Habitats and spatial pattern of solitarious desert locusts (*Schistocerca gregaria* Forsk.) on the coastal plain of Sudan

Gebremedhin WOLDEWAHID

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Abstract

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The Red Sea coastal plains of Africa and the Arabian Peninsula are an important breeding area for desert locust, *Schistocerca gregaria*. This area has been implicated as a source or transit area for locust swarms that threaten agriculture. The spatial distribution of the desert locust on the southern part of the Red Sea coastal plain of Sudan, between Port Sudan and Tokar, was investigated to determine habitat associations of the desert locust and collect information that might help in planning survey and control operations. Observations were made during three subsequent rainy seasons, from November till March, in 1999/2000, 2000/2001 and 2001/2002.

First of all, the main plant communities in the study area, a 120 km stretch of coastal plain, were classified and mapped. Sample sites were laid out in an approximately square 5 × 5 km grid of sample sites to collect vegetation data. Multivariate data analysis resulted in the delineation of four main plant communities, which were named after characteristic plant species: the *Suaeda monoica* scrubland near the coast, the *Acacia tortilis* scrubland near the Red Sea Hills, the *Panicum turgidum* grassland at intermediate location and altitude, and *Heliotropium*/millet, small pockets of cropland (mostly planted with millet) at the transition between the *Panicum* grassland and the *Suaeda* scrub. The croplands were characterized by relatively good moisture provision due to run-on water from spreading wadis, and high abundance and vegetation cover of the locust host plant *Heliotropium arbainense*.

Rainfall was markedly different between the three seasons: 158 mm in 1999/2000, 138 mm in 2000/2001 and 30 mm in 2001/2002. This resulted in substantial differences in observed locust densities. During the first and wettest season, solitarious adult locusts were observed in substantial numbers, up to 100 per ha, in the *Heliotropium/*millet plant community, but hardly in the plant communities characterized by *S. monoica*, *P. turgidum*, or *A. tortilis*. Egg laying and hopper development were found in the *Heliotropium*/millet plant community but not in the other communities. Gregarizing hoppers were found in one of the croplands. In the second year of the study, solitarious adult desert locusts were observed at low densities in the *Heliotropium*/millet plant community, and none were found in the other three communities. No egg laying or hopper development was observed in any community in the second season. In the third and driest season of the study, no adult locusts or hoppers were observed in the main study area. However, during the third season, it became possible to take samples in the delta of the wadi Baraka, near Tokar, to the south of the study area. This area receives more water than the main study area and adult solitary locusts were present here. They were associated with millet agriculture, as in the main study area.

Plant samples were taken in the central part of the main study area to compare nitrogen content of host plants in the two most suitable locust habitats: the *Heliotropium*/millet community and the *Panicum* grassland. Results showed a consistent difference in N content between host plants in the two plant communities, with the nitrogen content being approximately one percentage point higher in the *Heliotropium*/millet community than in the *Panicum* grassland. The difference in N-content is probably ecologically significant, as was demonstrated in a life table study in the laboratory, which compared survival, development and reproduction among gregarious locusts fed on millet leaves with 3.9% or 1.4% N. Net reproduction (65 versus 20 female offspring/female), intrinsic rate of increase (0.072 versus 0.047 day^{-1}) and generation time (58 versus 63 days) all indicate greater potential for population increase when nitrogen content in the food is high than when it is low.

Geostatistical methods were used to investigate whether it is possible to make predictions of locust densities at distant locations by spatial interpolation using kriging. Locust density maps were constructed, estimation errors were quantified and the relationship between sampling intensity and estimation error was established for the collected data sets.

This study shows a strong relationship between desert locust and the millet croplands on the coastal plain of Sudan. This habitat is characterized by better moisture status of the soil and higher nitrogen content in host plants, and contained the far majority of solitarious locusts in the area. All of the observed locust breeding was in millet croplands. Observations on other parts of the coastal plain confirmed the results. The millet croplands cover a very restricted portion of the coastal plain (only 5% of the area), and are relatively easy to survey.

Key words: Desert locust, plant community, spatial pattern, locust breeding, leaf N-content, Red Sea coast, Sudan.

Preface

This thesis is on desert locust, an ancient pest threatening crops and grazing over extensive areas in Africa, the Near East and south-west Asia. The aim of this thesis is to increase insight in the ecology of desert locust and contribute to an improved survey and control of this insect. The work described in this thesis was carried out in a collaborative project between Wageningen University (WU), The Food and Agriculture Organization (FAO) of the United Nations and the Plant Protection Directorate (PPD) of Sudan. The framework was the desert locust component of the EMPRES (Emergency Prevention System for Transboundary Pests and Diseases) programme of FAO. I am very grateful to all the people who contributed in various ways to the production of this thesis.

First I would like to thank my promoter Prof. dr. Joop C. van Lenteren and co-promoters Dr. ir. Arnold van Huis and Dr. ir. Wopke van der Werf, from Wageningen University, the Netherlands. Their unreserved professional guidance and supervision helped me to complete this thesis in its present shape. Arnold and Wopke, I sincerely appreciate your thorough understanding on the natural and political complexity of desert locust management which helped me a lot. You made a large contribution to this work and I am very grateful for your continuous encouragement and supervision at the workplace. Also I appreciate very much the warm-hearted welcome at your homes.

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Wageningen, October 2003

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Background

In the arid and semi-arid areas of Africa and Asia, the desert locust (*Schistocerca gregaria* Forsk.) can be a very destructive herbivore causing considerable loss to crops and pastures (Uvarov, 1957, 1977; Popov, 1958; van Huis, 1994; Bashir *et al.*, 1998). During plagues, the insect may occupy 20% of the earth land surface (29 million km^2) including 60 countries (Fig. 1) inhabited by a tenth of the world population (Steedman, 1988). The main focus of control organization is to search for outbreaks and devise means to control gregarizing populations before they develop into plagues. This requires monitoring of the build-up of solitarious desert locust populations in potential breeding areas. However, the breeding areas of the desert locust are vast, making effective monitoring of desert locust populations with ground survey teams extremely difficult. A better knowledge of the spatial relationship between desert locust populations and potential breeding habitats of the desert locust would improve desert locust survey and control operations.

Biology and ecology of the desert locust

Recession and plague populations, and weather

Weather, mainly rainfall in the arid and semi-arid area is low and variable. The variation in rainfall has a large random or unpredictable component (Noy-Meir, 1973). An effective rain event activates the emergence of green vegetation and breeding of animals (Noy-Meir, 1973) such as the desert locust (Magor, 1994; Pedgley, 1981; Dempster, 1963). When conditions in the desert habitat are not suitable for breeding, the desert locust exists in its solitary phase (phase *solitaria*). Solitarious populations are low in density and scattered over an area of nearly 16 million km^2 over 30 countries (Fig. 1). A period during which locusts predominantly occurs as solitaries is called recession. In the past, recessions have lasted from less than one year to seven years (Cressman, 1996b).

When the desert habitat becomes suitable for breeding, desert locust densities markedly increase, leading to gregarization (phase *gregaria*). Gregarization may occur when locusts concentrate and multiply in the desert with sufficient rainfall. Gregarization, unless checked, can lead to the formation of hopper bands and swarms

(Pedgley, 1981). This is commonly referred to as an outbreak. Suitable habitat conditions in successive breeding areas may lead to a dramatic increase in locust numbers. Simultaneous outbreaks may follow commonly referred to as an upsurge. Upsurges may eventually lead to a plague. Outbreaks often occur but they do not necessarily lead to upsurges. Similarly, most upsurges die out before leading to a major plague. There have been nine major plagues between 1860 to 1995 (Cressman, 1996b). They varied in length from one to 22 years. The last plague occurred in 1986-89.

The probability of desert locust populations developing into an outbreak cannot be reliably predicted (Dempster, 1963), because of limited knowledge of the factors that cause locust outbreaks. Outbreak records of migratory insects such as African armyworm and locusts are mostly associated with vegetation development following rains after extended periods of drought (Janssen, 1993; Lecog & Sukirno, 1999; White, 1976). The desert locust plague of 1986-89 occurred after the drought of 1983-1985 in Africa (Hare, 1987; Gruys, 1994).

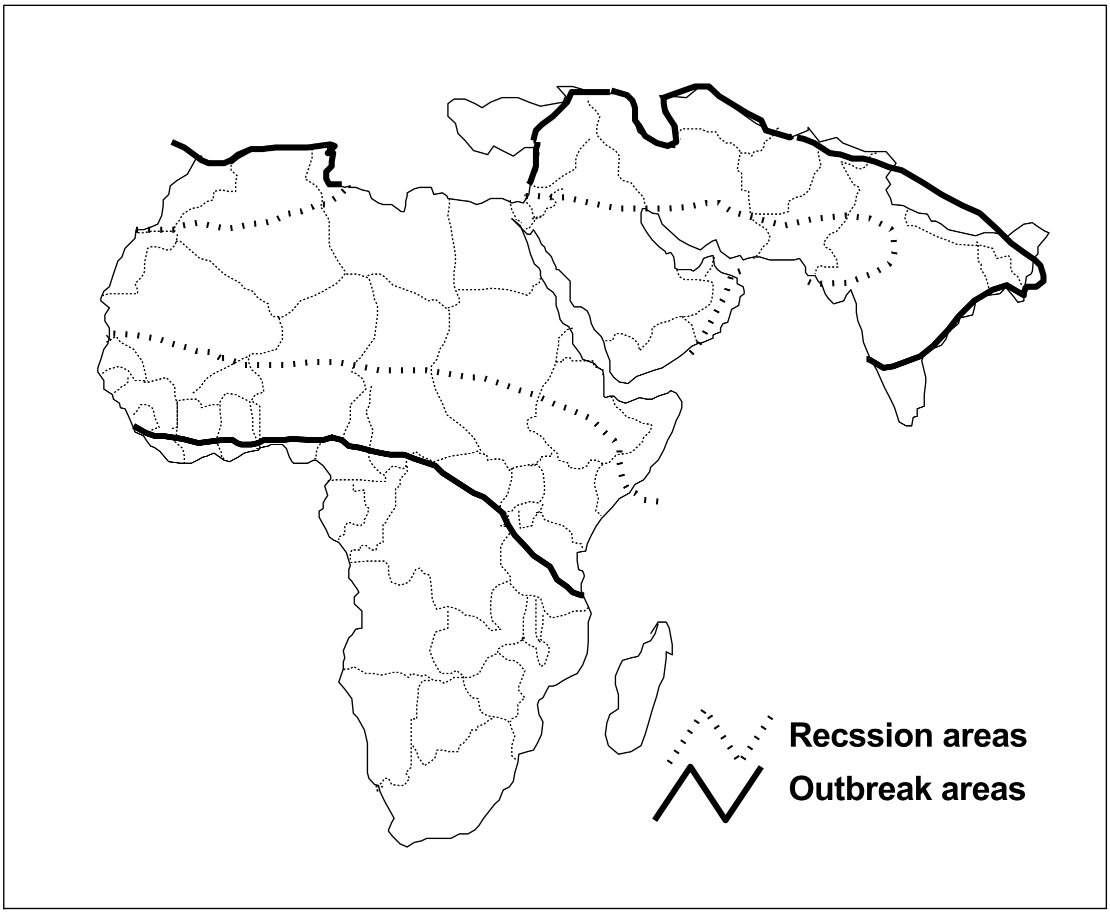

Fig. 1. Map showing extent of recession and invasion areas of desert locust.

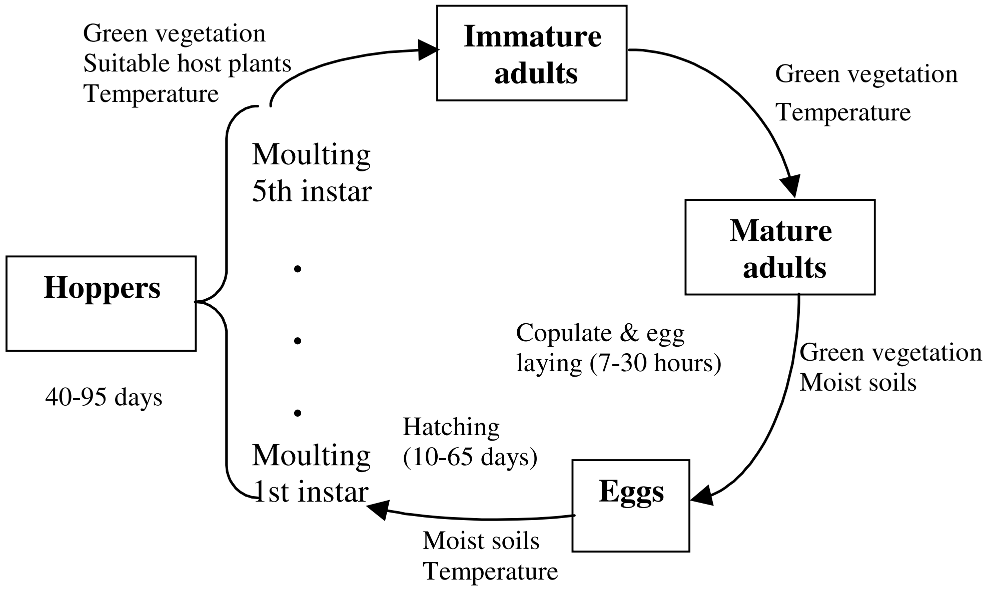

Fig. 2. Life cycle of the desert locust and relationships with major habitat factors for successful development and survival.

Relationship between desert locust biology and habitat factors

Desert locusts live three to five months depending on weather and habitat factors. The life cycle comprises three stages: egg, hopper (or nymph) and adult (Fig. 2). The relationship between the life cycle and environmental factors such as soil moisture, temperature and presence of suitable host plants are reviewed.

The egg stage. The female lays eggs in batches known as egg pods. Egg pods are deposited into bare, moist soil, 5-10 cm below the surface (Uvarov, 1977). A female usually lays about three egg pods in the field (e.g., Popov, 1958) and four to nine pods in the laboratory (Norris, 1952; Hunter Jones, 1958). A gregarious female lays up to 80 eggs per pod whereas a solitarious female lays 95 to 158 eggs. In the absence of suitable egg deposition sites (e.g., moist and non-salty soils), abnormal egg laying on the surface of the soil and on herbage has been reported in East Africa, Middle East and Asia (Lal, 1941; Popov, 1954; Uvarov, 1977). Deposited eggs develop and hatch in 10-65 days depending on temperature and soil moisture (Pedgley, 1981). In the desert, eggs develop and hatch successfully when there is enough moisture in the soil, whereas insufficient moisture may arrest egg development (Brown, 1947; Shulov, 1952, Shulov & Pener, 1963). Cases of widespread desiccation of deposited eggs were reported in Somalia (Joyce, 1962) and Libya (Brown, 1947). Moreover, 10-40% egg loss due to predation and parasitism has been reported (Joyce, 1962; Greathead, 1966).

The hopper stage. The emerging hoppers develop into five stages in the gregarious phase and into five or six stages in the solitary phase frequently over a period of 40-50 days and up to 95 days, depending on the ambient temperature (Wardhaugh *et al.*, 1969), and the quality of the host plant (Pedgley, 1981).

In the field, about 40 to 76% of the emerged hoppers die before they reach the adult stage (Greathead, 1966; Roffey & Stower, 1983). Hopper mortality is most likely related to habitat conditions such as presence of suitable host plants, cannibalism and predation. Hopper mortality due to predation has been recorded at the Red Sea coast (Greathead, 1966), in eastern Ethiopia and Somalia (Ashall & Ellis, 1962), and in West Africa (Wilps, 1997). The predators reported include birds (such as the wheatear *Oenanthe isabellina isabellina* and the desert sparrow *Passer simplex sahare*), jackals, rodents, reptiles and arthropods. Mortality due to predation is sometimes very high and can hasten the decline of small populations or delay upsurges in desert locust breeding areas such as the Red Sea coast (Greathead, 1966; Stower & Greathead, 1969).

Food shortage in a habitat due to inadequate rainfall was reported as the main cause of hopper mortality and failure of a generation in Rajasthan in 1968 (Bennett, 1976), and in Somalia in late 1955 (Pedgley, 1981). Similar results were reported for the Australian plague locust (*Chortoicetes terminifera*) nymphs from Australia (Bernays & Chapman, 1973). Suitability of host plants is also an important factor for hopper survival. For example, feeding on different host plants in the laboratory caused a variation in hopper mortality between 10 to 95% in solitarious and gregarious hoppers of the desert locust (Tawfik *et al.*, 1972; Abdel Rahman, 1999), and from zero to 92% in the grasshopper *Melanoplus mexicanus mexicanus* (Sanderson, 1939). Mortality of grasshoppers was greater when grasshoppers were fed on C_4 plants than when they were fed on C_3 plants (Caswell & Reed, 1976). This was attributed to differences in more readily available and higher protein content in C_3 plants than in C_4 plants (Caswell & Reed, 1976; Boutton *et al.*, 1978).

