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Relationships between food quality and fitness in the desert locust, *Schistocerca gregaria*, and its distribution over habitats on the Red Sea coastal plain of Sudan

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Abstract

The effect of millet, *Pennisetum typhoideum* Rich. (Poaceae), leaf nitrogen content on fitness parameters of the desert locust, *Schistocerca gregaria* Forsk. (Orthoptera: Acrididae), was studied under laboratory conditions. Locusts reared on high-nitrogen leaves were larger, developed faster, had higher survival, reproduced more and earlier, and showed greater synchronization than those fed on low-nitrogen leaves. Active and passive cannibalism contributed to mortality when locusts were reared on low-nitrogen leaves, but not when reared on high-nitrogen leaves. Elevated leaf nitrogen content of host plants increased net reproduction and intrinsic rate of increase, and lowered generation time. The findings show that nitrogen content of host plants affects the potential for population increase in the desert locust. Leaf samples of common plant species were collected in the *Heliotropium arbainense* (Fresen.) (Boraginaceae) and *Panicum turgidum* (Forssk.) (Poaceae) plant communities on the Red Sea coastal plain of Sudan during the winters of 1999 and 2000. The levels of leaf nitrogen in host plants were comparable to those in the laboratory studies and consistently higher in plant samples from the *Heliotropium* community than in samples from the *Panicum* community. Both in 1999 and 2000, locust densities were much higher in the *Heliotropium* than in the *Panicum* plant community. It should be assessed whether the desert locust would be attracted to sites where host plants have high leaf nitrogen content, as this would not only increase their fitness, but also the likelihood of gregarization and outbreaks.

Introduction

The desert locust, *Schistocerca gregaria* Forsk. (Orthoptera: Acrididae), lives generally as scattered solitarious individuals at low population densities in arid and semi-arid regions. It has a high requirement for food nitrogen or protein (Dadd, 1963; Hinks et al., 1993; Simpson et al., 2002; Raubenheimer & Simpson, 2003), and selectively feeds on host plants with high nitrogen (Chandra & Williams, 1983). Relationships between fitness parameters at population level (e.g., net reproduction, intrinsic growth rate) and nitrogen content of food plants have not been determined. However, in many herbivore insects, survival and fecundity are higher when food protein levels are high (McNeill & Southwood, 1978; Mattson, 1980; White, 1993; Awmack & Leather, 2002). This is also true for locusts and grasshoppers. For example, there was a positive correlation between both survivorship and fecundity and N concentration in *Melanoplus mexicanus mexicanus* (Saussure) (Orthoptera: Acrididae) fed on wheat with varying nitrogen concentrations (Smith & Northcott, 1951). In *Melanoplus sanguinipes* (Fabricius) (Orthoptera: Acrididae), fecundity was increased by a diet that was high in nitrogen (Krishna & Thorsteinson, 1972; Joern & Behmer, 1998), but survival was not affected by nitrogen

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content (Joern & Behmer, 1998). Similarly, when *Locusta migratoria migratorioides* (Reiche and Fairmaire) (Orthoptera: Acrididae) females were fed with a low protein diet, egg production dropped and terminal eggs were resorbed (McCaffery, 1975). Similar results were reported in the grasshopper *Ageneotettix deorum* (Scudder) (Orthoptera: Acrididae) in which more nitrogen in the diet significantly increased weight and egg production rate, and reduced the time until the first egg pod and the time between the first and the second egg pod (Joern & Behmer, 1997).

White (1976) suggested that survival of nymphs of desert locust and other locusts in desert environment is high at elevated leaf nitrogen. An elevated leaf nitrogen content of host plants could possibly contribute to the success of the build-up of desert locust populations, which subsequently could lead to upsurges and plagues. Knowledge on the response of desert locust life table statistics to leaf nitrogen of the host plants is therefore of interest for desert locust survey and control operations. The hypothesis to be tested in this study is that increased leaf nitrogen content in a host plant increases the fitness of desert locusts by changes in survival, development, and fecundity.

On the Red Sea coastal plain of Sudan, Woldewahid et al. (2007) described four plant communities: the *Suaeda monoica* Forssk. ex J.F. Gmel. (Chenopodiaceae) scrubland near the coast, the *Acacia tortilis* (Forssk.) Hayne, (Leguminosae, Mimosoideae) scrubland near the Red Sea Hills, the *Panicum turgidum* (Forssk.) (Poaceae) grassland at intermediate location and altitude, and *Heliotropium*–millet at the transition between the *Panicum* grassland and the *S. monoica* scrub. The croplands with millet (*Pennisetum typhoideum* Rich.) (Poaceae) are characterized by relatively good moisture provision because of runoff water from the spreading wadies, and high abundance and vegetation cover of *Heliotropium arbainense* (Fresen.) (Boraginaceae). This plant species is strongly associated with solitarious locusts (Woldewahid et al., 2004; van der Werf et al., 2005). A sharp decrease in locust density is seen when going from the *Heliotropium* plant community of the Gwob-Gabol area, which is a major millet-growing area in the southern part of the coastal plain of Sudan, to the immediately adjacent *P. turgidum* and *S. monoica* areas. The reason for the strong association of desert locust populations with the *Heliotropium* plant community is not known. Several explanations for herbivores to aggregate in certain habitats are possible. Certain plant species may provide shelter against adverse weather conditions, protection from natural enemies, or offer suitable conditions for egg deposition (Husein et al., 1946; Brown, 1947; Uvarov, 1966, 1977; Roffey & Popov, 1968; Chandra, 1985). It is also possible that herbivores respond to host-plant quality and choose host plants that maximize their fitness (McNeill & Southwood, 1978; Mattson, 1980).

