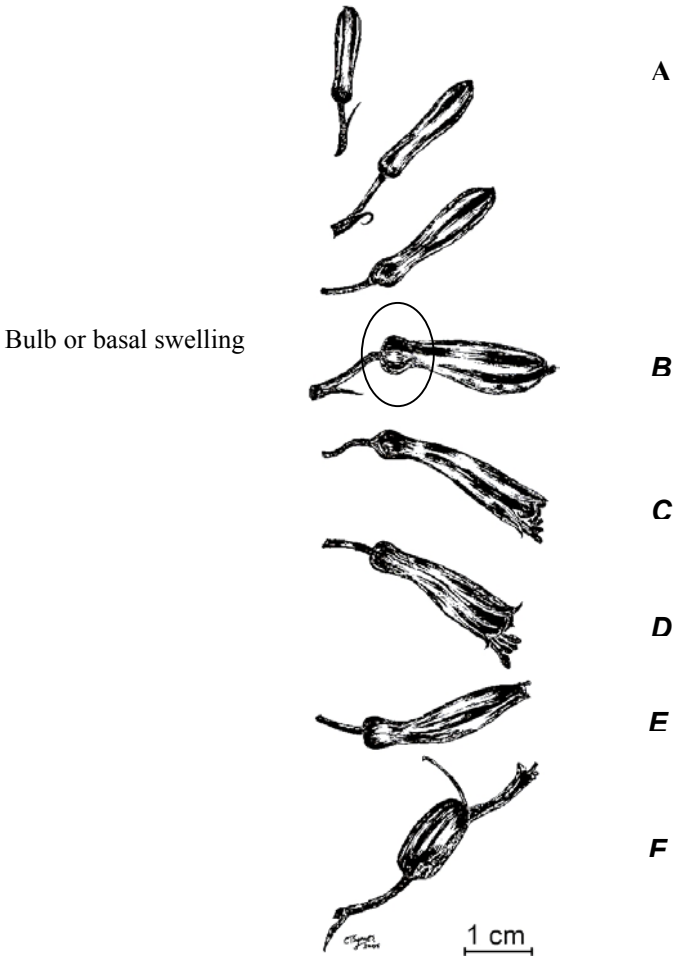


Figure 1. Flower development in *Aloe greatheadii* var *davyana*. Orientation of flowers changed from 0° to 120° then back to 80° with age. **(A)** Closed flower buds, with an upward orientation. **(B)** Flowers in which the corolla was just opening (stage 1), note the horizontal position. **(C)** Open flowers, 2-5 h, with the three long anthers exserted (stage 2), **(D)** The floral tube reached its maximum width, oriented downwards, with all six anthers exserted after 24 h (stage 3), **(E)** At 72 h the floral tube started to wilt while the style remained turgid (stage 4); flower in an upward position. Flowers were completely wilted after 96 h. **(F)** Fruit appeared approximately 3 weeks later.