Desert locust hoppers fed exclusively on *Heliotropium pterocarpium* and *Dipterygium glaucum* in field cages on the Red Sea coast of Eritrea appeared to thrive well, but others fed on *Zygophyllum simplex* died in large numbers and showed a high degree of cannibalism (Waloff, 1963). Hopper mortality in a field due to cannibalism was as high as 30 to 50% in Ethiopia (Ashall & Ellis, 1962), and up to 50% in the laboratory in India (Husain *et al.*, 1946; Bahitia, 1961). In the above reports, cannibalism in desert locust hoppers was observed in the presence of fresh vegetation. Uvarov (1931) linked cannibalism with shortage of water, whereas Husain *et al.* (1946) attributed it largely to lack of suitable food in a habitat. Cannibalism is also common in other Acrididae such as grasshoppers (e.g., Lockwood, 1989), the Australian plague locust (Farrow, 1982) and other herbivores especially those known for their preference for nitrogen rich plants (McNeill & Southwood, 1978; Mattson, 1980; White, 1993). For instance, Mattson (1980) suggested that herbivores could obtain high quality diet by resorting at least occasionally to cannibalism. Despite the frequent observations of cannibalism in the field and the laboratory, the relationship between the occurrence of cannibalism in hoppers and habitat factors remains elusive.

The adult stage. After the fifth or sixth instar, hoppers become fledglings or immature adults. In suitable habitats, adults, in general, mature in about three weeks although this process can take as long as eight weeks (Pedgley, 1981). In unsuitable habitats, immature adults can survive six months or longer. There is no clear information on habitat factors that delay or enhance maturation of the desert locust. Bodenheimer (1932; cf Rao, 1942) suggested that fresh succulent vegetation growing after rainfall might exert a powerful influence in enhancing the sexual maturation of the desert locust. In the Mekran areas of Indian, cage tests indicate that cultivated crops such as sorghum and maize, and wild plants such as *Heliotropium undulatum*, *Tribulus* sp., *Indigofera cordifolia* and *Sericostoma pauciflorum* increase the development rate and shorten the number of days to egg deposition and appearance of yellow hind wings (Rao, 1942). In the laboratory, hoppers reared on some host plants notably millet, *Heliotropium* and *Tribulus*, matured faster than those reared on other natural host plants at the Red Sea coast of Sudan (Abdel Rahman, 1999).

A locust is considered mature when it starts egg laying. Fecundity in desert locust varies as a function of population density and quality and availability of the host plant (Ashall & Ellis, 1962; Samah *et al.*, 1972; Abdel Rahman, 1999). Ashall & Ellis (1962) reported a significant drop in egg production from 74 to 59 per pod during field surveys under reduced green herbage availability in the arid areas of East Africa. Similar results were reported in the grasshopper *Austroicetes cruciata* Saussure in Australia (Andrewartha, 1944) and *Zonocerus variegatus* (L.) in Nigeria (Chapman *et al.*, 1979). Female fecundity varied when females were fed on different host plants (Ibrahim *et al.*, 1972; Abdel Rahman, 1999) and similar results were reported in the grasshopper *Melanoplus differentialis* (Thors.) (Sanderson, 1939) in the laboratory.

Spatial pattern of the desert locust distribution and its habitat

At the scale of seasonal breeding, egg deposition sites are largely confined to the moist and sandy cultivated wadies (e.g., Popov, 1958; Stower *et al.*, 1958). For instance, aggregated egg deposition, as high as 640-880 m^{-2} resulting from a single mass egg deposit, were found in wadi beds where moisture is accessible, while at the same time no egg pods were found in surrounding dry sands in East Africa (Popov, 1958). At micro scale or within the cultivated wadies, egg deposition is associated with the sandier part of the cultivated field in the Red Sea coast (Maxwell-Darling, 1936, 1937; Stower *et al.*, 1958; Waloff, 1963; Popov & Zeller, 1963).

A few researchers noted a relationship between the occurrence of both solitarious and gregarious hoppers, and millet and *Heliotropium* species along the Red Sea coasts of Eritrea, Saudi-Arabia and Sudan (Maxwell-Darling, 1936, 1937; Stower *et al.*, 1958; Stower & Greathead, 1969; Roffey & Stower, 1983). Association of desert locust hoppers with specific host plants such as *Heliotropium* and *Tribulus* were reported from Mauritania (Culmsee, 2002) and India (Chandra, 1984b). The distribution of gregarizing desert locust hoppers associated with *Tribulus* and *Schouwia* plants were reported from the Tamesna in Niger (Roffey & Popov, 1968). These reports are based on traverse notes and it is difficult to draw conclusions on the spatial relationship between hopper distribution and habitat factors.

Desert locust breeding in the Central Region

The habitat

In desert locust surveys, the locust breeding regions are classified into the East (southwest Asia), the West (West Africa) and the Central Region (Waloff, 1966). The Central Region consists of countries around the Gulf of Aden and the Red Sea. These countries are Djibouti, Egypt, Eritrea, Ethiopia, Oman, Saudi Arabia, Somalia, Sudan and Yemen. The arid and semi-arid areas of the Central Region share ecological characteristics. Potential evapotranspiration is less than rainfall in most of the months (Satakopan, 1965**;** Bruggeman, 1997). Rainfall at the coast occurs during the winter (November-January). Rainfall is erratic and scanty (averaging between 50 and 200 mm annually) with a variation coefficient of 50-70% (Satakopan, 1965; Bruggeman, 1997). The coastal landform of the Central Region, particularly the Red Sea coasts of Eritrea, Sudan, Saudi Arabia and Yemen is relatively similar. Within the Central Region, the best desert locust breeding habitats are at the coasts during the winter (November-January) and in the interior during the summer (June-August).

Desert locust survey and control in the Central Region

Desert locust populations are monitored using ground surveys in green habitats. Initially, a farmer was responsible to monitor and defend his crop from desert locust invasion. Due to the inability of a farmer to monitor and defend his crop, the responsibility shifted to governments and regional organizations (Magor, 1994; Cressman, 1996b). Regional organizations have been established to account for the supra-national scale of the locust problem, e.g., for the Central Region, it is the Desert Locust Control Organization for Eastern Africa (DLCO - EA) (Cressman, 1996b). In survey and control, the Desert Locust Information Service (DLIS) of FAO assists all locust-affected countries.

The strategy of desert locust control is to prevent the formation of hopper bands and swarms (Cressman, 1996a, b). This requires regular monitoring of locust breeding areas and the ability to quickly mount small scale control operations. Currently, most of the Central Region countries maintain regular survey programmes for monitoring the desert locust and other migratory pests.

Practically, desert locust surveys consist of three steps: (1) identification of a green habitat or a habitat with recent rainfall occurrence; (2) assessment whether the area is infested with locusts; and (3) search for locust infestations to control (FAO, 1994). Information on the green habitats is obtained from informers such as nomads and extension workers, and using aerial surveys or remote sensing imagery (Cressman, 1996a). The second step in the survey is assessment using ground teams. Assessment survey is guided by experience, the history of the sites with locust occurrence or recent reports. The purpose of the assessment survey is to identify green areas where locusts are likely to be found, and to determine whether locusts are present. Traverse notes of locust presence or estimates of locust densities at a survey stop can be used to identify those areas with a significant number of locusts. Once the area is identified, the third step in the survey is to estimate within the target areas the geographical extent and size of the infestations. From this information, the level and spatial extent of required control can be determined. Information from the three steps of survey is assumed to provide a picture of the overall locust situation in the green habitat (FAO, 1994; Cressman, 1996a). Once the infested area is identified and marked, a decision will follow how to control locusts using insecticides applied by a knapsack sprayer, car mounted sprayer or spray aircraft (Symmons & van Huis, 1997; van Huis, 1994).

Migration and herbivory

Green vegetation might be available at the coast during the rainy winter season and in the hinterlands during the summer season. Within each breeding habitat, spatial variation in land use (crop or grazing), soil texture and moisture, and species composition and cover abundance exist (El-Demerdash *et al.*, 1995; Popov & Zeller, 1963; Hemming, 1961; Vesey-Fitzgerald, 1955; Kassas, 1957; Maxwell-Darling, 1936). Herbivory differs spatially, following the presence of suitable herbs for grazing (McNaughton, 1988).

Bashir *et al.* (1998) found that on the coastal plain of Sudan, herbs and bushes, which are a valuable source of forage to livestock, took three years to recover after they had been eaten by desert locust hopper bands. During recessions, defoliation by solitarious locusts of herbs, bushes, crops, and pressure on primary productivity of the desert plants and competition with other herbivores is less conspicuous. During outbreaks or plagues, the impact on primary productivity and competition for host plants with other herbivores is extremely severe. During both recessions and outbreaks, locusts were reported to selectively forage on cultivated crops (Maxwell-Darling, 1936, 1937; Uvarov, 1957), and on valuable forage herbs such as *Heliotropium* and *Crotolaria microphylla* (Bashir *et al.*, 1998; Culmsee, 2002).

History of desert locust breeding in the Central Region

Several authors identified the Red Sea coast as a center of desert locust outbreaks (Johnson, 1926; Maxwell-Daring, 1936; 1937; Waloff, 1966). The 1986-89 plague of desert locust initially originated from the Red Sea coast (Walsh, 1988; Showler & Potter, 1991; Gruys, 1994). This plague incurred over US$ 300 million and about 26 million ha were sprayed (PANOS, 1993). The 1992-94 upsurges also originated from this region (Showler, 1995). The control of this upsurge cost about US$ 19 million and about 4 million ha were sprayed. Similar breeding trends were observed in the 1997 upsurge.

The Central Region is also a source of invasion to the other Sahelian, Persian Gulf, West African and Southwest Asian countries. Therefore, the FAO, the locust-affected countries and the international donor community started a project for developing a system for early intervention against desert locusts to be located in the Central Region (Showler, 1995). The desert locust project is part of the Emergency Prevention System (EMPRES) of FAO and initially concentrated their activities in countries around the Red Sea and Gulf of Aden. The research part of the project aimed at improving the desert locust survey operations and control strategies. The results of this thesis are a collaborative work between Wageningen University, The Netherlands, EMPRES/FAO and the Plant Protection Department of Sudan.

Desert locust breeding in the Sudanese Red Sea coast

The Sudanese Red Sea coast includes the coastal plain and the Red Sea Hills parallel to the Red Sea coast from Halaib (near Egyptian border) through northeastern Sudan into Eritrea. The Hills mark the boundary between the summer and winter breeding habitats of the desert locust. The winter desert locust breeding area covers 147, 200 km^2 along the Red Sea coast (El-Tom, 1994). In this area, the Beja and Rashida nomadic tribes rear livestock mainly camel, goats and sheep.

The Hills consists of mainly bare rocks, with vegetation growth in valleys, whilst the inland and the coastal plain are covered with sand. Between the Hills and the sea, there is a gradient in differentiation of plant community between diffuse natural vegetation near the foothills and cultivated crops at the outflow of the wadies (Maxwell-Darling, 1936; Kassas, 1957). The favorable sites are situated mostly at the outflow deltas. Nomads may construct earth dams across the dry riverbeds or wadies to store the floodwater, which they use to water their crops. These crops are millet (*Pennisetum typhoideum* Rich.) and sorghum (*Sorghum bicolor* L.), watermelon and other vegetables. Cultivated sites have been reported as breeding habitats of the desert locust (Maxwell-Darling, 1936, 1937; Stower *et al.*, 1958; Stower & Greathead, 1969), but available evidence is circumstantial.

Problem description

Despite the efforts of national, regional and international organizations to prevent outbreaks, occurrences of upsurges and plagues are still prevalent. So far, the outbreak of desert locust populations cannot reliably be predicted. The only means of monitoring desert locust population build up in the vast recession habitat is ground survey. Ground survey is guided by the recent occurrences of rainfall or green vegetation. However, ground survey teams have insufficient time to assess all green habitats. Therefore, desert locust outbreaks often go undetected. This led to the 1986-89 plague and 1992-94 and 1996-97 upsurges at the Red Sea coast. An improvement in the current ground survey operations of desert locust would reduce the threat of the desert locust to crops and pastures.

Aim and outline of the thesis

The main aim of this study was to establish spatial relationships between habitats and solitarious desert locust populations. This would enable to better target survey and control operations. This can be done by (1) characterizing the spatial association of locust density with habitat variables (soil texture, soil moisture, and plant community composition); (2) modelling the spatial pattern of locust distribution and estimate locust density in unvisited sites; and (3) searching for biological reasons for the spatial pattern of locusts, looking particularly at host plant quality. This study was carried out on the coastal plain of Sudan, a recession habitat of desert locust.

Chapter 2. Plant communities of the 20 × 120 km study area are defined based on cover abundance of individual plant species and sites with similar plant composition are separated. The relationship of plant community composition and habitat factors are quantified using multivariate analysis. The spatial extents of these plant communities are demarcated and mapped.

Chapter 3. The relationship between the density of adult desert locust and habitat factors, including plant community composition, is quantified using multivariate analysis. The spatial distribution of desert locust and plant community was displayed and mapped using data from 5 × 5 km and 1 × 2 km grids. The association of desert locust and plant community during the study period was quantified and the spatial extent of locust habitats was defined.

Chapter 4. The spatial distribution of locust breeding sites as ascertained by probing, egg deposition and the occurrence of hoppers were described and mapped in association with plant communities. The spatial relationship of both solitarious and gregarious hopper densities and host plants, and cover abundance of *Heliotropium arbainense* were quantified. Locust breeding sites were defined.

Chapter 5. The spatial correlation structure of adult locust distribution was described using variogram functions and using this information, locust densities in unsampled sites were estimated by kriging and cross validation. The relationship between sampling intensity and kriging variance was established to optimize sampling.

Chapter 6. The biological reasons why desert locust distribution is associated with certain plant communities but not with others are enumerated. The hypothesis is that locusts are concentrated in habitats with elevated levels of nitrogen in their food plants.

Chapter 7. A study of life table statistics was made to establish a relationship between the fitness parameters of the desert locust and the nitrogen content of the host plant millet.

Chapter 8. In the general discussion and summary, I first review the most important results from the studies described in the previous chapters. The findings were compared with past reports and ecological implications and its significance to improve the desert locust survey and control operations are discussed. Finally, I suggest directions of future research to further improve the desert locust survey and control operations.

Chapter 2

Description of plant communities on the Red Sea coastal plain of Sudan

Gebremedhin Woldewahid, Wopke van der Werf, Arnold van Huis, Tsedeke Abate, Bashir Mostofa & Karle Sykora, 2004. Description of plant communities on the Red Sea coastal plain of Sudan. submitted.

Chapter 2

Description of plant communities on the Red Sea coastal plain of Sudan

Abstract

Plant communities on the coastal plain of Sudan, between Port Sudan and Tokar, are quantitatively described, analysed and mapped. Data were collected at 60-64 sample sites, arranged in a 5 × 5 km grid in a 120 km stretch of coastal plain in 1999, 2000 and 2001. Four plant communities were distinguished by two-way indicator species analysis. They are named by the dominant plant species: *Suaeda monoica* Forssk., *Heliotropium* spp., *Panicum turgidum* Forssk., and *Acacia tortilis* (Forssk.) Hayne. The spatial extent of these plant communities during the rainy season is described. Correlation between plant community and soil particle size, moisture availability, grazing pressure and elevation are characterized by principal component analysis.

Key words: Plant community, classification, environmental variables, Red Sea coast.

Introduction

Knowledge of plant communities and their associated environmental factors is a prerequisite for defining habitats suitable for herbivores such as the desert locust (*Schistocerca gregaria* Forsk.) (Popov & Zeller, 1963; Launois & Lecoq, 1990; Popov *et al*., 1991). The Red Sea coastal plains are a well-known breeding area for the desert locust but some parts of the plain are probably more suitable than others (Maxwell-Darling, 1936; Pedgley, 1981).

Little quantitative or spatially referenced information is available on plant communities along the Red Sea coast. Kassas (1957) listed eight plant community types related to ‘salt marshes’ and six to ‘desert plain ecosystems’ along the northern coast of Sudan. The vegetation of the northern Eritrean coast has been described based on geomorphological classification with pedological subdivisions (Hemming, 1961). Vesey-Fitzgerald (1955, 1957) described the ecology of the Red Sea coast of Saudi Arabia under the two main categories of ‘the coastal plain’ and ‘the beach vegetation’ while he classified the more inland types as ‘the mountain’ and ‘the drainage system’. In the above studies, the sites are first classified based on geomorphology, pedology or physiographic features of the area and then the plant species associated to these sites were described and named as plant communities. More recently, eight major plant communities were quantitatively described on the Tihamah coastal plain of Saudi Arabia in relation to edaphic factors using ‘important values’ of the perennial plants to delineate communities (El-Demerdash *et al.*, 1995). This approach ignores annual plants, which represent 50 to 60% of the desert vegetation during the rainy season (Kassas, 1964). Therefore, a classification based on perennials may overlook aspects that are important for locust ecology, especially as most of the food plants are annuals (Pedgley, 1981).