Grasshoppers often select high-quality host plants, as measured by leaf nitrogen content, causing aggregation (Caswell & Reed, 1976; White, 1976, 1984, 1993; Boutton et al., 1978; Heidorn & Joern, 1987; Lockwood, 1989). The protein (27%) or nitrogen (4.5% N) requirement of the desert locust is very high (Dadd, 1963; Hinks et al., 1993; Fagan et al., 2002; Raubenheimer & Simpson, 2003). Despland & Simpson (2000) show that food quality and distribution interact to influence locust phase state through effects of crowding and locomotion. In the African Sahel, leaf nitrogen content of host plants is spatially variable (Breman & de Wit, 1983; Breman & Uithol, 1984). From an optimal foraging perspective, it would be profitable for desert locust to aggregate in the places where the host plants are the most nutritious. Thus, one of the factors responsible for the aggregation of solitarious desert locust to the *Heliotropium* plant community may be the presence of nutritious host plants with comparatively high leaf nitrogen content. Therefore, our objective was to determine whether differences in the density of desert locust between the *Heliotropium* plant community and the *Panicum* plant community were associated with differences in host-plant quality between those communities. Finally, we determined whether there were differences in microbial crusts between soils associated with these two plant communities, because those crusts can actively contribute to nitrogen fixation and, hence, help explain differences in soil and plant nitrogen (Belnap & Harper, 1994).

Materials and methods

Experimental design and host plants

The host plant used to feed the locusts in the life table study was millet (*P. typhoideum*), a staple food crop in semi-arid regions, and a suitable host plant for the desert locust (Abdel Rahman, 1999). Millet seeds were obtained from the Gwob-Gabol millet-growing area on the Sudanese Red Sea coast. There were 11 sowings of millet plants over a period of 13 weeks, starting 6 weeks before the life table study. Six- to 7-week-old plants were used to feed the locusts. Twenty 10-l pots (three plants/pot) per treatment per week were used. Pots were filled with commercial potting soil. In the elevated nitrogen treatment (N1), 10 g of calcium nitrate (15.5% N) was applied as solid fertilizer by mixing it with the upper soil of each pot at 1 week after sowing. Three weeks after sowing, ammonium nitrate (32% N) was applied as liquid fertilizer (2.3 ml pot^{-1}). No fertilizer was given to the low-nitrogen treatment (N0). Locusts were reared on millet leaves grown with (N1) and without (N0) nitrogen. Day length in the greenhouse was at

least 12 h. The daily mean day/night temperature was 28/22 °C. Relative humidity fluctuated between 54 and 70%.

Locust rearing and food supply

The locusts came from a gregarious stock that was originally obtained from the International Centre of Insect Physiology and Ecology (ICIPE) field station in Port Sudan and had been reared at the Laboratory of Entomology, Wageningen University, Wageningen, The Netherlands, for more than 10 generations. Five cohorts or replicates were started at intervals of 1–3 days. Per replicate, 100 24- to 48-h-old hatchlings were collected from the rearing, 50 of which were placed in a cage with high-nitrogen millet leaves, while the other 50 hatchlings were placed in a cage with low-nitrogen millet leaves. Cages ($0.14 \times 0.24 \times 0.29$ m) consisted of a transparent Perspex front, three opaque sides, and a bottom made of polyvinyl chloride, and a stainless steel wire mesh on top for aeration. At the rear, a round opening with a sleeve was fixed to handle plants and locusts, while two holes with a screw fitting were made in the bottom to attach glass jars (380 ml). One of the jars was filled with wet Oasis sponge to keep excised millet leaves fresh for at least 24 h. The other jar was filled with moist sand for egg-laying.

Every day, fresh millet leaves (25–40 cm length) ad libitum, a fresh sponge, and water were placed in the jar, while the old leaves were removed. Test cages were placed in a controlled climate room kept at a constant temperature of 30 °C, a r.h. of 46–54%, and a daylight regime of L12:D12.

Leaf nitrogen content

Each week, millet leaves of both treatments were oven dried, ground, and the amount of total leaf nitrogen (% N per dry weight) was determined by Dry Micro-Dumas Combustion Analysis (EA 1110 Elemental Analyser; CE Instruments, Milan, Italy).

Locust survival

Each day, the number in each stage was counted per cage until all individuals had either completed development or died. A precise record was made of live as well as dead individuals. Mortality due to handling or other causes was recorded. The total number of locusts eaten dead or alive by their conspecifics (i.e., passive and active cannibalism, respectively) could thus be determined on a daily basis. The proportion of locusts surviving through age x was calculated and a survivorship curve (l_x) was established in both treatments.

Stage duration and numbers entering a stage

The average duration of the five locust stages and the standard deviation (SD) of the time of recruitment to a stage were estimated from the life table records. The adult moult in locusts is referred to as fledging, and fledglings are the immatures, that is, pre-reproductive locust adults. Sexual maturity of males was assessed by the appearance of yellow coloration on the femur of the third leg (Hunter-Jones, 1956). Sexual maturity of the fastest-maturing females in a cage was signalled by the first egg-laying.

Female fecundity

Jars with moist sand (12% water by weight) were attached underneath each cage from the 10th day after fledging to enable egg-laying. Every 2 days, the jars were replaced and the number of females per cage, the number of egg pods laid, and the number of eggs per pod were counted. Observations on egg-laying were continued for 4 weeks. Egg pods that had been laid on the floor of the cage were cannibalized and could therefore not be counted.

Life table parameters including net reproductive number (R_0), mean generation time (T), and intrinsic rate of increase (r) were calculated with standard formulas (Keyfitz, 1977). Fecundity was calculated as the ratio between the total number of eggs laid in a cage and the initial number of female fledglings in the cage.

Morphometrics

Caput width, femur of the third leg, and length of first wing (six mature adults per cage: three females and three males) were measured as probes for the effect of food quality on the size of individuals.

Data collection in the Sudan

The site for the field study was located on the coastal plain of Sudan between Port Sudan and Tokar, near the wadis Gwob and Gabol (Figure 1). Sampling was conducted in the *Heliotropium* and *Panicum* plant communities during the winter season between December 1999 to February 2000 (1999 winter season or simply '1999') and during the winter of 2000/2001 (hereafter '2000').

In 1999, leaves were collected from specimens of 15 different plant species in the *Heliotropium* plant community, and of 12 different plant species in the *Panicum* community (Table 1). The leaves were collected from 34 *Heliotropium* sites and 24 *Panicum* sites, and there were seven collection dates: 18 and 25 December 1999; 8, 18, and 23 January, and 10 and 27 February 2000 (Figure 1A). Sampling frequency of plant species depended on their abundance in the sampling sites (Table 1). In general, sampling was terminated earlier in the *Panicum* sites than in the *Heliotropium* sites, because the foliage senesced earlier in the grassland due to lower moisture.