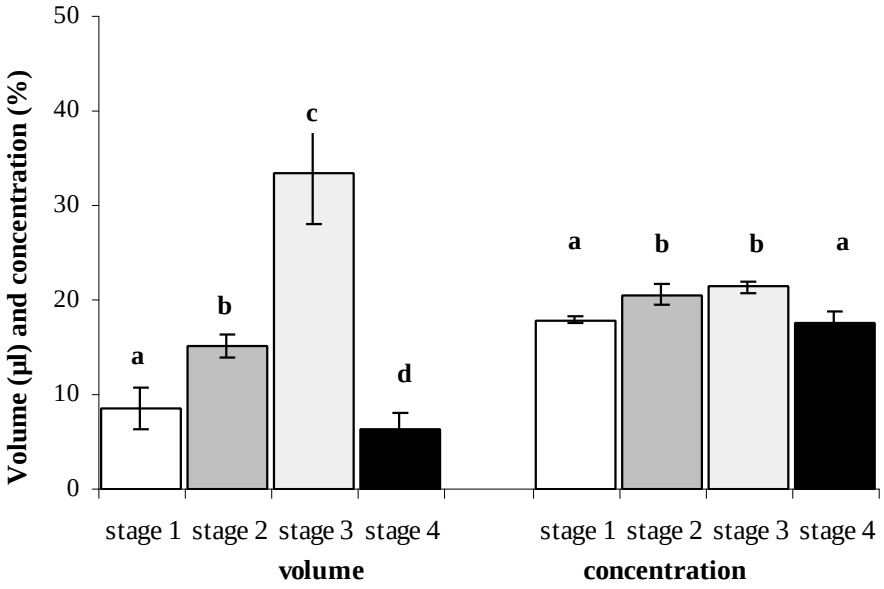


Figure 2. Average volume (combined values for nectar in the bulb and floral tube) and concentration of nectar produced in flowers of different flower stages (means ± SD, n = 5 per flower stage). All plants were screened (bees denied access). No letters in common denote significant differences at $P \leq 0.05$.

Differences between the bulb and floral tube

The average length of flowers (bulb and floral tube) of *A. greatheadii* var *davyana* is 28.1 ± 4.7 mm with the average bulb width and length of the flowers being 5.2 ± 0.7 and 6.8 ± 0.5 mm, respectively. The differences between nectar volumes in the bulb and tube were not significant (Fig. 3, Table 1), with the exception of the higher volume of nectar in flowers measured on the cool day. Although nectar concentration in the floral tube (19-22%) was higher than that in the bulb (18-21%) at both sites, the differences were not significant (Table 1). Temperature and humidity measured at Roodeplaat Nature Reserve on the warm day was 22°C and 17%, and on the cool day 16°C and 39%. At Rust de Winter the temperature was 25°C and RH was 15%.

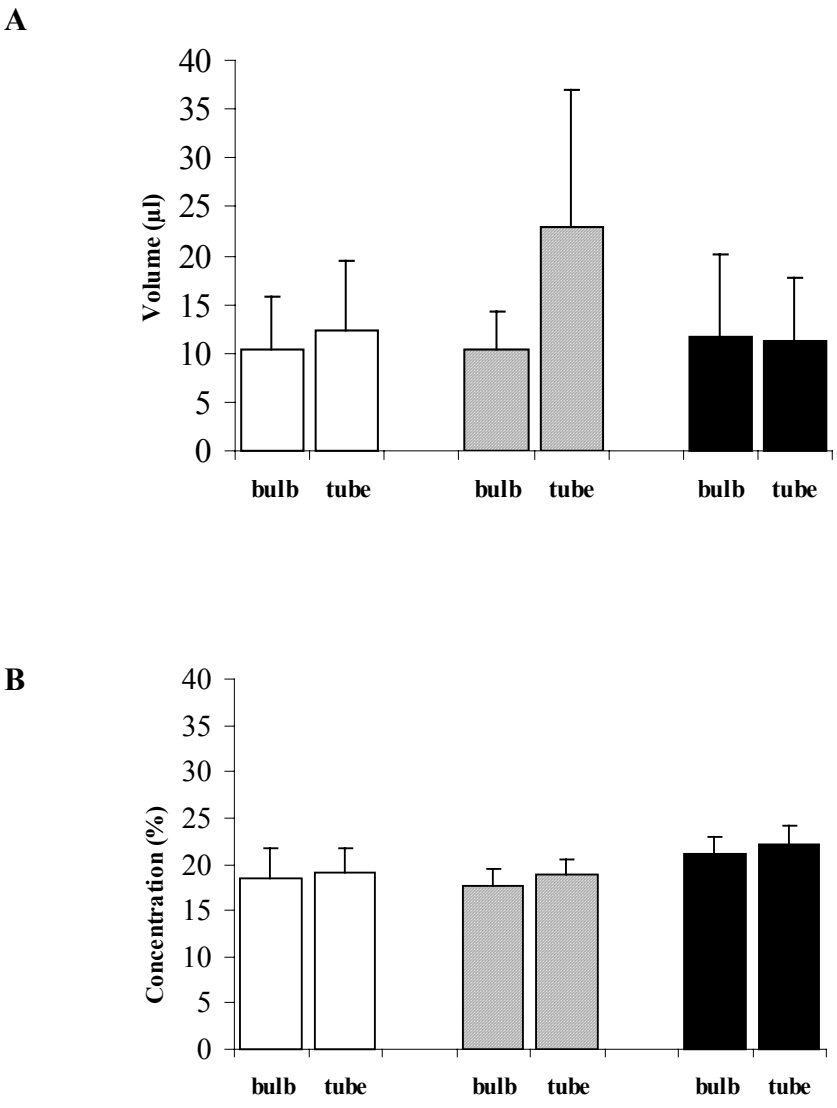


Figure 3. Average **(A)** volume and **(B)** concentration of nectar available in floral tube and bulb of *Aloe greatheadii* var *davyana* flowers measured at Roodeplaat Nature Reserve on a warm day (empty bars) and a cool, cloudy day (hatched bars), and at Rust de Winter (solid bars) (means ± SD, n = 20).