As part of a study on the spatial distribution of desert locust on the coastal plain of Sudan, and its relationship with habitat factors, especially food plants, we needed information on plant communities and their distribution. The previous studies did not provide this information as the description and classification was based on geomorphology or physiography of the sites rather than on abundance of plant species. Moreover, previous studies underemphasized annual plants and they did not result in maps that might be used in studies of locust distribution. The objective of the work described in this chapter is (1) to identify and describe plant communities on the coastal plain of Sudan; (2) to map these communities to provide a tool for survey of desert locusts; and (3) to characterize the interrelationships between plant communities, soil particle size, moisture availability, grazing pressure and elevation.

Materials and methods

Site description. The study was carried out in an approximately 120 km long stretch of Red Sea coast, between Port Sudan in the North and wadi Siterab in the South (Fig. 1). The coastal strip varies in width from 20-40 km, and in elevation from 0 m along the coast in the East, to 200 m in the West, where the bare rock faces of the Red Sea Hills rise steeply to an altitude of 800 to 1200 m above see level. The Red Sea Hills are largely bare and consist of Archean rocks (Kassas, 1957). Soil particle size in the plain varies from gravelly near the mountains to fine sand and silt towards the sea. The area is semi-arid with low and erratic rainfall (Satakopan, 1965). The warmest month is August with an average daily maximum of 41 °C and a minimum of 30 °C, while the coolest month is January, with an average daily maximum of 27 °C and a minimum of 20 °C. Most of the rain falls during the winter season, from October to January. In Port Sudan from 1985 through 2001, precipitation averaged 72 mm per winter, with a coefficient of variation of 73%. During this period, the lowest recorded seasonal rainfall was 3 mm (during the winter of 1998/1999) while the highest rainfall was 158 mm (during the winter of 1999/2000). Additional water on the coastal region is provided by run-off from the Red Sea Hills through the wadies, temporary riverbeds

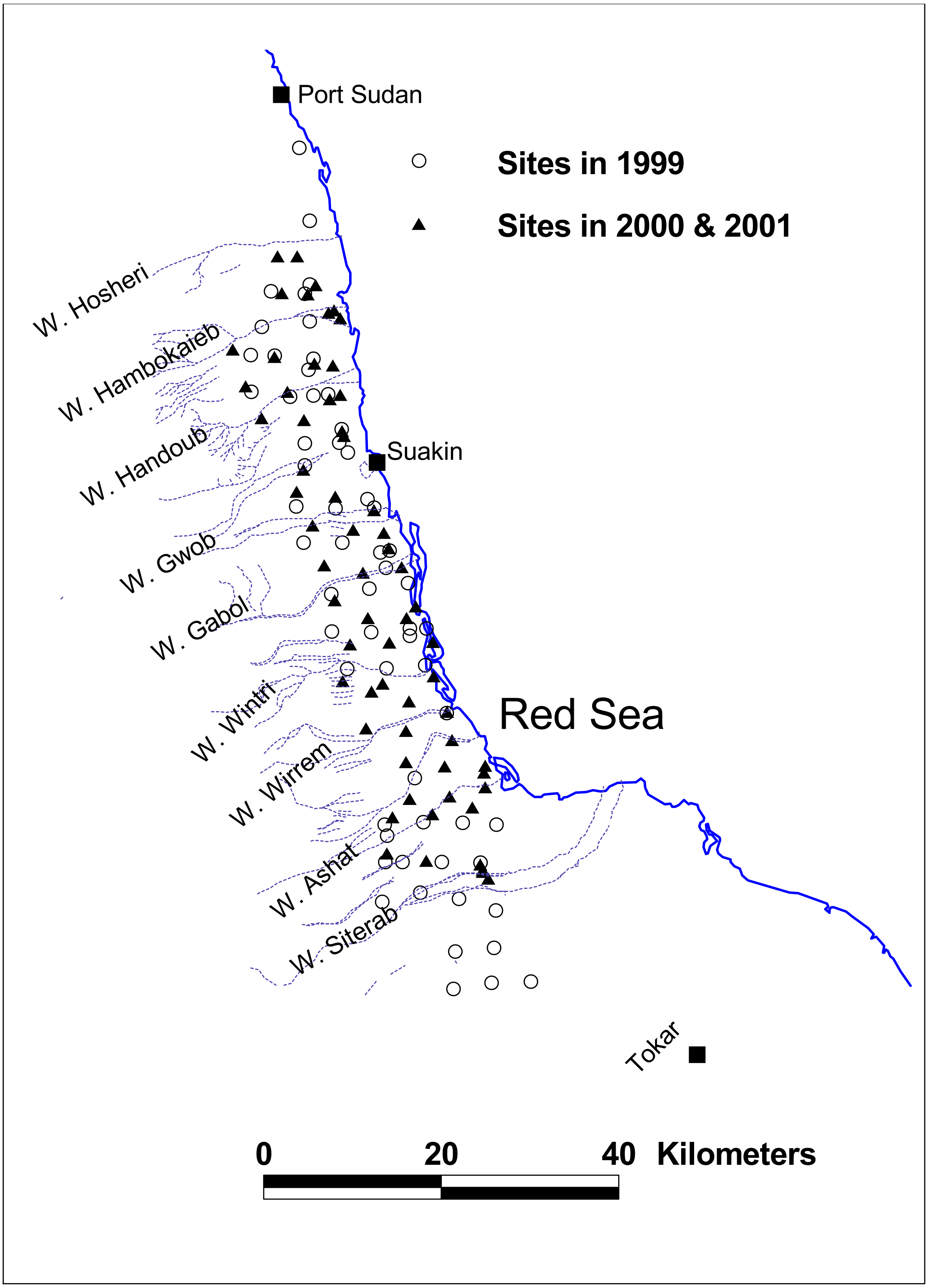

Fig. 1. Maps of the study area. Circles indicate sample sites in 1999 and triangles indicate sample sites in 2000 and 2001.

that drain much of their water in the lower course before reaching the Red Sea. The major wadies in the study area are Hosheri, Hambokaieb, Gwob, Gabol, Wirrem, Ashat and Siterab (Fig. 1). At the outflow of the wadies, soils are relatively fine and fertile. They support relatively lush vegetation growth. Therefore, nomads settle there during the winter, herding animals, mainly goats, sheep, camels, and cultivating crops.

Data collection. Vegetation and soil variables were estimated in an area of approximately 20 × 120 km using a 5 × 5 km grid for taking samples. The 1999 winter season, or simply 1999, refers to the period from November of 1999 to March 2000. The same terminology was used to describe the winters of 2000/2001 ('2000') and 2001/2002 ('2001'). During the winters of 1999, 2000 and 2001, rainfall was measured in the Port Sudan meteorological station.

Vegetation sampling. Cover abundance of all species present was scored at 60 sample sites in triplicate on 15**,** 22 and 29 December 1999 (Fig. 1). The following winter season, cover abundance was scored at 64 sample sites on 11 December 2000, and on 15 January and 6 February 2001 (Fig. 1). From 11 to 14 February 2002, cover abundance was scored at exactly the same sample sites as in the winter of 2000/2001. Cover abundance was scored using a modified version of the Braun-Blanquet 1-9 point scale (Appendix 1, van der Maarel, 1979). In 1999, cover abundance was scored on the whole of a 1 × 400 m transect per sample site whereas in 2000 and 2001, cover abundance was estimated in three 10 × 10 m plots, located at 50, 200 and 350 m along a 400 m transect. At each sample site, transects and plots were selected to represent relatively homogeneous vegetation. Transition zones were avoided. Plant species were identified using descriptions given by Collenette (1985) and Migahid (1996). Before analysis, cover abundance scores in the three plots per transect were averaged.

Soil sampling. In 1999 and 2000, particle size at each sample site was assessed using the 'feel' method (Brady, 1990). In 2001, however, at each sample site three 10 × 10 m plots were selected adjacent to the 'vegetation plots', and five soil samples from the top 15 cm were taken in each of them with a 7.6 cm diameter Auger. The five samples per plot were pooled to produce a 1-2 kg composite sample. The samples were thoroughly mixed, oven-dried at 100 °C for 48 h and then dry-sieved. The gravel fraction was estimated from 0.5 kg of the pooled soil sample using a 2.00 mm sieve. The size of the other particle size classes was estimated from a 50 g subsample, using four stacked sieves with mesh sieve size decreasing from the top to the bottom. The resulting particle fractions were classified as gravel (> 2.00 mm), coarse sand (> 0.420 mm), medium sand (> 0.210 mm), fine sand (> 0.105 mm), very fine sand (> 0.053) and silt + clay (< 0.053 mm). Before analysis of results, particle size fractions in the three plots per transect were averaged. Soil compaction in the upper 10 cm of soil was measured using a hand penetrometer (Eijkelkamp Agrisearch Equipment, The Netherlands) based on five readings per vegetation plot (15 per sample site).

Moist soil profile. Presence of moist soil was recorded every 7-14 days at five locations at each sample site: 0, 100, 200, 300 and 400 m along the 400 m transect. Soil was scooped away with a hand shovel to check presence of moisture at 0-5, 5-10 and 10-15 cm depth using 'touch and feel'. The results were coded as 0 (no moisture), 1 (moisture at 10-15 cm), 2 (moisture at 5-15 cm), or 3 (moisture throughout). The median score of the five points checked per sample site was used in the analysis.

Grazing and elevation. Grazing pressure at each sample site was classified as (0) none, (1) slight (2) moderate or (3) heavy. The elevation of sample sites was recorded from GPS, Garmin 12XL.

Separation and characterization of plant communities. Data collected during peak vegetation cover in each season were used in the analysis; this concerns the vegetation samples collected on 29 December 1999, 15 January 2001 and 11-14 February 2002. Three data sets with 99 plant species and 60 relevés in 1999, 79 plant species and 64 relevés in 2000, and 73 plant species and 64 relevés in 2001 were used in these analyses. Relevés or sample sites and plant species were classified using two way indicator species analysis (TWINSPAN) (Hill, 1979) for each of the three data sets. Following the delineation of plant communities with TWINSPAN, the species with significant difference in cover abundance among the distinguished plant communities (Wilcoxon test; $p < 0.05$) were categorized according to degree of fidelity. Degrees of fidelity were calculated using the PC program CLUTAB (WAU, 1994). Five degrees of fidelity were used, following the criteria of Barkman (1989): **selective** (species found most frequently in a certain community, and also, but rarely, in other communities), **preferential** (species predominantly found in one community with greater vigour but also abundantly found in other plant communities), **indifferent** (species without a definite affinity for any particular community)**, accidental** (species that are rare in a community) and **stray** (species not belonging to the community). Species with a significant degree of fidelity characterize a plant community.

Mapping. The transitions between the four main plant communities occurring in the study area were delineated by driving a car between the natural boundaries of any two adjacent plant communities. Co-ordinates of 320 GPS readings were recorded to describe the boundaries of the communities. Data were processed with Arc View 3.2 to produce a plant community map.

Multivariate analysis. Principal component analysis (PCA) was used to determine the association between plant communities and environmental variables: soil particle size, soil moisture, grazing pressure, compaction and elevation (ter Braak & Loomans, 1987). Monte Carlo tests within canonical correspondence analysis (CCA) were used to determine significance of relations between species composition and environmental variables. The computer package CANOCO 4 (ter Braak & Šmilauer, 1998) was used for all PCA ordinations.

Results

Rainfall. Rainfall in Port Sudan measured 158 mm from October 1999 to 30 March 2000; 138 mm from 1 October 2000 to 30 March 2001; and 29 mm from 1 October 2001 to 30 March 2002 (Fig. 2). In each of the three seasons, most of the rain fell in December.

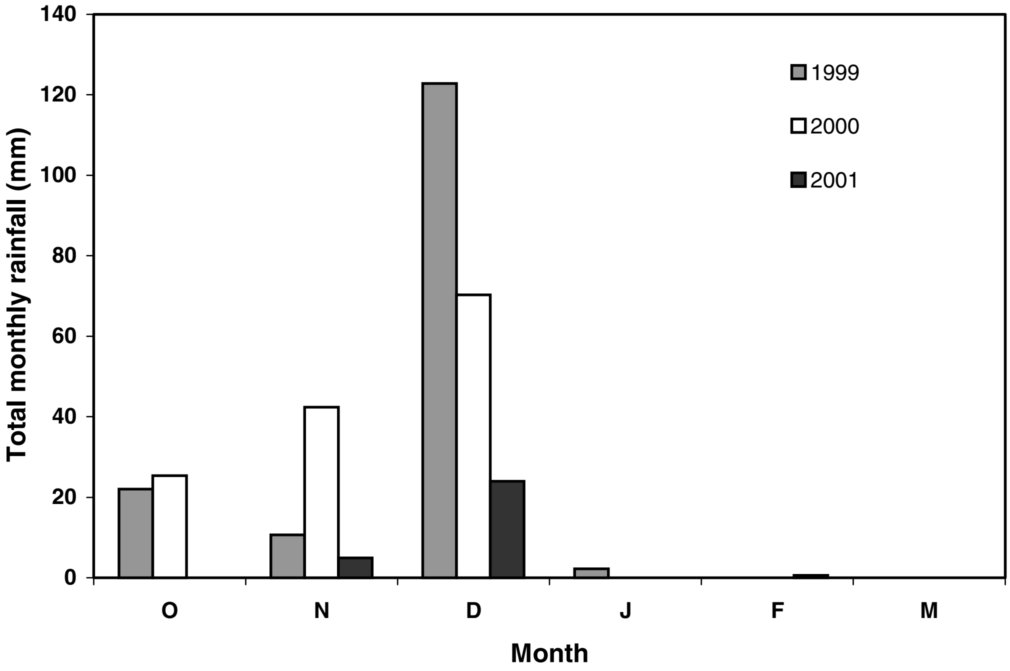

Fig. 2. Monthly total rainfall (mm) at Port Sudan during the winters of 1999, 2000 and 2001.

Vegetation classification. The classification of plant communities by TWINSPAN proceeded into two dichotomous steps. The first step distinguished between sites dominated by plant species of the ‘coastal’ area and those of the ‘foothills’ (Fig. 3). (Note that the classification of relevés is made on the basis of an objective analysis of species cover abundance and association.) In the second step, those sites with predominantly coastal plant species were further separated into those on saline soils near the Red Sea, (*Suaeda*) and those on non-saline soils at wadi outflows (*Heliotropium*). The foothill sites were further separated into grassland plain (*Panicum*) and scrub (*Acacia*) sites. We propose the selective or preferential species *Suaeda monoica*, *Heliotropium* spp., *Panicum turgidum* and *Acacia tortilis*, to name the resulting four plant communities.

***Suaeda monoica* plant community.** The community was dominated by three preferential species: *S. monoica* (12% cover), *Citrullus colocynthis* (L.) Schrad (< 5%) and *Euphorbia* spp. (Table 1). The succulent shrub *S. monoica* was the dominant plant species, with low cover of other plant species. ‘Indifferent’ scattered plant species such as *Halopeplis perfoliata* (Forssk.) Bunge ex Schweinf., and *Aeluropus lagopoides* (L.) Trin. ex Thw., were found in association with *S. monoica* (see Appendices 2 and 3).

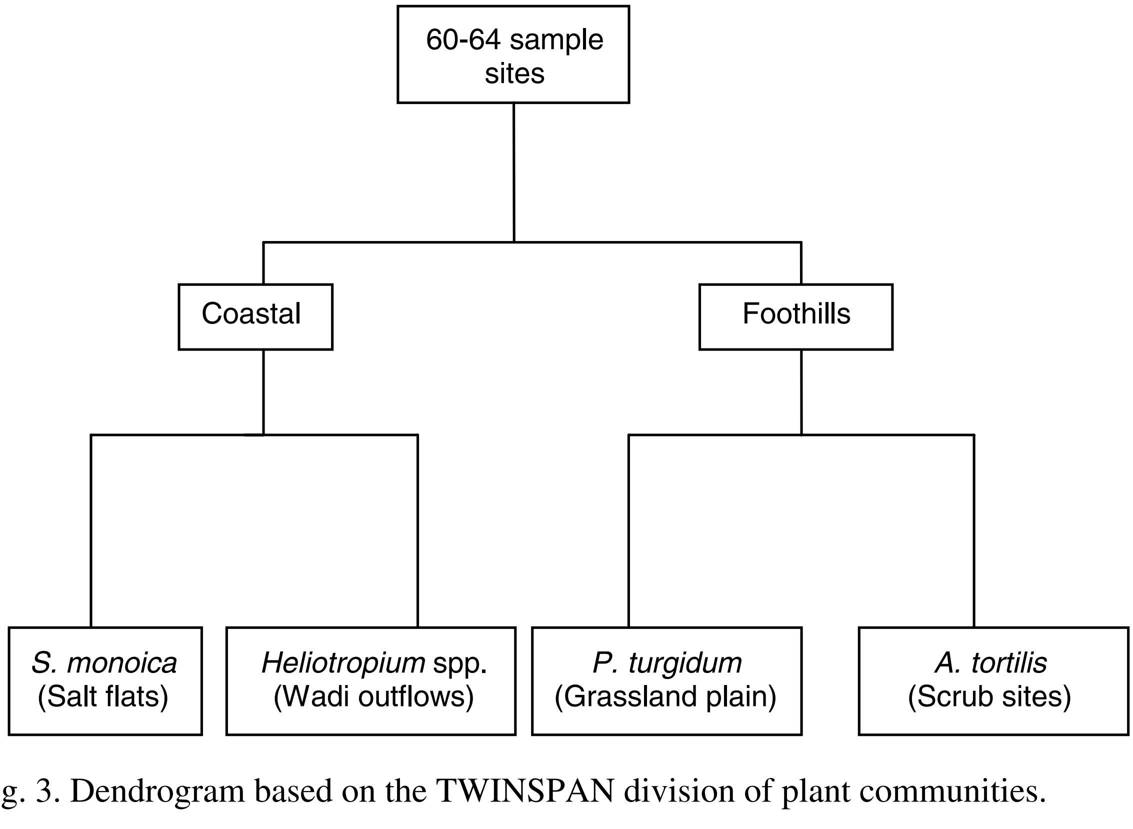

Fig. 3. Dendrogram based on the TWINSPAN division of plant communities.