In 2000, leaves were collected from eight different species of host plants in the *Heliotropium*, and from six

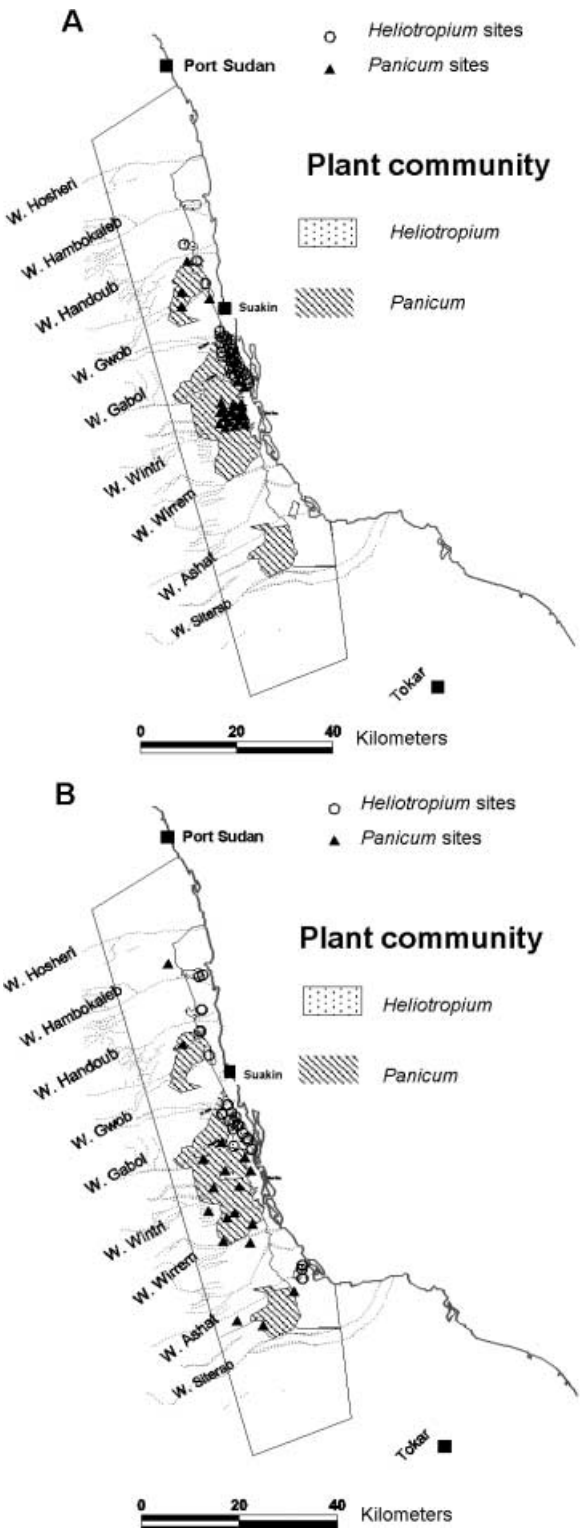

Figure 1 Location of sample sites in the *Heliotropium* (○) and *Panicum* (▲) plant communities in the winter seasons of (A) 1999 and (B) 2000 on the Red Sea coastal plain of Sudan (W., wadies).

species in the *Panicum* sites (Table 1). Leaves were collected at 22 *Heliotropium* sites and at 18 *Panicum* sites (Figure 1B). Leaves were collected on 6 and 20 December 2000; 3, 15, and 30 January, and 3 March 2001.

In 1999, at least three but not more than five composite leaf samples were collected per plant species at any given sample date. Each of those composite samples consisted of leaf material from 12–20 individual plants from one or more sample sites. In 2000, the number of composite samples per species and date varied from five to 15. A total of about 850 composite leaf samples were analysed in the winter of 1999, and 1200 in the winter of 2000. Fully grown upper leaves were sampled, and flowering or reproductive parts of the plant were avoided. During each sample occasion, host plants at a representative development stage were selected from the *Heliotropium* and *Panicum* plant community sites. There was no difference in development stage between the two plant communities. The collected leaves were immediately sun dried in a wire mesh and dry stored until further processing. The samples were oven dried to constant weight at 65 °C. After drying, the leaf total nitrogen content of each sample was analysed using the Micro–Kjeldahl method, at the Plant Nutrition Unit Sample Analysis Laboratory, Khartoum, Sudan.

Presence of microbial crusts observed as aggregates of fine soil particles was recorded in *Heliotropium* and *Panicum* sites. The microbial population was quantified from composite soil samples collected in five *Heliotropium* and *Panicum* sites. Each composite soil sample consisted of soil collected from 10 boreholes of the upper 10 cm. The number of colony-forming units (CFU) (propagules) was estimated by incubation in the laboratory of the Department of Biofertilizers, Environment and Nature Research in Khartoum, Sudan.

Data analysis

All quantitative characteristics of locusts were calculated separately for each cohort per cage, resulting in five replicate values per treatment. As the obtained data satisfied normality requirements, significance of differences was assessed by paired t-test, using cages of N0 and N1 started at the same date as a pair. All analyses were conducted with SPSS (1999).

Results

Leaf nitrogen content – laboratory study

The total leaf nitrogen content (g N per g dry green leaf) of millet plants grown on soils with (N1) and without (N0) nitrogen application were significantly different (paired t-test: $P \leq 0.05$) in all of the 11 weekly sowings (Figure 2). On average, the leaf nitrogen content was 3.9% (range

Plant species	1999		2000	
	Heliotropium sites	*Panicum* sites	*Heliotropium* sites	*Panicum* sites
Aerva javanica	3	3	–	–
Amaranthus spec.	4	–	5	–
Cassia senna	1	3	–	–
Cenchrus ciliaris	4	2	6	4
Citrullus spec.	4	2	–	–
Crotalaria microphylla	4	4	–	–
Cyprus spec.	4	1	–	–
Eleusine spec.	2	1	–	–
Heliotropium arbainense	7	4	7	5
Launaea capitata	1	–	4	–
Panicum turgidum	–	4	–	4
Pennisetum typhoideum	7	–	7	–
Phaseolus spec.	2	–	–	–
Tephrosia spec.	2	4	5	4
Trianthema spec.	–	–	6	4
Tribulus terrestris	7	4	6	5
Zygophyllum simplex	1	3	–	–

Table 1 List of plant species sampled for leaf nitrogen analysis in the 1999 and 2000 winter seasons on the coastal plain of Sudan. The number of sample occasions of individual plant species is indicated

2.7–4.9%) in the N1 treatment vs. 1.4% (0.9–2.1%) in the N0 treatment.