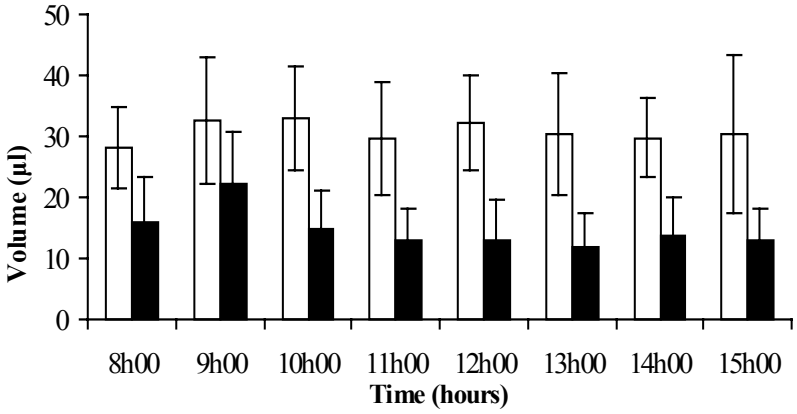
Table 1: Results of Student's t-tests comparing nectar volume and concentration measured in the bulb and floral tube of *A. greatheadii* var *davyana* flowers. Significance is shown by italics.

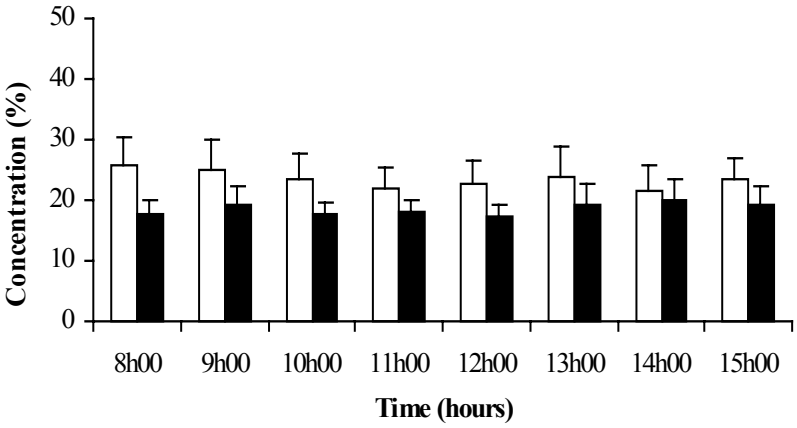
		t	df	P
Roodeplaat Nature Reserve (warm day)	Volume	1.02	38	0.32
	Concentration	0.70	38	0.50
Roodeplaat Nature Reserve (cool day)	*Volume*	*3.90*	*38*	*0.001*
	Concentration	1.91	38	0.07
Rust de Winter	Volume	-0.12	38	0.90
	Concentration	1.92	38	0.06

Screened and unscreened flowers

Treatment had a significant effect on both volume ($H_{1, 480} = 266.361$, $P < 0.001$) and concentration of nectar ($H_{1, 480} = 172.059$, $P < 0.001$). The average volumes and concentrations of nectar available throughout the day in screened flowers (30.7 ± 9.2 µl, 23.5 ± 4.4%) were significantly higher (for volume $U = 4024.0$, $P < 0.001$, and for concentration $U = 8906.5$, $P < 0.001$) than those in unscreened flowers (14.7 ± 7.1 µl, 18.6 ± 2.7%) (Fig. 4). The nectar volume available in screened flowers was slightly higher early in the morning and around noon while the volume in unscreened flowers showed a peak at 09.00 h. However no significant differences were observed (after Bonferroni adjustments) for hourly comparisons of nectar volumes or concentration throughout the day within screened and unscreened flowers.