Table 1. Degrees of fidelity (Barkman, 1989) of plant species to four plant communities: *S. monoica* (A), *Heliotropium* spp. (B), *P. turgidum* (C) and *A. tortilis* (D) in the 1999 winter season.

Group	A	B	C	D
Number of samples:	10	13	19	18
Suaeda monoica	+			
Citrullus colocynthis	+			--
Euphorbia aegyptiaca	+			
Euphorbia sp.	+			
Leptadenia pyrotechnica	--			
Heliotropium spp.		+		
Amaranthus graecizans		+		
Portulaca oleracea		+		
Ricinus communis		++		
Pennisetum typhoideum		++		
Sorghum bicolor		++		
Sorghum halepense		++		
Medicago sp.		++		
Amaranthus spinosus		++		
Trianthema sp.		++		
Cucumis melo		++		
Datura innoxia		++		
Chenopodium murale		++		
Schouwia purpurea		++		
Phaseolus vulgaris		++		
Dipterygium glaucum		++		
Sesamum indicum		++		
Sesbania sp.		++		
Cicer sp.		++		
Fumaria parviflora		++		
Hypoestes forsskalei		++		
Capparis decidua			+	--
Panicum turgidum			+	
Aerva javanica			--	
Salvadora persica				+
Lycium shawii				+
Ochradenus baccatus				+
Cyphostemma sp.				++
Tribulus terrestris				-
Echinochloa colona				-

++ = selective

+ = preferential

- = accidental

-- = stray

***Heliotropium* plant community.** The plant community was characterized by the preferential species *Heliotropium arbainense* (12-25% cover), *Amaranthus graecizans* L., *A. spinosus* L., and *Portulaca oleracea* L. (Tables 1 and 2). Other *Heliotropium* species, *viz. H. longiflorum* and *H. ovalifolium* were occasionally found, but records at the sample sites were made considering *Heliotropium* spp. as a group. *Heliotropium arbainense* was the most common species. Annual grasses such as *Pennisetum typhoideum* Rich. (cultivated millet) (25% cover), *Sorghum halepense* (L.) Pers., and *S. bicolor* (L.) Moench, and annual dicots such as *Medicago* sp., *Phaseolus* spp., and *Trianthema* spp., *Cucumis melo* L., *Ricinus communis* L., *Schouwia purpurea* Schweinf. and *Dipterygium glaucum* Decne. were selective to this community (Table 1).

***Panicum turgidum* plant community.** The community is characterized by the preferential species *P. turgidum* (5-12% cover) and *Capparis decidua* (Forssk.) Edgew (Tables 1 and 2). The community is often referred to as ‘Panicum plain’, or ‘Panicum grassland’. *P. turgidum* is a perennial tussock grass that is yellow during summer but produces green sprouts in the rainy season. *Salsola spinescens* Forssk., *Schoenfeldia gracilis* Kunth, *Argemone mexicana* L., and *Cenchrus ciliaris* L., were indifferent species for this plant community (see Appendices 3 and 4).

***Acacia tortilis* plant community.** The plant community was dominated by the widely spread perennial desert shrub *A. tortilis* (< 5% cover). This community consisted of a sparse, open scrub characterized by the preferential species *A. tortilis*, *Lycium shawii* Roem. et Schult., and *Salvadora persica* L. (Tables 1 and 2). *Ochradenus baccatus* Del., *Cyphostemma* sp., and *Cassia senna* L., *Indigofera spinosa* Forssk., were selective for this group.

Comparisons among seasons. The classification of species in 2000 was quite similar to that of 1999 (Table 2). Some differences occurred, possibly because of variation in moisture availability, grazing pressure and slight shifts in the location of some sample sites. For instance, *Eleusin*e spp. in 2000 was a preferential species to the *Heliotropium* community, and *C. ciliaris* to the *P. turgidum* community while these species were not selective to these respective communities in 1999. Similarly, *Rumex* sp. became preferential, while *Convolvulus* spp., and *Indigofera spinosa* became selective to the *A. tortilis* community. In 2001, the cover abundance of annuals was much lower and shorter alive than in 1999 and 2000, because of much lower rainfall. Nevertheless, the vegetation classification was essentially similar to that of 1999 and 2000 (Table 2). *Launaea capitata* (Spreng.) Dandy in 2001 became selective to the *Heliotropium* community and *Cassia senna* to the *A. tortilis* community.

Table 2. Degrees of fidelity (Barkman, 1989) of plant species to four plant communities: *S. monoica* (A), *Heliotropium* spp. (B), *P. turgidum* (C) and *A. tortilis* (D) in the 2000 and 2001 winter seasons.

Group	A	B	C	D
Number of samples:	16	17	17	14
2000				
Suaeda monoica	+			
Eleusine spp.	--	+		
Medicago sp.		+		
Pennisetum typhoideum		++		
Panicum turgidum			+	
Cyperus spp.		--	+	
Blepharis ciliaris			++	
Corchorus olitorius			++	
Zygophyllum simplex			-	
Acacia tortilis				+
Rumex sp.				+
Convolvulus spp.				++
Indigofera spinosa				++
Number of samples:	10	14	30	10
2001				
Heliotropium spp.		++		
Tephrosia spp.		++		
Medicago sp.		++		
Trianthema spp.		++		
Launaea capitata		++		
Eleusine spp.		++		
Salsola spinescens		--		
Lycium shawii				+
Acacia tortilis				++
Cassia senna				++

++ = selective

+ = preferential

\- = accidental

-- = stray

Variation of environmental variables in the plant communities. The soil particle size in the four plant communities varied from fine to coarse in the order *Heliotropium* - *S. monoica* - *P. turgidum* - *A. tortilis* (Fig. 4a). The soils in the *Heliotropium* community had the greatest fraction of fine and very fine sand (> 0.105 mm and > 0.053 mm, respectively) while they contained the smallest fraction of coarse sand (> 0.420 mm). Soils in the *A. tortilis* community had the greatest fraction of coarse sand and gravel (> 2 mm). Soils in the *S. monoica* and *P. turgidum* areas had intermediate particle size. Soil penetrability decreased, as soil particle size became coarser (Fig. 4b).

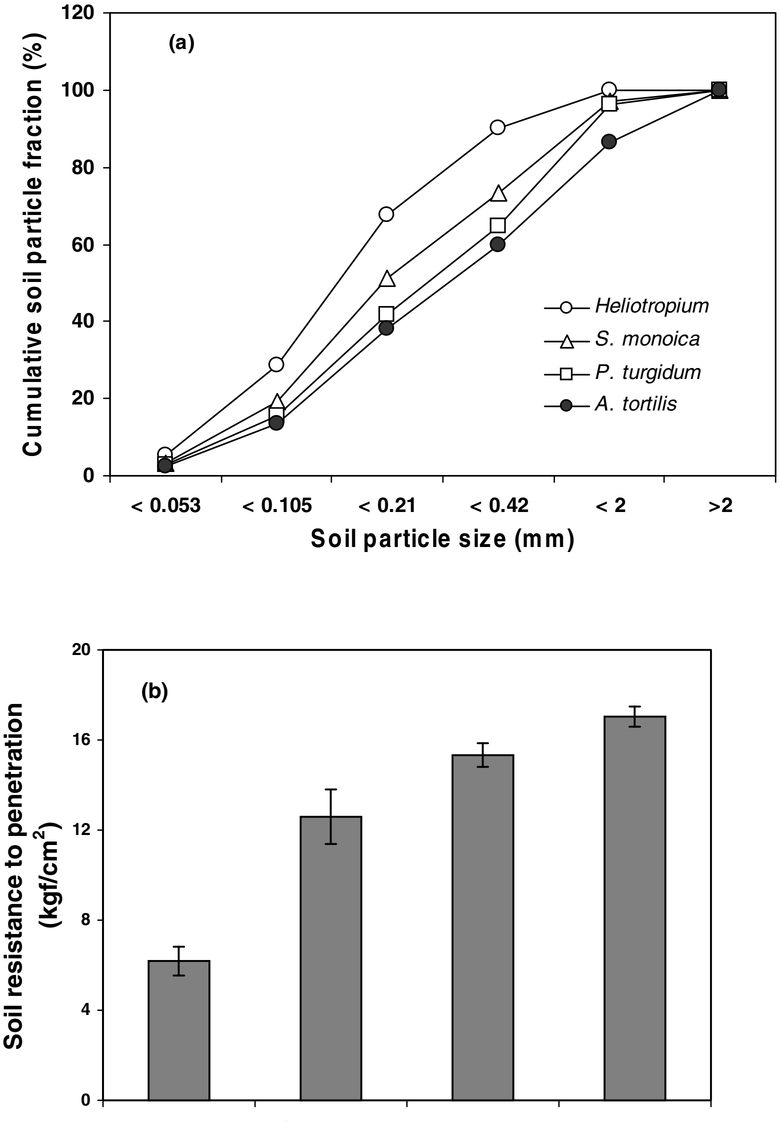

Fig. 4. Cumulative soil particle size distribution (%) (a) and soil resistance (kgf/cm^2) to penetration (b) in sites with different plant communities.

The highest scores for presence of soil moisture were found in the *Heliotropium* community in all three seasons (Figs. 5a, b and c). In the 1999 winter season, with reasonable rainfall (158 mm) the highest score (2.06) was in the *Heliotropium* community while the moisture score in *S. monoica* was lower (1.89) and still lower in *P. turgidum* and *A. tortilis* (both 1.78) (Fig. 5a). In 2000 with 138 mm rainfall, the median moisture score found in the *Heliotropium* plant community was lower than in 1999, but substantially higher than in the other communities (Fig. 5b). In 2001, rainfall (30 mm) was less than in 1999 and in 2000. Correspondingly, the moisture scores were low and the highest median score (0.50) for soil moisture was found in the *Heliotropium* community (Fig. 5c).

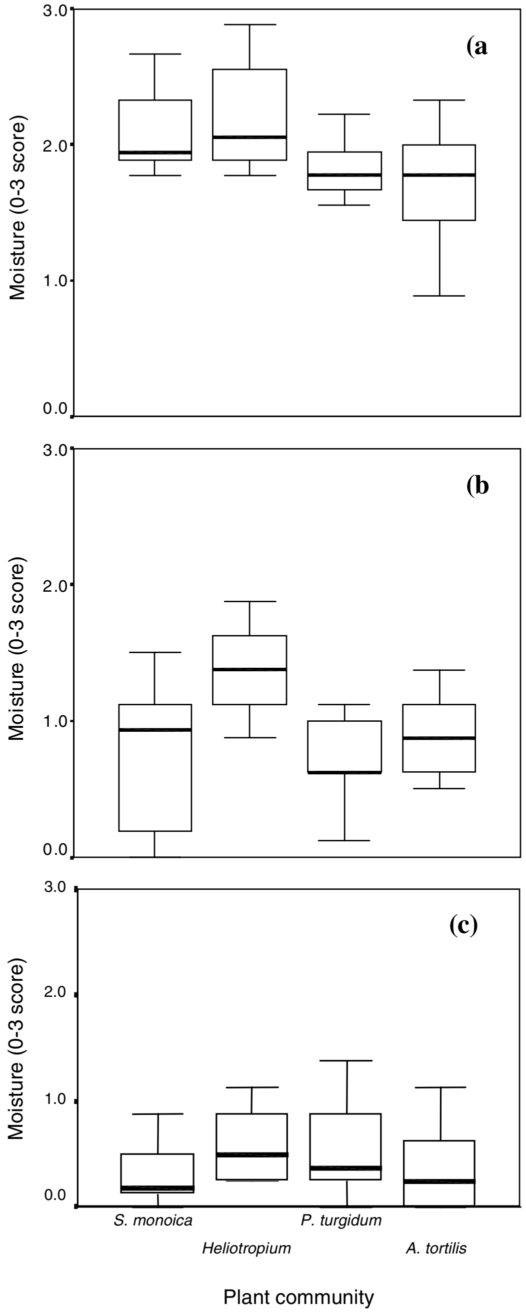

Fig. 5. Depth of moist soil in four plant communities in 1999 (a), 2000 (b) and 2001 (c). Scores indicate: (0) no moisture, (1) moisture at 10-15 cm, (2) moisture at 5-15 cm, (3) moisture at 0-15 cm. Box plot indicates 25, 50, and 75 percentile and whiskers indicate minimum and maximum values.

Grazing pressure varied among plant communities (Fig. 6). For instance in 1999 and 2000, the highest median scores (2.96 in 1999 and 2.89 in 2000) were found in the *P. turgidum* community, followed by the *S. monoica* and *A. tortilis* communities whereas grazing was virtually absent in the *Heliotropium* community (Figs. 6a and b). In the dry winter of 2001, the median score of grazing intensity was almost the same for all plant communities (Fig. 6c).

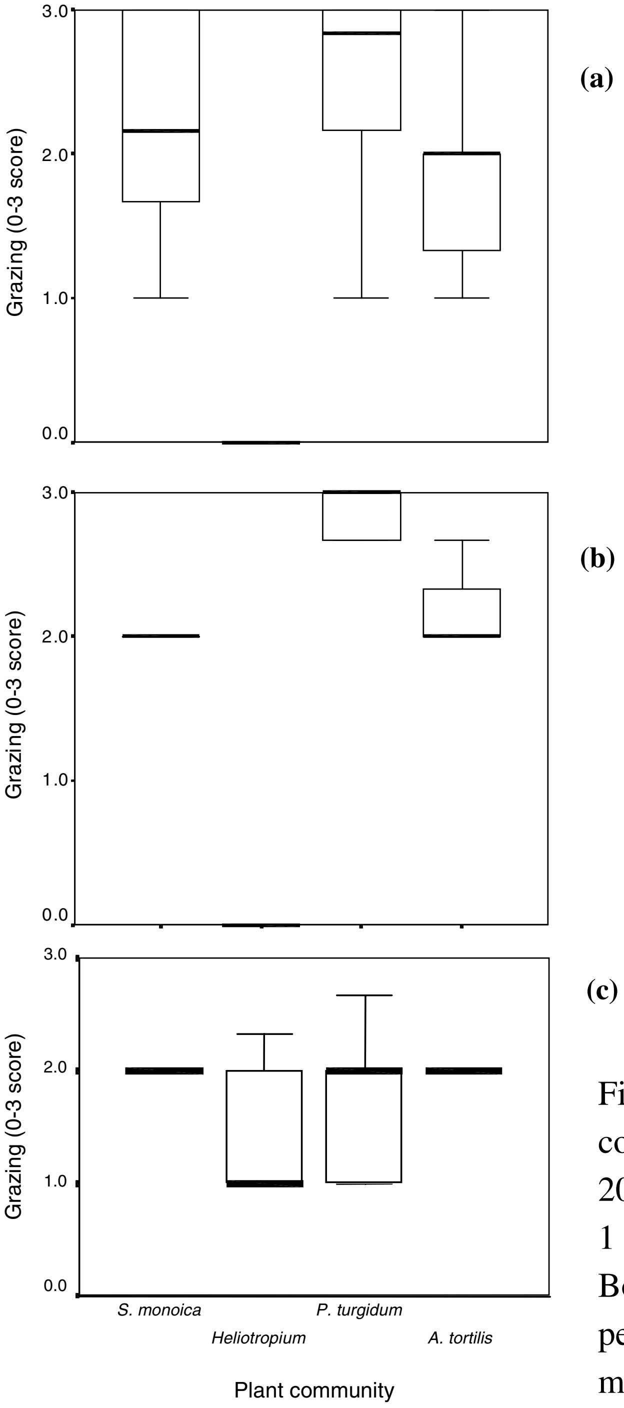

Fig. 6. Grazing pressure in four plant communities in 1999 (a), 2000 (b) and 2001 (c). Grazing scores are 0 = none, 1 = slight, 2 = moderate and 3 = heavy. Box plot indicates 25, 50, and 75 percentile and whiskers indicate minimum and maximum values.