Locust survival to the adult stage

Mortality was 8% in locusts reared on high-nitrogen foliage vs. 36% in locusts reared on low-nitrogen foliage. Survival of locusts until average time of fledging is shown in Figure 3. There were highly ($P \leq 0.01$) significant (L2, L3, and L4), weakly ($P \leq 0.10$) (L1), or no significant (L5) differences in mortality between locusts fed on high- and low-nitrogen leaves (Figure 4). Active cannibalism was observed in the low nitrogen treatment, but never in the high nitrogen treatment. Active cannibalism was mostly observed when the victims were vulnerable to attack during moulting. Moreover, scavenging on bodies of dead individuals must also have occurred. No passive cannibalism happened in the high nitrogen treatment, as the few cadavers in this treatment were all retrieved, untouched by scavenging siblings.

Stage duration and synchronization

L2 to L4 locusts reared on millet leaves with high leaf nitrogen content (N1) had significantly shorter instar durations (paired t-test: $P \leq 0.05$) than locusts reared on low nitrogen leaves (N0) (Table 2). Total time in the five locust stages was also significantly different, amounting to

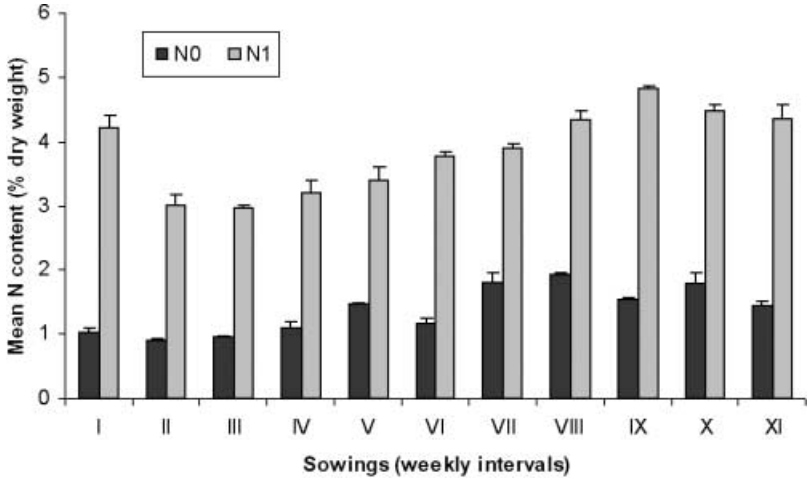

Figure 2 Leaf nitrogen content (mean + SE) of weekly sowings of millet at high (N1) and low (N0) levels of nitrogen in the soil.

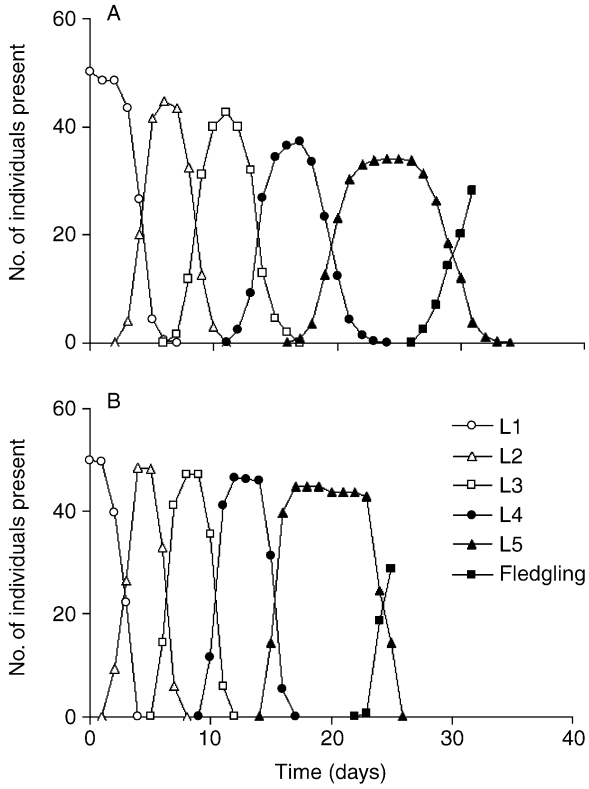

Figure 3 Stage dynamics in *Schistocerca gregaria* (average of five cages) reared on (A) low-nitrogen (N0) and (B) high-nitrogen (N1) millet leaves.

almost 3.5 days shorter in N1 than in N0. The locusts fed on N1 millet moulted in a significantly more synchronized manner than locusts fed on N0 millet, as shown by significant differences in the SD of the time of recruitment to the next stage (Table 2).

Locusts reared on high-nitrogen foliage had a shorter mean (± SE) time from hatch to first egg-laying (48 ± 3 days) than locusts reared on low-nitrogen foliage (56 ± 5 days). The time between adult moult and first egg-laying did not differ significantly between locusts reared on high- and low-nitrogen foliage (21 ± 2 and 23 ± 2 days, respectively; t-test: $P>0.05$).

Females reared on leaves with a high nitrogen content laid more eggs (mean ± SE: 156 ± 18 eggs/female) (weakly significant: paired t-test: $P\leq0.10$) than those reared on leaves with a low-nitrogen content (92 ± 10 eggs/female) (Table 3). There was no difference in the number of pods deposited per female (2.2 ± 0.2 vs. 2.1 ± 0.2) between the two nitrogen treatments. The mean (± SE) number of eggs per pod, however, was significantly higher in the high nitrogen treatment (73 ± 3; paired t-test: $P\leq0.01$), than in the low nitrogen treatment (42 ± 2), as were the maximum and minimum number of eggs per pod (Table 3).