These data were collected on a windless day. Temperature measured at the screened inflorescence throughout the day was not significantly higher (± 4.5°C) than that measured at the unscreened inflorescence ($U = 21.0$, $P = 0.248$) (Fig. 4C). Relative humidity was not significantly lower in the screened inflorescence ($U = 15.0$, $P = 0.074$), but this seemingly constant RH in the screened raceme for most of the day is possibly due to the limited operating range of the HOBO dataloggers.





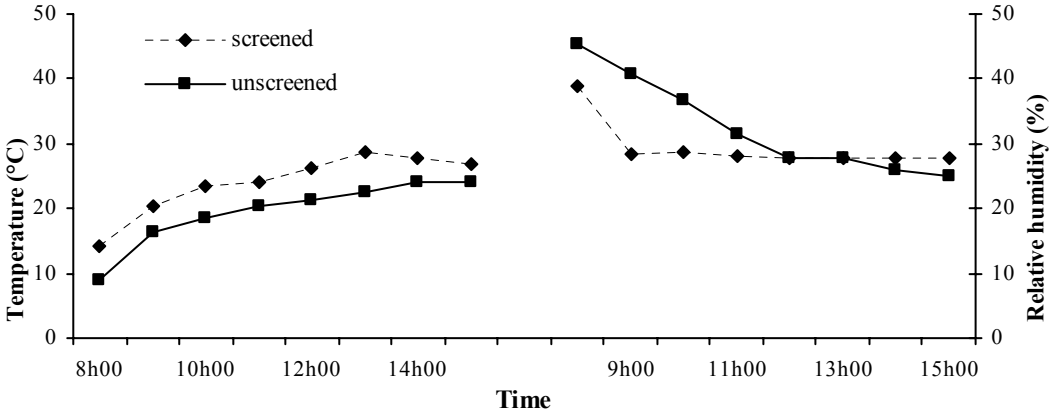


Figure 4. Nectar volume **(A)** and concentration **(B)** and temperature and humidity **(C)** measured in screened (blank bars) and unscreened flowers (solid bars) over a full day (means ± SD, n=30).

Plants in the sun and shade

The average hourly volume and concentration of nectar secreted in the sun (18.1 ± 6.7 µl, 19.4 ± 3.2%) was significantly higher (for volume $H_{1, 360}$= 20.335, P < 0.001; for concentration $H_{1, 360}$ = 10.965, P < 0.001) than that secreted in the shade (14.6 ± 6.3 µl, 17.8 ± 2.6%). Mann-Whitney U-tests showed that volumes of nectar for plants in the sun were higher in mid morning (11.00 h) and late afternoon (15.00 – 16.00 hrs) than for plants in the shade (volume at 11.00 h U = 91.50, P = 0.026; at 15.00 h U = 82.50, P = 0.011; at 16.00 h U = 40.50, P < 0.0001). Nectar concentration in plants in the sun was significantly higher between 08.00 and 12.00 h as compared to that in plants in the shade (concentration at 08.00 h U = 94.0, P = 0.031; at 10.00 h U = 77.0, P = 0.007; at 11.00 h U = 91.50, P = 0.0257). The temperature ranged between 11 and 25°C and RH decreased from 24 to 7% during the day.

Nectar production through the flowering season

Daily temperatures were very similar for the three sampling days at Roodeplaat Nature Reserve spaced throughout the flowering season. The mean minimum daily temperature was 9.8 ± 0.8°C and the maximum was 23.3 ± 1.5°C. RH decreased through each day, with the average maximum value being 32.1% and the minimum value 5.3%.

The mean volume of nectar produced throughout the day was 14 ± 2.6 µl early in the season, 17 ± 1.9 µl in the middle and 12 ± 1.8 µl late in the season. The concentration of nectar increased from 17 ± 0.7% to 21 ± 1.7% over the flowering season. These values were significantly different; for volume ($H_{2, 900}$ = 68.956, P < 0.001) and concentration ($H_{2, 900}$ = 175.665, P < 0.001).

The volume of nectar produced in the middle of the season was significantly higher than that produced early (U = 35589.5, P < 0.001) and late in the season (volume U = 27153.5, P < 0.001), while the volume of nectar early in the season was significantly higher than that produced late in the season (U = 37061.5, P < 0.001). The average concentration of nectar produced late in the season was significantly higher than the concentration of nectar produced early (U = 16997.5, P < 0.001) and in the middle of the season (U = 28336.0, P < 0.001). Nectar concentration early in the season was significantly lower than that of nectar in the middle of the season (U = 34146.5, P < 0.001).