Mapping. A map of the plant communities, based on GPS tracking of their border is provided in Fig. 7. The *A. tortilis* community covered the areas near the Red Sea Hills, bordered by areas of *P. turgidum* towards the Red Sea. *Heliotropium* areas were situated at the wadi outflows. They often border *P. turgidum* at all sides except the East, where salt tolerant *S. monoica* covered the areas nearest to the coast. A West to East zonation of communities was related to elevation: *A. tortilis* community occupied the highest elevations (117 ± 13 m) with *P. turgidum* at intermediate elevation (73 ± 7 m) and *Heliotropium* (33 ± 2 m) and *S. monoica* communities at the lowest elevations (37 ± 7 m).

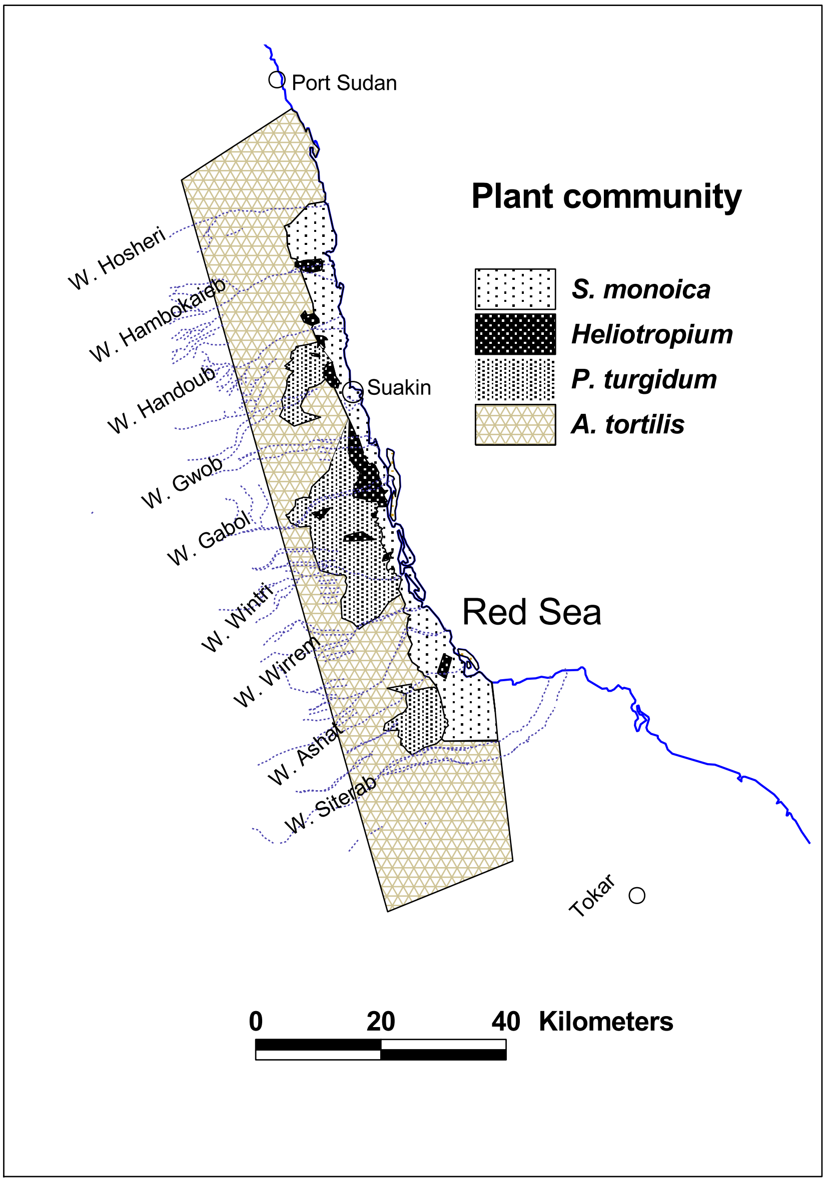

Fig. 7. Map showing the spatial distribution of plant communities in the study area on the coastal plain of eastern Sudan.

Table 3. Weighted correlation matrix of environmental variables with the first two PCA species axes, 1999-2001.

Variables	1999		2000		2001	
	Axis 1	Axis 2	Axis 1	Axis 2	Axis 1	Axis 2
Soil particle size	$+0.820^{**}$	$+0.189^{NS}$	$+0.661^{**}$	-0.075^{NS}	$+0.474^{**}$	-0.065^{NS}
Moist soil profile	$+0.515^{*}$	$+0.069^{NS}$	$+0.422^{*}$	-0.429^{*}	$+0.129^{*}$	+0.321
Elevation	-0.622^{**}	-0.321^{NS}	-0.602^{**}	-0.029^{NS}	-0.075^{NS}	–0.197
Grazing	-0.596^{**}	$+0.434^{NS}$	-0.837^{**}	$+0.261^{NS}$	-0.029^{NS}	-0.054^{NS}
Soil resistance	-	-	-	-	$+0.506^{NS}$	-0.098^{NS}
Eigenvalue	0.229	0.108	0.202	0.107	0.256	0.103
% of variance explained in species	23	11	20	11	26	10

* Significant at $p \leq 0.05$;

** Significant at $p \leq 0.01$ otherwise not significant (NS) using CCA permutation test.

Multivariate analysis of species composition and environmental variables. Relationships between species composition and environmental variables were analysed using PCA (Fig. 8). In the PCA ordination diagram, each point represents a relevé or sample site. The axes 1 and 2 represent species composition as orthogonal axes and arrows represent the relationship between environmental variables and the plant community, as represented by the orthogonal axes 1 and 2. The cosine of the angle between species axes and the arrow of the environmental variables indicate the degree of correlation. The arrow points in the direction of maximum correlation and its length is proportional to the correlation coefficient. In 1999, relevés of the *S. monoica* and the *Heliotropium* communities were plotted near moist, fine soils in the PCA ordination graph, whereas those of the *P. turgidum* and *A. tortilis* communities were positioned in the direction of coarse sand and gravely dry sites (Fig. 8a). A similar arrangement of plant communities was observed in 2000 (Fig. 8b). In 1999 and 2000, relevés of the *Heliotropium* and *S. monoica* communities were clearly separated, while those of *P. turgidum* and *A. tortilis* overlapped.

In general, axis 1 was more strongly correlated with environmental variables than axis 2 (Fig. 8; Table 3). Axis 1 was positively and significantly correlated with finer soil texture and higher moisture availability, and negatively correlated with grazing pressure and elevation (Fig. 8a; Table 3). Axis 2 was positively correlated with grazing pressure. In 2000, similar correlations were observed as in 1999 with a slightly increased correlation of axis 1 to grazing pressure ($r = -0.837$) and of axis 2 to moisture availability (*r* = –0.429) (Fig. 8a; Table 3). In 2001, the correlation between species axes and environmental variables was comparatively low (Table 3). Axis 1 was positively correlated with increased fine particle size and moisture availability and negatively correlated with soil compaction.

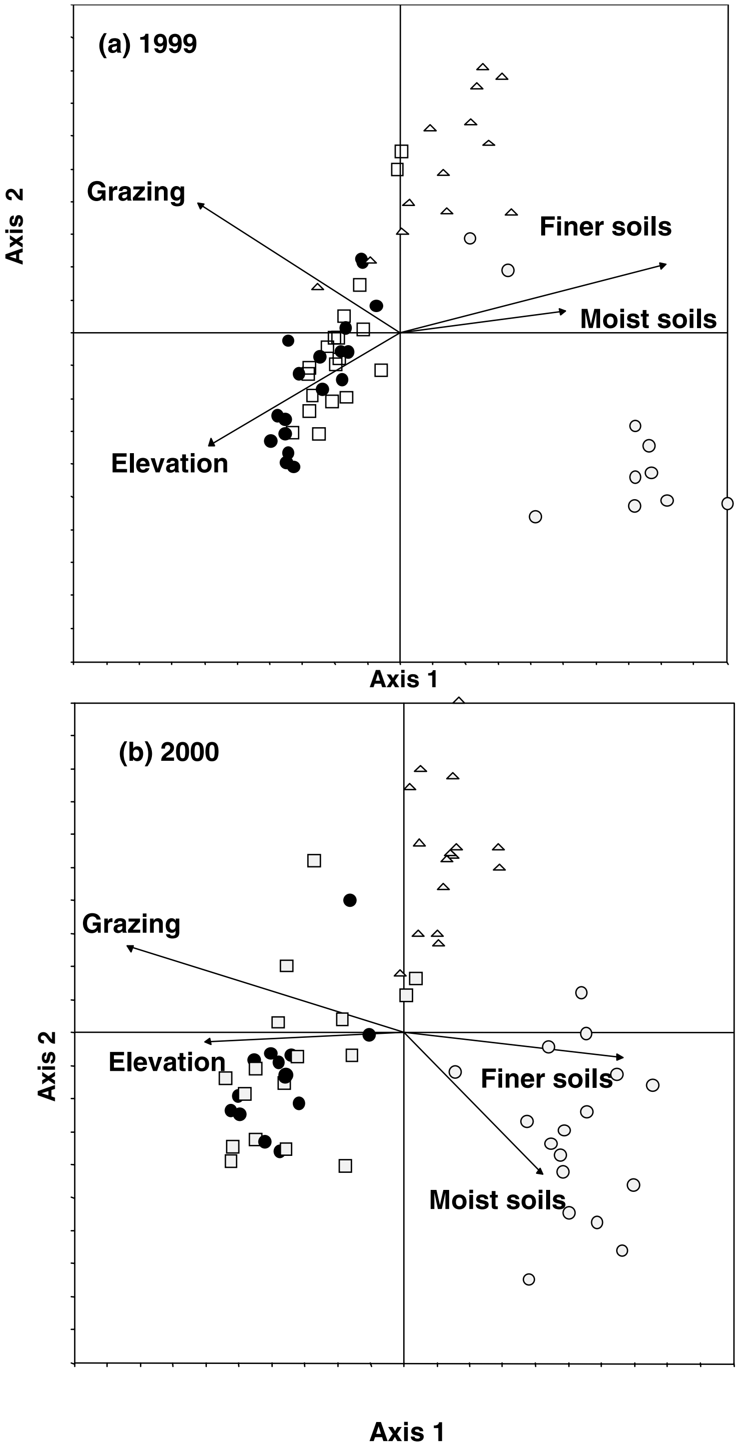

Fig. 8. PCA ordination of plant community relevés in relation to soil texture, soil moisture, grazing pressure and elevation, in 1999 (a), 2000 (b). Axes 1 and 2 represent scores of plant communities. Symbols indicate classification of relevés in plant communities as derived by TWINSPAN classification: *S. monoica* (Δ), *Heliotropium* spp. (o), *P. turgidum* (□) and *A. tortilis* (●).

Discussion

Four plant communities, viz. *S. monoica*, *Heliotropium*, *P. turgidum* and *A. tortilis* were identified between the sea and the foothills on the coastal plain of Sudan using a 5 × 5 km grid of sample points at which species scores were made in three years, along with accompanying observations on soil particle size, soil moisture, elevation and grazing intensity (Pictures 1-4). The *S. monoica* community dominated the coastal sites while the *Heliotropium* community was found at outflow areas in the lower courses of the wadies. The *P. turgidum* community occurred on coarse sands while the *A. tortilis* community dominated the gravely foothills, further west. In this area covering 20 × 120 km of the Sudanese coast, there was no earlier floristically based description of plant communities to compare our results to. Kassas (1957) reported a reconnaissance survey of habitats between December 1953 and April 1954. He first divided the area into 'salt marsh' and 'coastal plain' ecosystems. Within the salt marsh, he listed eight plant communities: *S. monoica*, the raised beach, *S. fructicosa*, *Avicennia marina* Forssk., *Arthrocnemum glaucum* (Delile) Ung., *H. perfoliata*, *A. lagopoides*, and *Sporobolus spicatus*. On the coastal plain, Kassas identified six plant communities namely *P. turgidum*, *A. tortilis*, *A. nubica*, *Indigofera spinosa*, *Capparis decidua*, and *Calotropis procera*. The *S. monoica*, *P. turgidum* and *A. tortilis* plant communities are similar to those described here whereas the species that Kassas used to characterize the other three communities in the plain are indifferent, selective or preferential species in our classification. Hence, our data indicate that these three communities can be lumped with the *S. monoica*, *P. turgidum* and *A. tortilis* plant communities. Based on cover abundance of the plant species, the 14 plant communities reported by Kassas (1957) are lumped into four plant communities in our classification. These four plant communities are physically observable and distinctly associated with habitat factors and seem practically useful for the study of desert locust distribution.

El-Demerdash *et al.* (1995) identified *Ziziphus spina-christi* (L.) Willd, *C. procera*, *L. pyrotechnica*, *Tamarix mannifera* (Ehrenb.) Bunge and *C. conglomeratus* Rottb., *A. tortilis*, *P. turgidum* and *S. monoica* plant communities along the Arabian Red Sea coast. The latter three plant communities are similar to those that we describe here; the others are either indifferent or preferential species to the plant communities described here. Thus, based on our data, a further split in plant communities was not indicated. El-Demerdash *et al.* (1995) further reported the existence of *H. arbainense* but did not classify it as a plant community. The important values of the perennial plants were scored using '10 m line transect', and this may underestimate the abundance of herbs plus no allowance was made for annual plants.

Picture 1. The *Acacia tortilis* plant community with the Red Sea Hills in the background.

Picture 2. The *Panicum turgidum* plant community in Gwob-Gabol.

Picture 3. The *Heliotropium*/millet plant community. Photo shows young millet hills with *Heliotropium arbainense* underneath.

Picture 4. The *Suaeda monoica* plant community.

The climate on the coastal plain is arid to semi-arid (Satakopan, 1965), the pattern and composition of the plant communities appeared to be related to the pattern of soil particle size, soil moisture status, elevation and grazing pressure of the sites. This pattern seems to follow the process of run-off water from the western hills and deposition of soils and addition of water on the coastal plain. The coastal plain is a zone of deposition, starting with gravel near the foothills (*A. tortilis* community), then the coarser grits (*P. turgidum* community) and, lastly the fine soil particles in the low elevation wadi outflows (*Heliotropium* community). Presence of soil moisture as modified by absorption of water from run-off and retention follows the same pattern as the soil particle size. The pattern of plant community composition and associated habitat factors observed along the Sudanese coast appear to be similar to that of northern Eritrean (Hemming, 1961) and South Arabian (Vesey-Fitzgerald, 1955, 1957) Red Sea coasts, although the description and classification method used is entirely different. Similar relationships between plant communities and edaphic factors were reported from the deserts of the Red Sea coast of Saudi Arabia (Younes *et al.*, 1983; El-Demerdash *et al.*, 1995), Egypt (Abd El-Ghani, 1998) and the Negev desert of Israel (Hillel & Tadmor, 1962; Whittaker *et al.*, 1983; Yair & Danin, 1980).

In conclusion, the new approach of sampling plant species in a spatial grid helps to explore the spatial pattern of plant community composition and associated habitat factors. The description and classification of habitats using cover abundance of plant species resulted in four plant communities, each distinct in terms of associated habitat factors. This description and classification is less complex and more discernible in the field than the earlier classifications (Hemming, 1961; Kassas, 1957). Consequently, it was possible to delineate and produce a defined plant community map showing the spatial extent and pattern of the four plant communities in a 20 × 120 km coastal area. We think this description and classification is useful for studying the spatial distribution of desert locust in relation to plant communities and to identify and localize the most likely locust habitats. Furthermore, this description and classification may serve for conservation of natural resources and grazing management and lay a basis for further vegetation research. The same approach of plant community description and classification can be extended and verified on the Eritrean, South Arabian and Yemeni Red Sea coasts, a common habitat of the desert locust.

Chapter 3

Relationships between the occurrence of solitarious desert locusts (*Schistocerca gregaria* Forsk.) and plant communities on the Red Sea coastal plain of Sudan

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Chapter 3

Relationships between the occurrence of solitarious adult desert locusts (*Schistocerca gregaria* Forsk.) and plant communities on the Red Sea coastal plain of Sudan

Abstract

Systematic surveys were conducted during three years in an area of 20 × 120 km on the coastal plain of Sudan to quantify the relationship between the occurrence of solitarious adult desert locusts (*Schistocerca gregaria* Forsk.) and habitat factors. Data on locust density, cover abundance of plant species and other habitat indicators were collected in 60-64 sample sites in a 5 by 5 km grid during the winters of 1999, 2000 and 2001. Locust samples were taken every 7-14 days. Cover abundance and other habitat indicators were scored in each season. Principal component analysis (PCA) showed that in each of the three winter seasons, locust densities were associated with the *Heliotropium* plant community, fine soil texture and relatively high moisture availability, and negatively correlated with increased grazing pressure and elevation. The *Heliotropium* plant community contained 93% of the locusts found in 1999 and 100% in 2000 while this plant community made up to 27% of our samples and covered only 5% of the surveyed area, mostly at the cultivated wadi outflows. The localized distribution of locusts in cultivated wadi outflows was confirmed by observations in parts of the coastal zone outside the main study area. For instance in the Tokar delta, locusts were restricted to cultivated sites and the highest locust density was found in association with millet cropping and to a lesser extent, with sorghum. These results provide clues for enhancing the efficiency of locust survey and control and raise questions as to why certain habitats are preferred.