Adults (both fledglings and matures) reared on high nitrogen millet suffered lower mortality than locusts reared on a low nitrogen millet (Figure 5A). Cannibalism was a major cause of mortality in adults reared on low-nitrogen foliage. During the fledgling stage, cannibalism was only observed in locusts reared on low-nitrogen foliage. After the adults matured and started egg-laying, cannibalization of egg-laying females occurred both at high and low nitrogen.

The impact of leaf nitrogen content on stage duration, survivorship, and fecundity translated into differences between treatment effects on the aggregate life history parameters R_0, T, and r (Table 4). The expected number of female offspring was higher and earlier in females reared on high-nitrogen foliage than in females reared on low-nitrogen foliage (Figure 5B,C). Female offspring per female (R_0) was three times as high on high-nitrogen food (64.8) as on low-nitrogen food (19.5). The generation time (T) was shorter in locusts reared on high-nitrogen foliage than in locusts reared on low-nitrogen foliage (58 vs. 63 days). The intrinsic rate of increase (r) was greater on high-nitrogen leaves (0.072/day) than on low-nitrogen leaves (0.047/day). Doubling time was 15 days on low-nitrogen leaves and 10 days on high-nitrogen leaves.

Adult morphometrics

Adults reared on high nitrogen food were larger than those reared on low nitrogen food. Morphometrics showed that

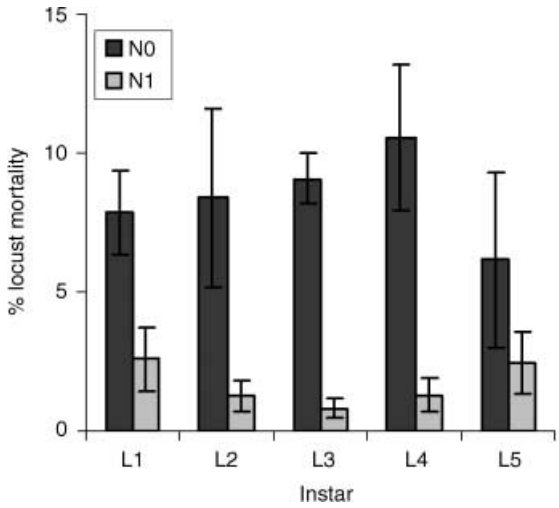

Figure 4 Percentage (mean ± SE) dead *Schistocerca gregaria* per instar when reared on high- (N1) and low-nitrogen (N0) millet leaves.

	Stage duration		SD time recruitment to a stage	
Stage	N0	N1	N0	N1
L1	4.09 ± 0.20	3.24 ± 0.44ns		
L2	4.48 ± 0.15	3.69 ± 0.23**	0.68 ± 0.08	0.46 ± 0.09***
L3	5.17 ± 0.15	4.26 ± 0.20*	0.72 ± 0.09	0.47 ± 0.07***
L4	5.86 ± 0.10	5.19 ± 0.27**	0.90 ± 0.16	0.50 ± 0.06**
L5	9.25 ± 0.49	9.04 ± 0.41ns	1.11 ± 0.11	0.47 ± 0.05***
Fledging			2.63 ± 1.37	0.52 ± 0.04ns
L1–L5	28.85 ± 0.41	25.43 ± 1.26***		

Differences of treatment means of average stage duration within rows are significant: ***P≤0.01, **P≤0.05, *P≤0.10, and ns, not significant (P>0.10) using paired t-test.

Table 2 Average stage duration (mean ± SE; days), and standard deviation of time (SD ± SE, days) of recruitment into a stage of *Schistocerca gregaria* reared on millet leaves with low (N0) and high nitrogen (N1) content

the hind femur, caput width, and elytron lengths of males and females reared on high leaf nitrogen content (N1) were significantly (paired t-test: P≤0.01) longer than those of individuals reared on low-nitrogen leaves (Table 5).

Nitrogen content of host plants in two contrasting plant communities

In both years of the study, leaf nitrogen content was consistently higher in host plants at *Heliotropium* sites than in host plants at *Panicum* sites (Figure 6). During the winter of 1999, nitrogen percentage, pooled over all plant species sampled, was about 2.5% in the *Heliotropium* sites, decreasing to less than 2.0% in February 2000 (Figure 6A). In *Panicum* sites, nitrogen percentage was stable around 1.8% until 15 January; after that the vegetation dried and no more samples were taken. The leaf nitrogen content of the host plants *H. arbainense* and *Tribulus terrestris* that were found in both plant communities were compared (Figure 6B,C). In December, the leaf nitrogen content of *H. arbainense* was similar in both communities (Figure 6B). From January onwards, the leaf N content of *H. arbainense* was about 1% higher at *Heliotropium* sites than at *Panicum* sites. A similar trend was observed in leaf nitrogen content of *T. terrestris* at *Heliotropium* and *Panicum* sites (Figure 6C). The cereal millet is cultivated and dominant in the *Heliotropium* sites, while the perennial grass *P. turgidum* is the dominant plant in the *Panicum* sites. Both plant species were similar in nitrogen content in early December. Thereafter, the nitrogen content declined in both plant species, but more rapidly and to a greater extent in *P. turgidum* than in millet. On 15 January, the difference between both species was greater than 1% (Figure 6D).

In December 2000, the pooled nitrogen percentage in plants at *Heliotropium* sites was approximately 3.7%, and it decreased gradually in the course of January and February 2001 to 2.6% (Figure 6A). At *Panicum* sites, the nitrogen percentage varied between 2.8 and 3.0%; and no green vegetation was present after the end of January. In December and January, the leaf nitrogen content of *H. arbainense* and *T. terrestris* at *Heliotropium* sites was higher than the leaf nitrogen content of the same host plants at *Panicum* sites (Figure 6B,C). This difference in leaf nitrogen became negligible after January. The leaf nitrogen content of the millet at *Heliotropium* sites and the *P. turgidum* at *Panicum* sites were similar in early December, and, thereafter, the nitrogen content declined in both plant species, but in the *P. turgidum* more than in the millet, as in the 1999 winter season (Figure 6D).