Nectar production across the distribution range

There were significant differences in volume ($H_{2, 270} = 265.572$, $P < 0.001$) and concentration ($H_{2, 720} = 55.090$, $P < 0.001$) of nectar across the distribution range *of A. greatheadii* var *davyana* (see map page 4 of Introduction), from Zeerust in the west to Marble Hall in the east (Fig. 5A, B). Different populations may contribute to these differences. The volume and concentration of nectar were not significantly different at Zeerust and Roodeplaat (for volume $U = 26617.0$, $P = 0.151$; for concentration $U = 55582.0$, $P = 0.934$). However, the volume of nectar produced at Mable Hall was significantly lower that at Roodeplaat Nature Reserve ($U = 6542.5$, $P < 0.001$) and Zeerust ($U = 8396.5$, $P < 0.001$) (Fig. 5A). The average concentration of nectar available at Marble Hall was significantly lower than that of nectar at Roodeplaat Nature Reserve ($U = 12131.0$, $P < 0.001$) and Zeerust ($U = 11458.5$, $P < 0.001$).

Average daily temperatures were 15.9 ± 3.8°C at Zeerust, 18.0 ± 4.4°C at Roodeplaat Nature Reserve and 25.7 ± 3.8°C at Marble Hall. The range of relative humidity during the day was similar at Zeerust and Marble Hall (29.5 - 15.4% and 25.6 - 18.2% respectively) but lower at Roodeplaat Nature Reserve (23.7 - 6.7%).