Key words: Desert locust, *Heliotropium*, plant community, Red Sea coast, Sudan.

Introduction

In the arid and semi-arid areas of Northern Africa, the Arabian Peninsula and South West Asia, the desert locust (*Schistocerca gregaria* Forsk.) occurs in a solitarious phase when population densities are low and in a gregarious phase when population densities are high. The high locust densities that lead to outbreaks occur when there are favourable conditions for breeding and survival during several generations (Pedgley, 1981). Desert locust outbreaks give rise to large and dense groups of hopper bands or adult swarms that are a threat to agriculture. To reduce this threat, locust management is based on monitoring the build-up of gregarizing populations and to control those outbreaks (Cressman, 1996a, b). The build-up of locust populations is routinely monitored using ground searches (FAO, 1994). This is a difficult task, since the breeding area to be searched is vast. Therefore, it has been suggested that outbreaks often remain undetected (Symmons, 1992). Monitoring the population build-up of early outbreaks in a vast area requires knowledge about the most likely locust habitats, where the resources for breeding and survival are favourable. Locusts need an upper 15 cm of moist soil for the deposition and development of eggs, and green vegetation for the development of nymphs (Uvarov, 1957; Popov, 1958). Moreover, it has been shown for other locust species that locusts are associated with certain habitats and plant communities (Kemp *et al.*, 1990; Launois & Lecoq, 1990).

The Red Sea coastal plains were first identified as an important breeding area for desert locust by Johnston (1926) and Maxwell-Darling (1936 and 1937). There are several reports that, within the Red Sea coastal plain, desert locusts are mostly observed in areas with millet (*Pennisetum typhoideum* Rich) and *Heliotropium* spp. (Maxwell-Darling, 1936, 1937; Stower *et al.*, 1958; Waloff, 1963; Roffey & Stower, 1983). Unfortunately, the available evidence is based on occasional visits and ‘traverse notes’. No systematic survey of desert locust habitats has been carried out in this region or elsewhere. No quantitative or spatially explicit relationship between solitarious adult desert locust occurrence and habitats is therefore established.

Recently, plant communities of the locust habitat were distinguished and their relationship to soil particle size, soil moisture availability, elevation and grazing pressure at the Sudanese Red Sea coast were described using multivariate analysis (Chapter 2). Four plant communities were distinguished: *Suaeda monoica* Forssk., *Heliotropium* spp., *Panicum turgidum* Forssk., and *Acacia tortilis* (Forssk.) Hayne. The objective of the study reported here is: (1) to relate the density of desert locusts to these plant communities and associated habitat variables; (2) to delimit the spatial extent of the most likely locust habitat where survey should be targeted at the Sudanese Red Sea coast.

Materials and methods

Study site. The study area is delimited by Port Sudan (19°35' N, 37°13' E) in the north, the Tokar delta (18°26' N, 37°44' E) in the south, the Red Sea in the east and the Red Sea Hills in the west of Sudan. The 20 to 40 km wide areas between the hills and the sea is called the coastal plain. The coastal plain has an arid to semi-arid climate with low and erratic rainfall (Griffiths & Hemming, 1963, Satakopan, 1965). Precipitation occurs in the winter months from October to January. During this period the desert locust breeds. Additional water for plant growth in the plain is provided by run-off from the Red Sea Hills via 'wadies' (temporary riverbeds) such as Hambukaeb, Gwob, Gabol, and Ashat. The wadies slowly spread in the plain forming deposits of fine soil particles at their outflows before they reach the sea. These deposits are used for cultivation of millet during the winter season.

The warmest month of the year on the coastal plain is August with an average daily maximum of 41 °C and a minimum of 30 °C, while the coolest month is January, with an average daily minimum of 20 °C and a maximum of 27 °C. Average total winter rainfall (October to February) at the Port Sudan Airport Meteo Station was 70 mm from 1985-2001, with a maximum of 158 mm in 1999 and a minimum of 3 mm in 1998 (coefficient of variation 73%). During our sampling, from October through March during three subsequent winters (1999-2001), rainfall and average daily temperature were measured at the meteorological station of Port Sudan, at the northern end of the study area. Total rainfall during these winter periods amounted to 158 mm in 1999/2000, 123 mm of which fell between 15 and 30 December 1999, 138 mm in 2000/2001, 70 mm of which fell on 18 December 2000, and only 30 mm in 2001/2002 (Fig. 1). Comparatively, the heaviest rain fell in December in each of the three seasons.

Four plant communities were identified in the plain: *S. monoica*, *Heliotropium* spp., *P. turgidum* and *A. tortilis* (Chapter 2). The *S. monoica* plant community is found near the sea, often on salty soils. The *P. turgidum* plant community is found on coarse sand and is used by nomadic herders for grazing goats, and camels. In between these two communities, there are pockets of the *Heliotropium* plant community, on fine and moist sand soil, at low elevation at the outflows of wadies. These areas are used for agriculture in years with sufficient rainfall. The *A. tortilis* community is prevalent on coarse sand and gravel near the Red Sea Hills.

Data collection. In the 1999 winter season, solitarious adult locusts were counted between December 1999 and February 2000. This period will be referred to as the 1999 winter season or simply 1999. The same terminology was to describe the winters of 2000/2001 ('2000') and 2001/2002 ('2001'). In this paper the term locust refers to solitarious adult desert locust unless otherwise specified.

Locusts count. Locusts were counted using a 5 × 5 km grid of sample sites in the 1999, 2000 and 2001 winter seasons. The sites were spread as evenly as possible in space, and rather evenly over the four plant communities, with 10 of the 60 sites in the *Heliotropium* plant community, 13 in the *S. monoica* community, 19 in the *P. turgidum* community, and 18 in the *A. tortilis* community (Fig. 2a). In the 1999 winter

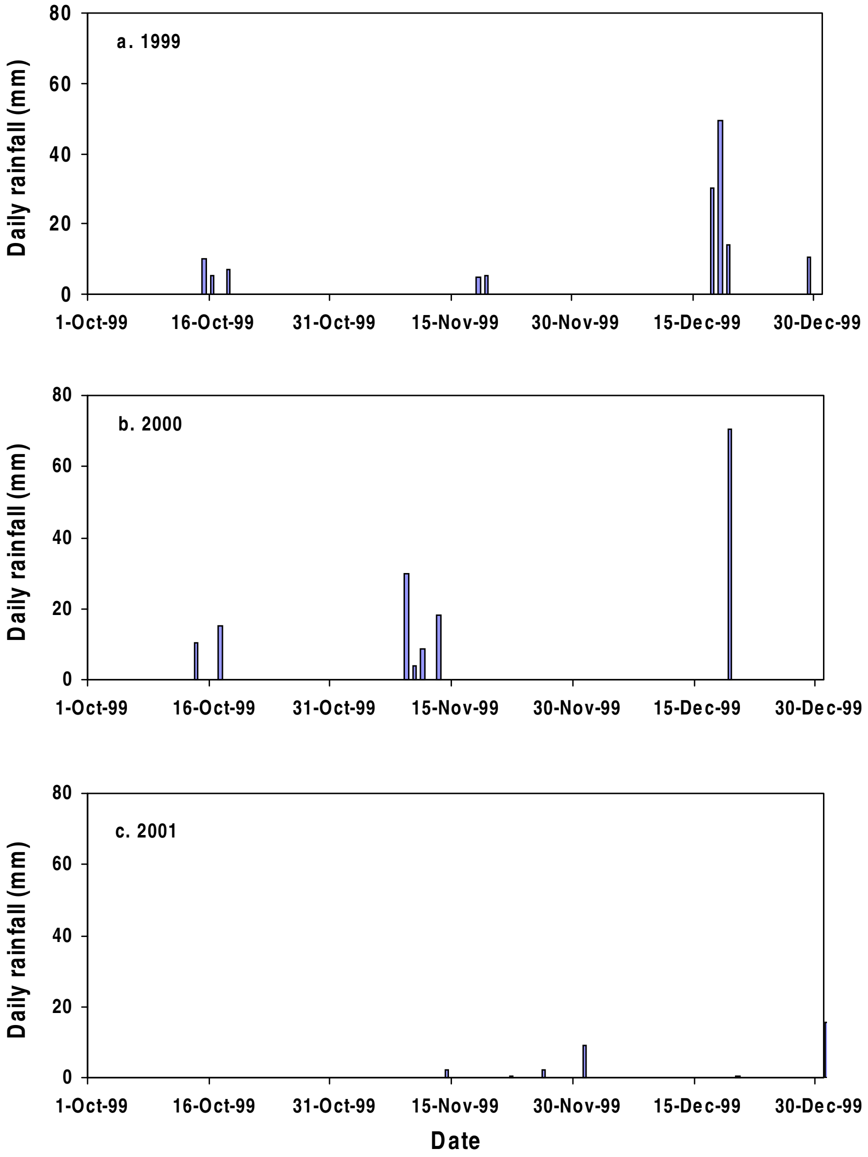

Fig. 1. Daily total rainfall (mm) at Port Sudan during the winters of 1999 (a), 2000 (b) and 2001 (c).

season, locusts were counted on nine occasions: 7, 15, 22 and 29 December 1999; 3, 13, 19 and 26 January 2000; and 9 February 2000. In the 2000 winter season, there was a slight shift in some sampling sites and 17 of the 64 sample sites were in the *Heliotropium* community, 16 in the *S. monoica* plant community, 17 in the *P. turgidum* community, and 14 in the *A. tortilis* community (Fig. 2b). Locusts were counted on 1, 15 and 31 December 2000; 13 and 27 January, 10 and 24 February and 10 March 2001. In the 2001 winter season, the same 64 sample sites as in 2000 were visited on 10 and 24 November, and 8 and 21 December 2001; and on 5 and 19 January; and 2 and 14 February 2002. The survey was performed using two teams, each consisting of three observers plus a driver and an all terrain vehicle. Sampling the 5 × 5 km grid required three days. The middle day of those is quoted as the date of sampling.

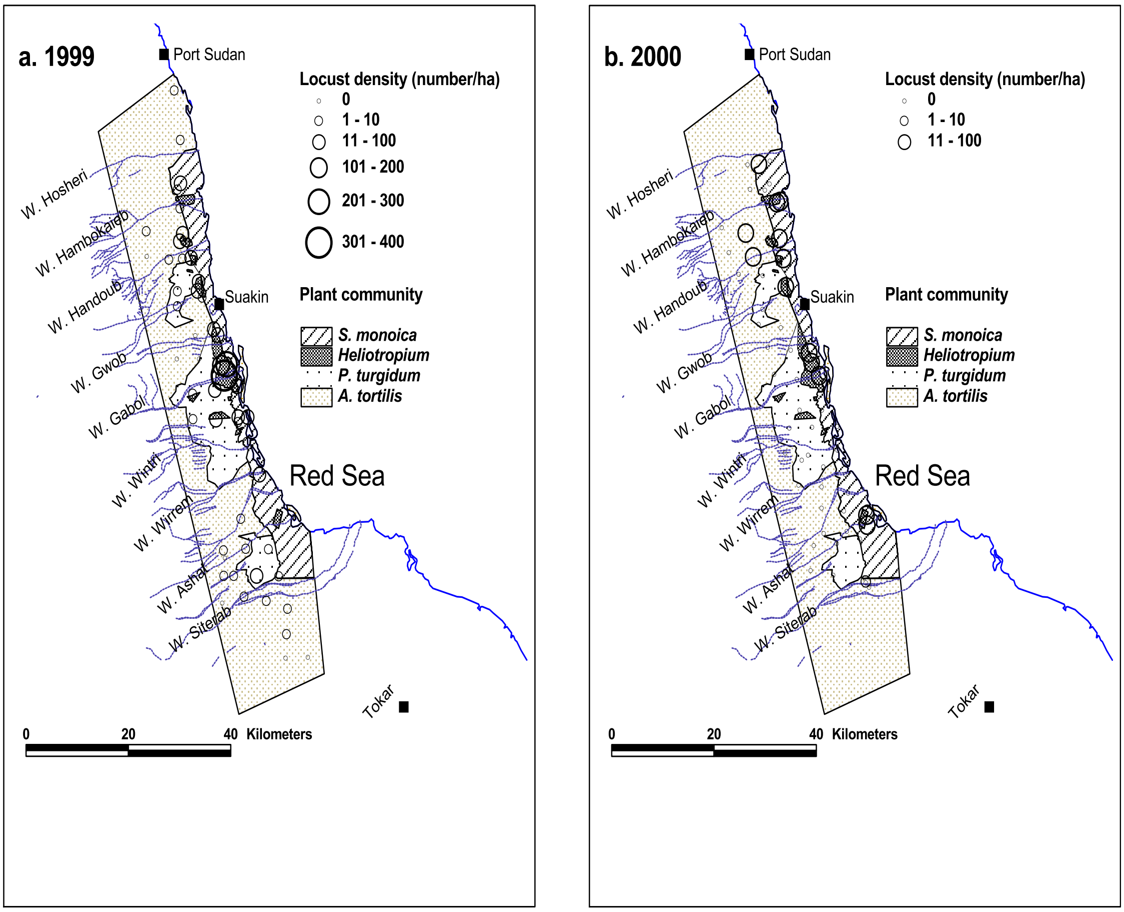

Fig. 2. Spatial distribution of locust density (number/ha) and plant communities in 1999 (a) and 2000 (b). The radius of circles represents the average locust density (number/ha) at a sample site over eight to nine sample occasions.

Locusts count in the Gwob-Gabol area. In the winters of 1999 and 2000, locusts were counted at a 1 × 2 km resolution in the *Heliotropium* plant community in the Gwob-Gabol area (the main cropland in our study area) and adjacent *S. monoica* and *P. turgidum* areas. This 1 × 2 km grid was embedded in the 5 × 5 km grid of the main study. The objective was to compare the locust densities in the *Heliotropium* plant community with those immediately outside this community. In the winter of 1999, 60 sample sites, 34 of which were in the *Heliotropium* plant community, five in the *S. monoica* community and 21 in the *P. turgidum* community, were visited on 6, 17, 22 and 30 January and 4, 9, 17 and 24 February 2000. In the winter of 2000, the number of sample sites was 33, 21 of which were in the *Heliotropium* community, four in the *S. monoica* community and eight in the *P. turgidum* community. The sites were visited on 8 and 24 December 2000; 6 and 20 January; 3, 17 and 28 February and 14 and 21 March 2001. The same 33 sample sites were visited in the following winter: on 17 November; and 1, 11 and 29 December 2001.

Locust counting protocol. At each sample site, a walking direction was chosen that would ensure a straight 400 m walking path in the same plant community. Three observers each walked a 400 m transect in parallel, with 10-20 m between transects. The observers swayed a stick to flush and count adult solitarious locusts on a 1 m wide swath. Transect length was standardized at 400 m by tallying the number of steps with a hand counter. To avoid bias, counts were made between 10.00 h a.m. and 5.00 h p.m., provided that temperatures were above 24 °C and wind speed below 20 m/s. The total number of locusts counted was converted to a number per ha. Air temperature was measured with a Sling Psychrometer (BACHARACH, INC) and wind speed with an anemometer (Dwyer ® wind meter, Dwyer Instruments, INC). Position and elevation of each sample site was ascertained with Global Positioning System (GPS, Garmin 12XL). The same locust counting protocol was used throughout the study.

Vegetation sampling. Cover abundance of plant all species was scored using a modified version of the Braun-Blanquet 1-9 point scale (van der Maarel, 1979). In 1999, cover abundance was assessed on the whole of a 1 × 400 m transect per sample site whereas in 2000 and 2001, cover abundance was estimated in three 10 × 10 m plots, located at 50, 200 and 350 m along the 400 m transect. At each sampling site, transects and plots were selected to represent relatively homogeneous vegetation. Transition zones were avoided. Vegetation assessments (‘relevés’) were made at least once per season. All plant species were identified using descriptions given by Migahid (1996). Cover abundance scores in the three plots per transect (2000, 2001) were averaged. During each sample, the status of the vegetation was recorded as greening, green, drying or dry.

Spatial extent of plant communities. The spatial extent of each plant community was delineated by tracing the border with a car and taking GPS co-ordinates with a Garmin 12XL GPS.