Variable	N0	N1
Mean number of eggs/female	92.4 ± 10.3	156.1 ± 18.0*
Mean number of pods/female	2.2 ± 0.2	2.1 ± 0.2ns
Mean number of eggs/pod	41.8 ± 1.9	73.2 ± 2.6***
Maximum number of eggs/pod	69.7	112.7**
Minimum number of eggs/pod	18.0	37.0**

Differences of treatment means within rows are significant using paired t-test: ***P≤0.01, **P≤0.05, *P≤0.10, and ns, not significant (P>0.10).

Table 3 Fecundity (mean ± SE) of *Schistocerca gregaria* females reared on millet leaves with low (N0) and high (N1) nitrogen content

Locust distribution in the coastal plain of Sudan

Comparatively high locust densities were found in the *Heliotropium* plant community and low densities, or virtually no locusts, in the *Panicum* plant community in both seasons (Figure 7). In 1999, locust density amounted to 332 ± 56 individuals/ha (mean ± SE) in the *Heliotropium* plant community, and 21 ± 5 individuals/ha in the *Panicum* plant community. In 2000, the density was 56 ± 5 locusts/ha in the *Heliotropium* plant community, and no

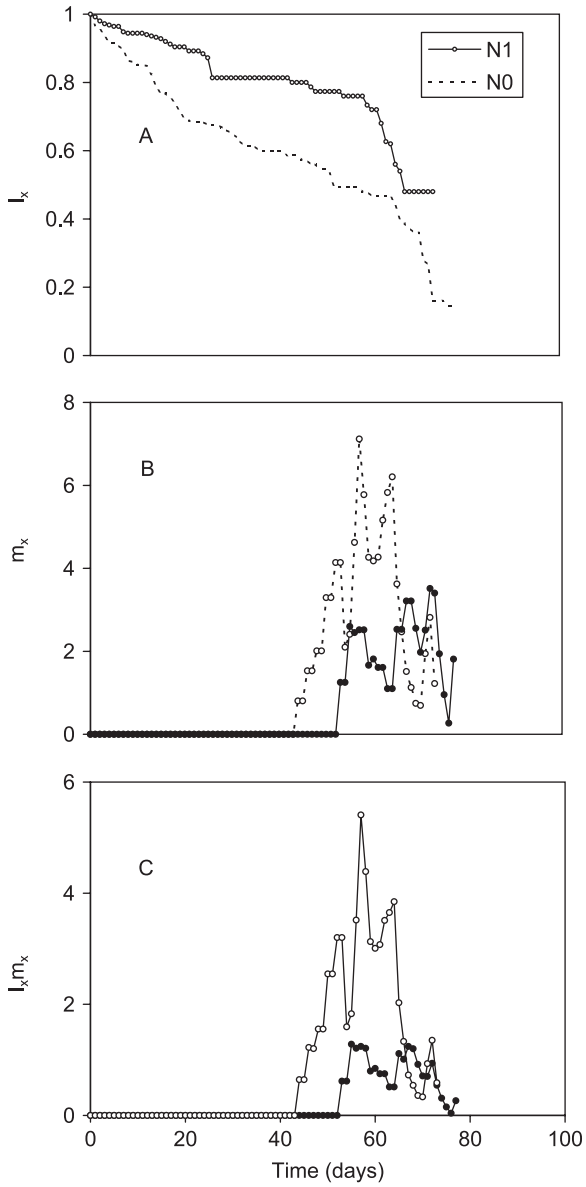

Figure 5 Age-dependent survival (l_x; A) and egg production (m_x; B) of *Schistocerca gregaria* reared on high- (N1) and low-nitrogen (N0) millet. (C) The age-dependent egg production, corrected for survival (l_x m_x). Net reproduction (R_0) is the summation of l_x m_x.

locusts were observed in the *Panicum* plant community (Figure 7).

Microbial crusts in the coastal plain of Sudan

Microbial crusts were observed in almost half of the *Heliotropium* sites and they were rarely found in *Panicum* sites (data not shown). The density of CFUs of microbiota was 26 times higher in *Heliotropium* sites than in *Panicum* sites (Figure 8). The mean number of CFUs per μg soil (log10-transformed for analysis) in the *Heliotropium* sites was 3.53 ± 0.20, which is significantly higher than the density of CFUs in the *Panicum* sites (2.11 ± 0.28; t-test: t = 4.20, d.f. = 8, and P = 0.003).

Discussion

Fitness and synchronization

Locusts reared on millet with high leaf nitrogen content showed better survival, greater synchronization, faster development, larger size, and higher fecundity than locusts fed on millet with low nitrogen content. As a result, the potential for population growth, as expressed by the intrinsic rate of natural increase (r), was substantially greater when the locusts were fed with high-nitrogen leaves (r = 0.072/day) than when they were fed with low nitrogen leaves (r = 0.047/day). Rapid rate of development and an early production of eggs in locusts reared on high-nitrogen millet leaves might allow for a more optimal use of green vegetation after rainfall as the longevity of green vegetation following rain may be short in deserts (Noy-Meir, 1973).

The processes of moulting, maturation, and egg-laying were more synchronized in locusts that received high-nitrogen food than in those that received low-nitrogen food. Synchronization is implicated in the process of gregarization (Collett et al., 1998) and the possibility exists that greater synchronization, found in this study at higher-nitrogen levels in the host plant, could enhance gregarization.

Mortality and cannibalism

Substantial mortality of locusts is common in laboratory and field studies and cannibalism is often an important component of this mortality. In the field, locust mortalities of 40 (Stower & Greathead, 1969) and 76% (Roffey & Stower, 1983) have been reported in the presence of green

Table 4 Effect of feeding of *Schistocerca gregaria* on millet leaves with low (N0) and high (N1) nitrogen content on its life history parameters: net reproductive number (R_0, female offspring/female), generation time (T, days), doubling time (DT, days), and intrinsic rate of increase (r, day^{-1})

Parameters	N0	N1
R_0	19.5	64.8
T	63.2	58.1
r	0.047	0.072
DT	15	10

	Male		Female	
	N0	N1	N0	N1
Femur length	22.6 ± 0.2	24.9 ± 0.2**	25.1 ± 0.3	28.0 ± 0.2**
Caput width	6.0 ± 0.1	6.9 ± 0.1**	6.8 ± 0.2	8.3 ± 0.1**
Elytron length	50.2 ± 0.6	53.4 ± 0.4*	56.3 ± 0.5	62.4 ± 0.3**

Differences of treatment means within a row are significant using paired t-test: **P≤0.01 and *P≤0.05.