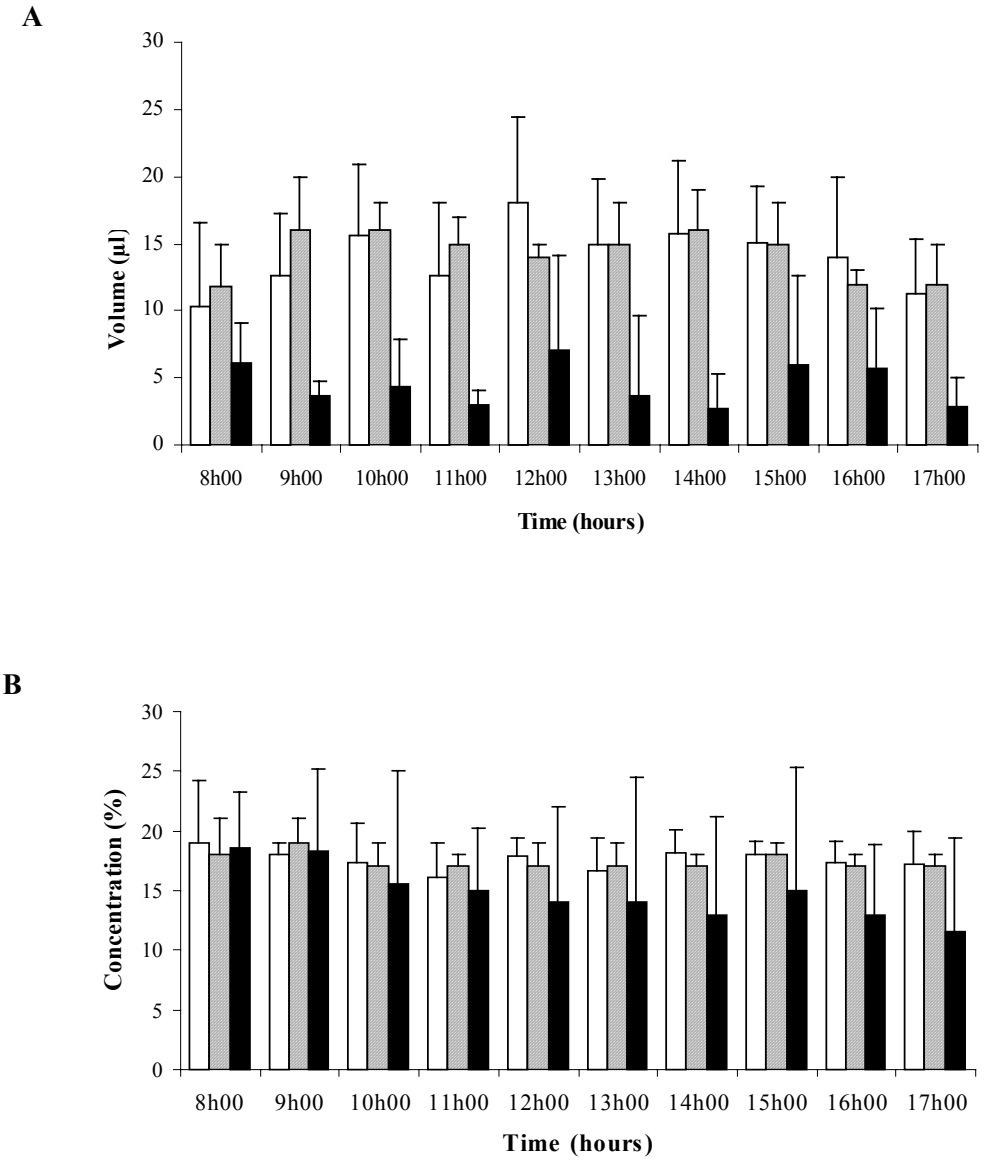


Figure 5. Nectar volume **(A)** and concentration **(B)** of *Aloe greatheadii* var *davyana* available throughout the day at Zeerust (blank bars), Roodeplaat Nature Reserve (hatched bars) and Marble Hall (solid bars). Nectar was sampled early in the flowering season (means ± SD, n=30).

Discussion

The dilute nectar of *A. greatheadii* var *davyana* is available to foragers throughout the day in spite of extremely low ambient humidities during the flowering season. The low humidity is likely to increase evaporation from the nectar, but tubular flowers modify the humidity gradient and slow the exchange of water between the air and nectar (Plowright, 1987). The tubular flowers of *A. greatheadii* var *davyana* may explain the more constant concentration of its nectar compared to the greater variation seen in the more open flowers of *A. castanea* and the shorter tubular flowers of *A. ferox*, even though both the latter aloes have more dilute nectar (Hoffman, 1988; Nicolson and Nepi 2005). It is known that the shape of flowers helps to determine their nectar concentration. This is clearly illustrated by comparing nectar concentrations measured on a summer day: from an initial concentration of about 20%, in the tubular flowers of *Echium vulgare* concentration remain below 50% while it reaches 60% in the cup-shaped flowers of *Crataegus* (Corbet et al., 1979), while in the open umbelliferous flowers of *Heracleum* nectar evaporates freely, and even becomes crystalline (Willmer, 1983). The internal microclimate of more humid air in tubular flowers helps to slow the rate of equilibration of nectar with ambient conditions. Floral features that contribute to delayed evaporation from nectar include elongated corollas, hairs within and constrictions of the corolla beyond the nectary (Corbet et al., 1979; Nicolson, 2002). Therefore, although slow, some evaporation may occur from nectar in the tube of *A. greatheadii* var *davyana* flowers, explaining the slight difference in nectar concentrations between the bulb and floral tube.

Flower stages observed in *A. greatheadii* var *davyana* are similar to those in other *Aloe* species, e.g. *A. castanea* and *A. ferox* (Hoffman, 1988; Nicolson and Nepi 2005) and nectar volume also varied significantly between the different stages, reaching a peak in stage 3 flowers with a substantial decline in stage 4 flowers. Contrary to observations for *A. castanea* and *A. ferox,* the nectar concentration of *A. greatheadii* var *davyana* flowers remained more constant with flower age and declined only slightly in stage 4 flowers. Bernadello et al. (1994) and Torres and Galetto (1998) interpreted the decline in nectar volume, but not concentration, with age in flowers of *Combretum fruticosum* (Combretaceae) and *Mandevillea pentlandiana* (Apocynaceae) as an indication of reabsorption. Nectar of *A. greatheadii* var *davyana* flowers remains in contact with the

nectary, therefore the lower volume and concentration in stage 4 flowers may be suggestive of reabsorption.