Soil texture. In 1999 and 2000, soil texture at each sample site was assessed using the ‘feel’ method (Brady, 1990). In 2001, particles size distribution was determined by collecting five soil samples from each of three 10 × 10 m plots at each sample site. The sample plots were adjacent to the plots that were used for making vegetation relevés. Soil samples were taken from the top 15 cm in each plot, using a 7.6 cm diameter auger. The five samples per plot were pooled to produce a 1-2 kg composite sample. The samples were thoroughly mixed, oven-dried at 100 °C for 48 h. and then dry-sieved using five stacked sieves with mesh size decreasing from top to bottom. The resulting particle fractions were classified as gravel (> 2.00 mm), coarse sand

(> 0.420 mm), medium fine sand (> 0.210 mm), fine sand (> 0.105 mm), very fine sand (> 0.053) and silt + clay (< 0.053 mm). The gravel fraction was estimated from 0.5 kg of the pooled soil sample. The small particle size class was estimated from a 50 g subsample. Before analysis of the results, particle size fractions in the three plots per transect were averaged.

Soil compaction in the upper 10 cm of soil was measured using a hand penetrometer (Eijkelkamp Agrisearch Equipment, The Netherlands). Five readings were made in each vegetation plot, i.e., 15 per sample site.

Moist soil profile. Presence of moist soil was recorded every 7-14 days at five locations at each sample site: 0, 100, 200, 300 and 400 m along the 400 m transect. Soil was scooped away with a hand shovel to check presence of moisture at 0-5, 5-10 and 10-15 cm depth using 'touch and feel'. The results were coded as 0 (no moisture), 1 (moisture at 10-15 cm), 2 (moisture at 5-15 cm), or 3 (moisture throughout). The median score of the five points checked per sample site was used in analysis.

Grazing. Grazing pressure at each sample site was classified as (0) none, (1) slight, (2) moderate, or (3) heavy.

Elevation. The elevation of sample sites was measured with Garmin 12XL GPS.

Association between locust density and site factors. Association between locust density and habitat variables such as plant composition, soil particle size, soil moisture, grazing pressure, elevation were quantified and visualized with Principal Component Analysis, using the software program CANOCO (ter Braak & Šmilauer, 1998), and by the use of univariate descriptive statistics, using SPSS for windows v10.

Verification in the whole coastal plain. Observations on the presence of locusts outside the 5 × 5 km grid were made in the winters of 2000 and 2001 to validate our findings in the study area. The survey covered sites between Halaib near the Egyptian border and the Tokar delta near the Eritrean border, a distance of about 400 km. Presence of locusts was checked by taking 'traverse notes', taking samples in three types of habitat, across the coast based on experience gained during the survey of the 5 × 5 km grid in 1999. The three habitats were cropland (unlikely habitat), green grazing (possible habitat) and dry grazing land (unlikely habitat). The cultivated wadi outflows, in general, are deposits of fine texture soils and are relatively moist and green sites, similar to the sites in the *Heliotropium* plant community in the main study area. The major cultivated sites visited included wadi Diib, Oko, Arbaat (north of Port

Sudan), and Siterab and wadi Baraka in the Tokar delta (south of Port Sudan). In the validation study there was no systematic classification of sites based on plant composition and other habitat factors except for the Tokar delta.

In 2000, 22 of the 59 sample sites were situated in cultivated wadies, 25 in grazing green areas and 11 in grazing dry areas. The sites were visited between 24 November and 17 December 2000. In 2001, 35 of the 60 sample sites were in cultivated wadies, 9 in green grazing areas and 16 in dry grazing areas each site was visited on 1-3 November and 21-24 December 2001; 19-22 January and 12-15 February 2002. In all sites, locusts were checked by scouts on three parallels 400 m transects and they were recorded as absent or present.

Locust counts in the Tokar delta. During the validation study, the Tokar delta cultivated wadi outflow was among the visited sites were presence of locusts was observed. As part of the confirmation of the results obtained in the main study area, we made a detailed case study in this wadi outflow. The Tokar delta is located 155 km south of Port Sudan, 40 km south of the most southern sample points of the 5 × 5 km grid. The soil is more fertile and suitable for agriculture than that at other parts of the coast. There is dependable supply of floodwater during summer from the highlands of Eritrea and Ethiopia through the wadi Baraka. Crops are grown under flood recession farming, which is planting crops in flood plains after the floodwater recedes. Locusts were counted on three 400 m parallel transects similar to the 5 × 5 km grid in the Tokar delta. We used 45 sample sites in a 2 × 2 km arrangement and visited these on 25 December 2001; and on 5 and 20 January, 2 and 13 February; and 3 March 2002.

Data on cover abundance of plant species, soil texture, presence of moist soil and compaction were recorded in the same way as in the 5 × 5 km grid. Plant community composition in the Tokar delta was analysed using two-way indicator species analysis (TWINSPAN) (Hill, 1979). Following the delineation of plant communities with TWINSPAN, the species with a significant difference in cover abundance among the distinguished plant communities (Wilcoxon test; $p \leq 0.05$) were categorized according to fidelity. Five degrees of fidelity were used, following the criteria of Barkman (1989): **selective** (species found most frequently in certain community and also, but rarely, in other communities), **preferential** (species predominantly found in one community with greater vigour but also abundantly found in other plant communities), **indifferent** (species without a definite affinity for any particular community)**, accidental** (species that are rare in a community) and **stray** (species not belonging to the community). Species with a significant degree of fidelity characterize a plant community. Details on plant communities and the degree of fidelity of species for the 5 × 5 km grid are reported elsewhere (Chapter 2). The relationship between plant composition and other habitat factors was analysed as for the 5 × 5 km grid data.

Results

Relationship between solitarious locusts and plant community. In 1999, the highest locust densities were found at sites with the *Heliotropium* plant community on fine grained and moist soils in wadi outflows, cultivated with *P. typhoideum* (millet) (Fig. 2a), in particular around the outflows of the wadies Gwob and Gabol. The lowest locust densities were found in the *A. tortilis* plant community on relatively dry gravel soils near the foothills. In 2000, locusts were exclusively found in the *Heliotropium* plant community in cultivated wadi outflows (Fig. 2b). In 1999, the percentage area covered with *Heliotropium* plant community was about 5%, compared to 14% for the *S. monoica* plant community, 21% for the *P. turgidum* plant community and 60% for the *A. tortilis* plant community (Fig. 2a).

Multivariate analysis of relationships between locust distribution, site factors and plant communities. The association between locust density, plant communities and associated habitat variables in the 5 × 5 km grid is displayed using PCA ordination diagrams (Fig. 3). The ordination diagrams show the main variation in species composition along axis 1 and 2. Arrows of locust density and habitat variables pointing in the same direction indicate a positive correlation and arrows pointing in the opposite direction indicate a negative correlation. The cosine of the angle between the arrow of locust density, the PCA species axes (axis 1 and 2), and those of habitat variables represent the degree of correlation. Correlation coefficients are given in Table 1. In 1999, the *S. monoica* and the *Heliotropium* communities were associated with moist and fine textured soils, whereas the *P. turgidum* and the *A. tortilis* communities were associated with coarse sand and gravel (Fig. 3a). Locust density was correlated positively and significantly with the first PCA species axis ($r = 0.67$) in the direction of *Heliotropium* sites, with fine textured soils ($r = 0.54$) and comparatively high moisture availability ($r = 0.55$) (Table 1). Locust density was negatively correlated with grazing pressure ($r = -0.50$), and to a lesser extent with elevation ($r = -0.25$). The PCA results for 2000 were broadly the same as in 1999 (Fig. 3b, Table 1). In the dry winter of 2001, however, the correlation between locusts (at low density levels) and the first PCA species axis was much lower than in the other two years (although significant), and the correlation with other habitat factors was weak (Table 1).

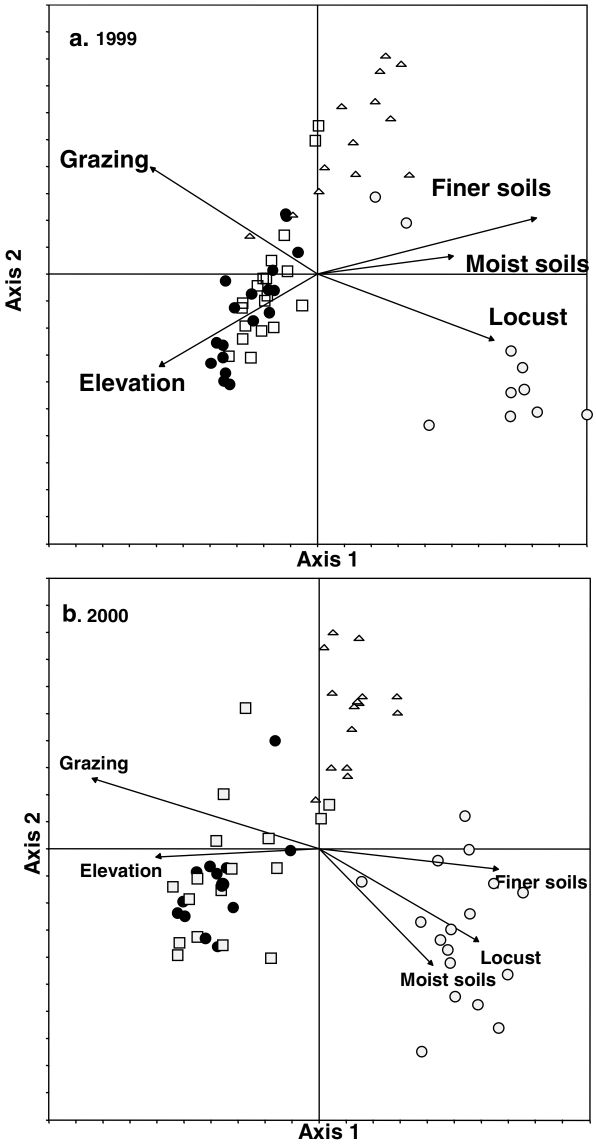

Fig. 3. PCA ordination plot, based on plant community composition, showing the relationship of locust density (number/ha), plant composition (axis 1 and 2) and other habitat variables in the 5 × 5 km sampling grid as indicated by arrows in 1999 (a) and 2000 (b). Symbols in the ordination plot indicate plant communities at sample sites: *S. monoica* (Δ), *Heliotropium* (o), *P. turgidum* (□) and *A. tortilis* (●).

Table 1. PCA correlation matrix (*r*) between locust density (number/ha), species (first two PCA axes) and habitat variables, 5 × 5 km grid main study area, 1999 through 2001 winter seasons and in the Tokar delta in 2001.

Habitat	Winter seasons			
variables	1999	2000	2001	Tokar delta (2001)
Axis 1	$+0.667^{**}$	$+0.589^{**}$	$+0.325^{*}$	$+0.608^{**}$
Axis 2	-0.249^{NS}	-0.341^{**}	-0.012^{NS}	$+0.467^{**}$
Soil particle size	$+0.535^{**}$	$+0.475^{**}$	$+0.114^{NS}$	-0.663^{**}
Moist soil	$+0.553^{**}$	$+0.589^{**}$	$+0.181^{NS}$	$+0.385^{**}$
Elevation	-0.253^{*}	-0.377^{**}	$+0.007^{NS}$	-
Grazing	-0.504^{**}	-0.628^{**}	-0.037^{NS}	-
Compaction	-	-	-0.161^{NS}	$+0.114^{NS}$

** Significant at $p \leq 0.01$, * significant at $p \leq 0.05$, and ^{NS} not significant at $p > 0.05$.

Relations between temporal trends in locust density, soil moisture and state of the vegetation. In 1999, Locust densities were greatly and consistently higher ($p \leq 0.05$) in the *Heliotropium* plant community than those in the other plant communities (Fig. 4a). For instance, on 15 December, the number of locusts/ha (mean locust density ± SEM) was 115 ± 43 in the *Heliotropium*, 15 ± 4 in the *S. monoica*, 19 ± 9 in the *P. turgidum* and 3 ± 1 in the *A. tortilis* plant community. Due to 123 mm of rain between 15 and 30 December, the soil was moist and the vegetation green at the end of December (Fig. 5a). The locust density reached its peak on 22 December 1999. After December 1999, soil moisture levels in most sites were low and the annual plants started to dry out towards the end of January, except at the outflows of the wadies (Fig. 6a). On 26 January 2000, the ratio of locust densities in the *Heliotropium*, *S. monoica*, *P. turgidum* and *A. tortilis* plant communities was 134 : 7 : 2 : 1.

In 2000, high locust densities were again associated with the *Heliotropium* plant community ($p \leq 0.01$) (Fig. 4b). About 42 mm of rain fell between 9-13 November and about 70 mm on 18 December. The percentage of sites with moist soil was lower (Fig. 5b) and the duration of green vegetation cover shorter (Fig. 6b) than in the preceding year. On 31 December 2000, about 53 ± 13 locusts/ha were found but only in the *Heliotropium* plant community. During the whole season, no locusts at all were observed outside the *Heliotropium* plant community.

In 2001, the soils were quite dry (Fig. 5c), due to low rainfall and the vegetation stayed green for a shorter time than in the 1999 and 2000 winter seasons (Figs. 5c and 6c). The locusts observed were scattered and their number was too low to make comparisons among plant communities (Fig. 4c).

Locusts in the Gwob-Gabol area. The locust distribution was compared in adjacent plant communities over three winter seasons (Fig. 7). In the three winter seasons, there was an abrupt drop in locust densities immediately outside the *Heliotropium* plant community (Fig. 8). In 1999, comparatively high locust densities were found in the *Heliotropium* community and quite low densities in the *P. turgidum* and *S. monoica* plant communities (Fig. 8a). At the peak, locust density amounted to 358 ± 63 individuals/ha (mean ± SE) in the *Heliotropium* community and 68 ± 19 in the *P. turgidum* and 25 ± 14 in the *S. monoica* plant communities. In 2000, the peak density was 53 ± 13 in the *Heliotropium* community and virtually no locusts were found in the *P. turgidum* and *S. monoica* plant communities (Fig. 8b). In 2001, only two locusts were counted on 17 November, two on 1 December and three on 11 December (Fig. 8c). All were found in the *Heliotropium* plant community.

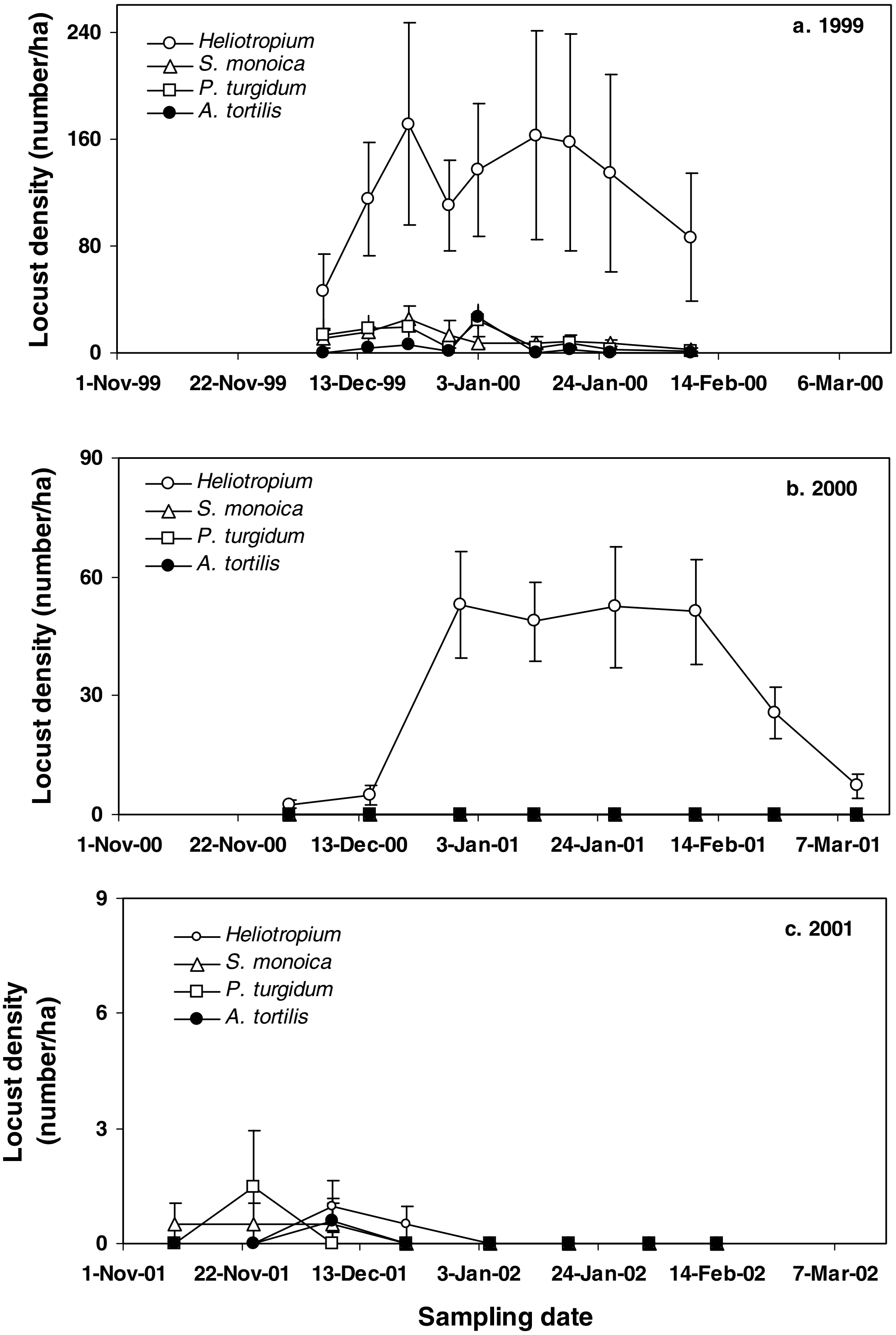

Fig. 4. Locust density (number/ha; average ± SEM) in relation to plant community in the 1999 (a), 2000 (b) and 2001 (c) winter seasons in a 5 × 5 km grid on the coastal plain of Sudan (cf. Fig. 3). Bars indicate standard error of the mean.