Table 5 Morphometrics (mean ± SE, mm) of adult *Schistocerca gregaria* reared on millet leaves with low (N0) and high (N1) nitrogen content

vegetation. In both cases, the causes of mortality were not reported. Ashall & Ellis (1962) found 30–50% locust mortality in east Africa, due to cannibalism, and Husain et al. (1946) reported 50% locust mortality due to cannibalism in the presence of green vegetation. In our life table study, we observed that the locusts reared at low nitrogen ate their entire casted exuviae, whereas those reared at high leaf nitrogen content did not eat their casted skins.

Lack of moisture in the diet has been mentioned as a cause of cannibalism (Uvarov, 1977). Husein et al. (1946), however, indicated that locusts ate the dead parts of the victim in the presence of moist and green leaves, which might indicate that they were in need of nitrogen rather than water, supporting White's (1993) conclusion that cannibalism is due to shortage of nitrogen in the food. The protein requirement of the desert locust is in the order of 20–40% protein of the plant dry matter (corresponding to approximately 3.3–6.7% N) (Dadd, 1963). Thus, the 1.4% total N in the low-nitrogen millet leaves of our experiment is very low compared to the nitrogen requirement of desert locust, whereas the 3.9% N in the high nitrogen treatment is in the range of satisfactory N contents mentioned by Dadd (1963). As 50% of the cuticle or exuviae in desert locust and grasshoppers is protein (Hinks et al., 1993), cannibalism and the eating of exuviae may provide an essential nutritional resource to locusts feeding on low-nitrogen plant food. In this sense, cannibalism might be a survival mechanism for insects in a nitrogen-limited environment (Mattson, 1980; White, 1993). The extra nitrogen through cannibalism could have mitigated the effects of the low-nitrogen crop diet. However, the incidence of cannibalism, an increase from 4 (L1) to 10% (L4), is probably too low to show an effect. The better synchronization observed for locusts reared on high-nitrogen leaves may have prevented cannibalism in this treatment as cannibalism mainly occurred when victims are immobile due to moulting.

Microbial crusts

Microbial crusts consisting of a shallow (1.0 cm) layer of fine soil particles, bound together in a stable aggregate, were frequently observed in the *Heliotropium* plant community, but rarely in the *Panicum* plant community. These crusts help to absorb water from runoff and retain moisture (Fattom & Shilo, 1984; West, 1990; Mazor et al., 1996). Moreover, certain microbes living in these crusts can fix atmospheric nitrogen (de Ridder et al., 1982), making it available to host plants after mineralization. (Belnap & Harper 1994). The last authors further reported that plants grown in microbial crusted soils showed a significant increase in NPK and trace elements compared to plants from non-crusted sites in the deserts of southeastern Utah, USA. They further observed that microbial crusts can trap fine soil particles that are more nutrient rich than the coarser sand particles. Moreover, microbial crusts stabilize the soil, protecting it against wind erosion, and improving moisture absorption and retention, thereby supporting the growth of higher quality host plants.

Desert locust distribution on the Red Sea coastal plain of Sudan

In both winter seasons on the coastal plain of Sudan, the total leaf nitrogen content of locust host plants, particularly *H. arbainense* and *T. terrestris*, was consistently higher in the *Heliotropium* plant community than in the *Panicum* plant community. The sites of the two plant communities differ in grazing pressure, soil particle size, presence of moist soil in the upper 0–15 cm soil layer, and microbial crust. The *Panicum* plant community was grazed during the rainy season, whereas the *Heliotropium* plant community with millet was not. Reduction of leaf nitrogen of plants in grazed sites is common in sub-Saharan Africa due to nutrient mining (Stoorvogel & Smaling, 1990). Grazed plants may also produce secondary compounds (Mattson, 1980) not favoured by locusts. The moist and fine soil particle size in the *Heliotropium* plant community could be a better source of nitrogen for host plants than the coarse sand particles in the relatively dry *Panicum* plant community.

The leaf nitrogen content of the host plants in the *Panicum* plant community (less than 3.5% N per g dry weight) was below the nitrogen requirement for desert locust (4.5% g N per g dry weight). In both winter seasons, breeding of desert locust populations was largely confined to the