Table 2. Volume and concentration of nectar (standing crop) measured in flowers of four *Aloe* species of the section Pictae (n = 10). Data presented as means ± SD. (Human & Nicolson, unpublished data)

***Aloe* species**	**Volume**	**Concentration**
Winter flowering		
A. branddraaiensis	8.0 ± 4.1	17.2 ± 1.3
A. grandidentata	22.7 ± 21.1	12.5 ± 1.7
A. maculata	21.6 ± 8.5	14.6 ± 1.0
Summer flowering		
A. zebrina	33.2 ± 17.1	22.4 ± 1.4

The nectar concentration of *A. greatheadii* var *davyana* corresponds to nectars taken by birds (Nicolson & Fleming, 2003), but is unusually high compared to most *Aloe* species. Nectar concentration of the summer flowering *A. zebrina* is also relatively concentrated. It was thought that the high concentration observed in these two species might have a phylogenetic basis rather than being an adaptation for pollinator type, but other spotted aloes have lower concentrations (Table 2). Other aloes with tubular flowers produce nectar with much higher volumes, e.g. *A. ferox* and *A. marlothii,* 180 µl and 250 µl respectively, and lower concentrations (12.5% and 12.1% respectively) (Hoffman, 1988; C.T. Symes, unpub data). These species have much larger flowers and nectaries than that of *A. greatheadii* var *davyana,* which explains the higher volumes of nectar (Opler, 1983). Flowers of *A. castanea,* on the other hand, are smaller and more open (campanulate) and the increased exposure might be expected to lead to more evaporation and higher nectar concentrations. However, this species has very dilute nectar of below 10% throughout the day (Nicolson & Nepi, 2005). Aloe flowers are frequented by sunbirds and larger passerine birds (Oatley & Skead, 1972) as well as by bees. The most dilute *Aloe* nectars appear to be associated with pollination by generalised passerines rather than by sunbirds (S.D Johnson & S.W. Nicolson, in prep).

It is foraging by bees that lead to substantially lower volumes of nectar in unscreened flowers than in screened flowers. Although the standing crop volume is low (15 µl), a large proportion (10-12 µl) of this nectar is inaccessible to bees and remains in the bulb of the flowers. The observed differences in volume and concentration of nectar between screened and unscreened flowers were similar to those observed by Corbet and Willmer (1981) and Wyatt et al. (1992). Even though insects may affect the volume of nectar, it is unlikely that they will have a direct effect on the concentration of the remaining nectar. The increased concentration of nectar in screened flowers may be the result of increased ambient temperature and decreased relative humidity in bags (Dafni, 1992), especially during the windless conditions of our study.

Variability in nectar rewards is also an effect of ambient conditions such as sun and shade. Higher ambient temperature may explain the significantly higher nectar volume of plants in the sun, and although the concentration was slightly higher in the sun the difference was not significant. In Israel Goldstein et al. (1987) observed higher volumes of nectar for *A. arborescens* in the shade compared to plants in the sun, but concentrations remained the same. They found that sunbirds preferred to feed on flowers in the sun in spite of the smaller volume of nectar and attributed this preference to energy saving. Nicolson and Nepi (2005) observed marked differences in flower development in *A. castanea* on the sunny and shady side of racemes, with higher volumes and lower concentrations in nectar of flowers in the shady side.

Seasonal patterns of nectar production have seldom been investigated. Pleasants (1983) observed a seasonal decline in nectar volume of *Ipomopsis aggregata* (Polemoniaceae), but no change in concentration. He attributed the decline in nectar volume to increased energy demands on plants as a result of seed development. McDade (2004) hypothesised that nectar production would be higher early in the season in order to entrain hummingbirds, while later in the season plants only need to produce enough nectar to keep them returning. According to local beekeepers, *A. greatheadii* var *davyana* nectar is more abundant at the end of the flowering season (A Schehle, pers. comm.); however, we measured the lowest volumes and highest concentration late in the season. The northern provinces of South Africa are summer rainfall regions with dry winters, therefore as winter progresses water stress increases and this may contribute to the increase in concentration. According to Carroll et al. (2001) and Wyatt et al. (1992),

drought indirectly influences floral rewards and thus pollinator visitation; plants experiencing water stress may produce less nectar. Leiss and Klinkhamer (2005) demonstrated a decrease in nectar production with low water availability with a resultant decrease in pollination. However, leaf succulence enables *A. greatheadii* var *davyana* to provide abundant nectar during winter when alternative sources are scarce thus making it an ideal resource for beekeepers.

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