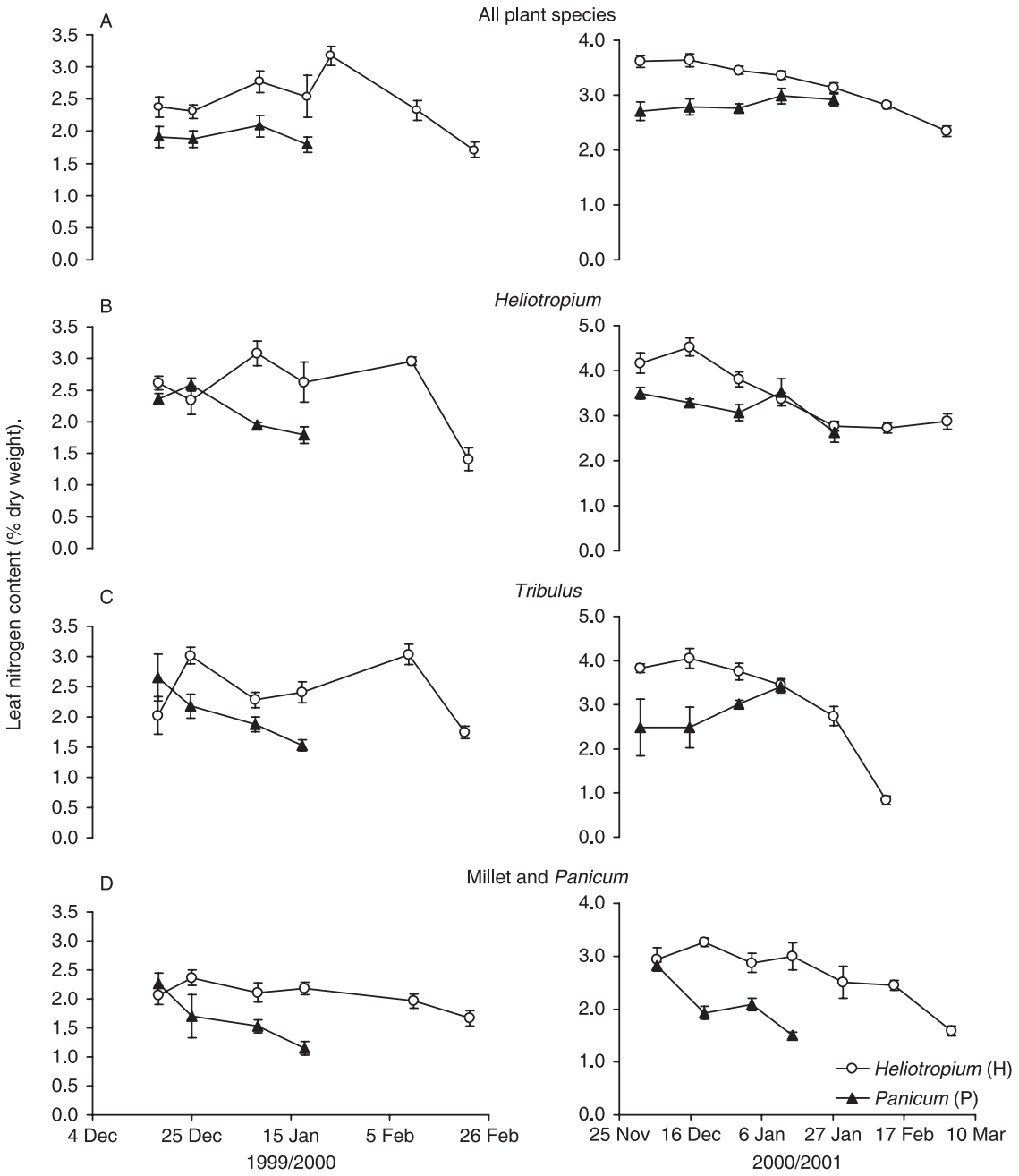

Figure 6 Leaf nitrogen content (mean ± SE) of *Schistocerca gregaria* host plants in *Heliotropium* (H) and *Panicum* (P) sites: (A) all species combined, (B) *Heliotropium arbainense*, (C) *Tribulus terristris*, and (D) millet from *Heliotropium* sites and *Panicum turgidum* from *Panicum* sites. Data collected in two subsequent winters: 1999/2000 and 2000/2001.

Heliotropium plant community, where the leaf nitrogen of host plants is higher than that in the adjacent *Panicum* plant community (van der Werf et al., 2005). When sufficient rains created good conditions for egg-laying in the *Panicum* community in late December 1999 and 2000, locusts were still concentrated in the *Heliotropium* community. The findings are congruent with the idea that the difference in locust density between the two plant communities is not due to a difference in the suitability of the soil for egg-laying, but to a difference in host plant quality, resulting in a different potential for locust development, survival, and reproduction.

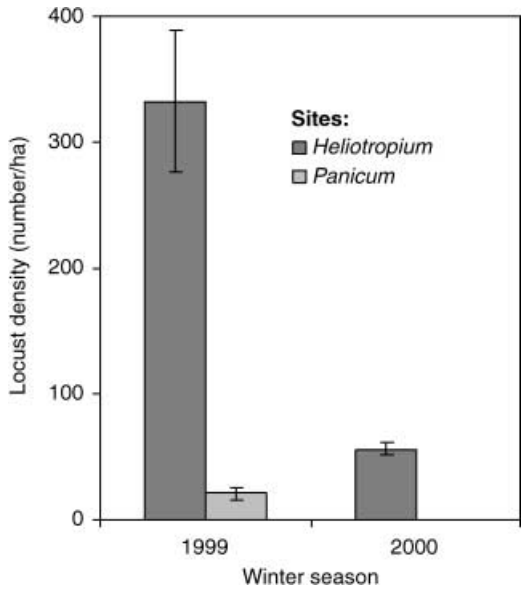

Figure 7 Density of *Schistocerca gregaria* (mean ± SE number/ha) in *Heliotropium* and *Panicum* sites in 1999 and 2000.

Conclusion

Our laboratory results demonstrated that increased leaf nitrogen content of the host plants may enhance population growth and synchronize development of the desert locusts. Furthermore, we showed a correlation between host plants having high leaf nitrogen content (i.e., the *Heliotropium* plant community) and the occurrence of elevated locust densities. Interactions between locust densities, vegetation abundance, and vegetation distribution (Collet et al., 1998; Despland & Simpson, 2000; Despland et al., 2000) trigger gregarization (Simpson et al., 2000). The concentration of high-quality vegetation in relatively small patches in the landscape (5% of the Red Sea coastal area in Sudan being occupied by the *Heliotropium*/millet plant community – van der Werf et al., 2005) could force locust populations to aggregate and foster gregarization and swarm development (Kennedy, 1939; Ellis & Ashall, 1957; Roffey & Popov, 1968; Despland et al., 2004). If elevated nitrogen leaf content of host plants would contribute to higher population densities and a more aggregated distribution, then chances or gregarization and localized outbreaks would also increase.

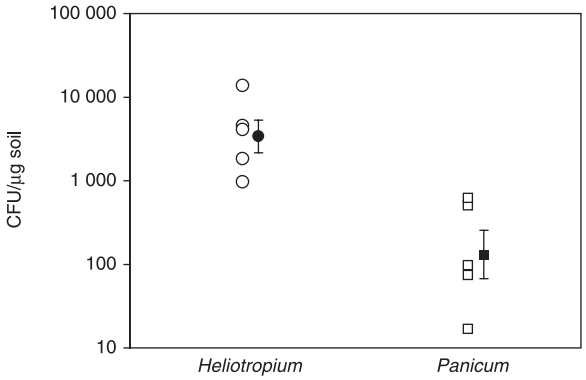

Figure 8 Density of microbial propagules (colony-forming units, CFU) in soils in the *Heliotropium* and *Panicum* communities. Open symbols represent the five sites of each community, and the closed symbols with whiskers are the mean ± SE.

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