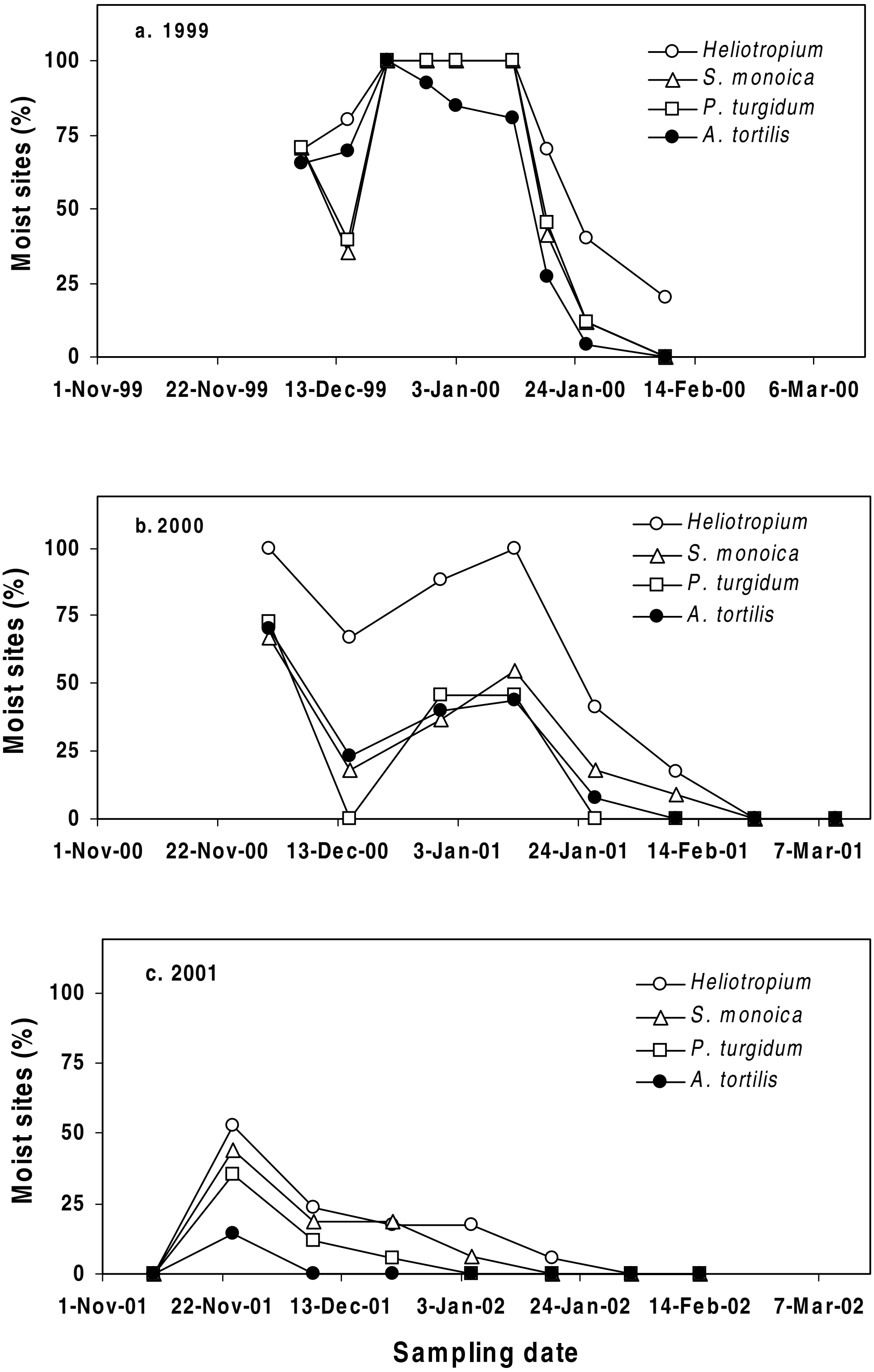

Fig. 5. Percentage of sample sites with 0-15 cm moist soil profile in four plant communities in 1999 (a), 2000 (b) and 2001 (c) winter seasons.

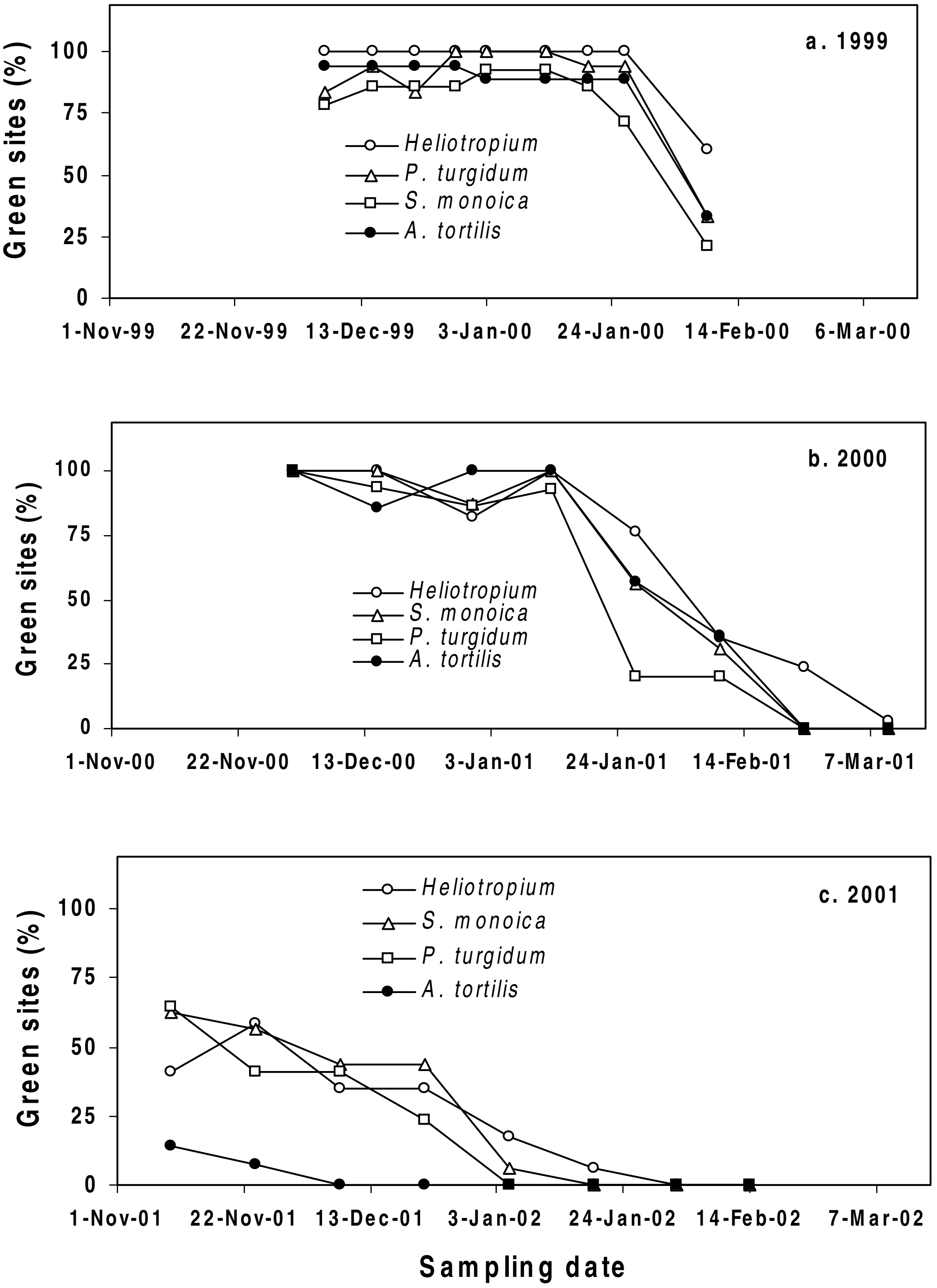

Fig. 6. Percentage of sample sites with green vegetation in four plant communities in the 1999 (a), 2000 (b) and 2001 (c) winter seasons.

Verification in the whole coastal plain. In 2000, locusts were observed in 82% of the sites situated in wadies cultivated with millet or sorghum whereas locusts were rarely detected in adjacent green and dry grazing sites (Fig. 9). In 2001, locusts were detected in 92% of the cultivated sites while locusts were only rarely found in green or dry grazing sites (Fig. 9).

Plant community in the Tokar delta. In the Tokar delta in 2001, four plant communities were identified by TWINSPAN, and characterized by species of different degree of fidelity (Table 2). The *Dipterygium/Medicago* plant community was characterized by the preferential species *Dipterygium glaucum* Decne and *Medicago* L. and occurred mainly on fine sandy soils on which millet (*P. typhoideum)* was cultivated. The *Sorghum/Solanum* plant community was characterized by the

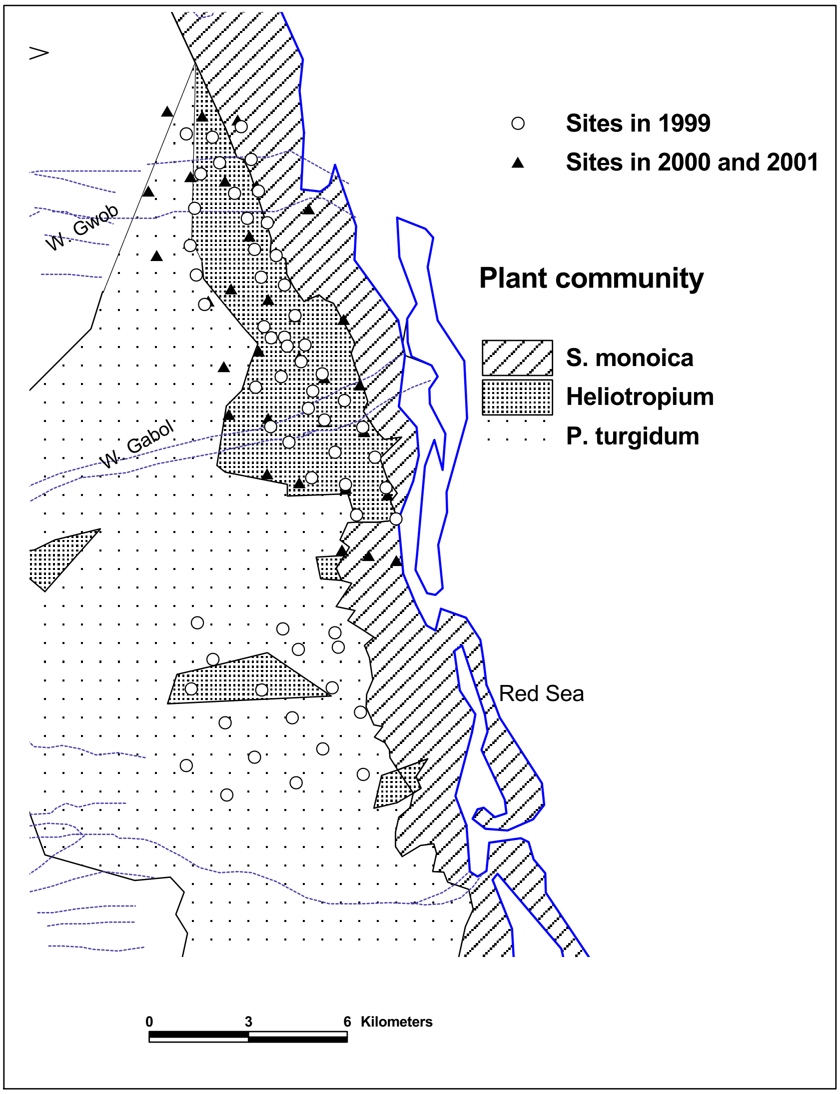

Fig. 7. Map of sample sites in the Gwob and Gabol area.

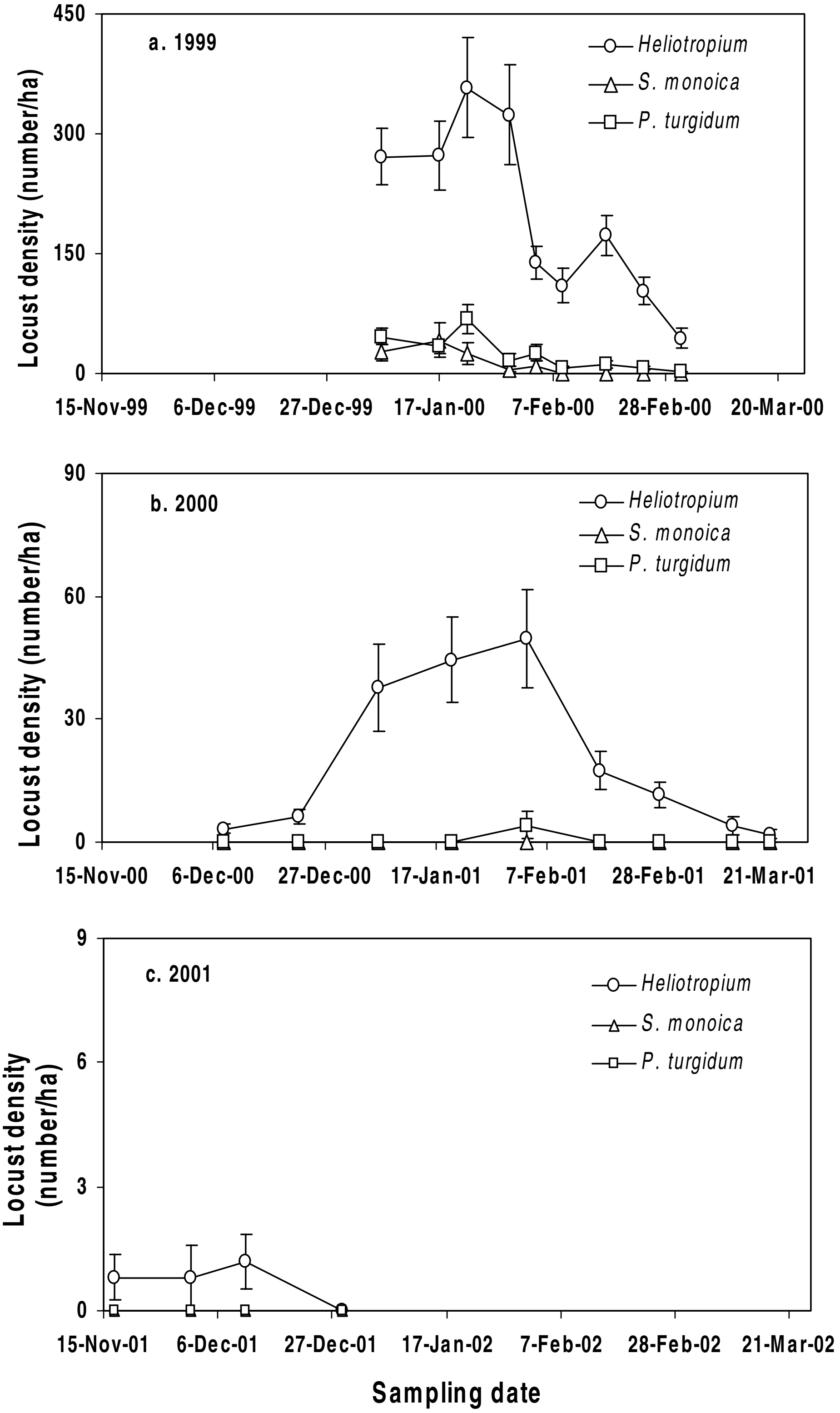

Fig. 8. Comparison of locust density (number/ha) in the *Heliotropium* plant community and in the immediate adjacent *P. turgidum* and *S. monoica* plant communities in the Gwob-Gabol cropland adjacent areas in 1999 (a), 2000 (b) and 2001 (c). Bars indicate standard error of the mean.

Table 2. Selective, preferential and stray plant species characterized four plant communities in the Tokar delta according to two-way indicator species analysis (Barkman, 1989).

Plant species	Plant communities*			
	Dipterygium/ Medicago	*Sorghum/Solanum*	*Brachiaria*	*P. chilensis*
Medicago sp.	++			
Dipterygium glaucum	++			
Brachiaria sp.			+	
Sorghum halepense		+		
Solanum dubium		+		
Gossypium barbadense		+		
Prosopis chilensis				+
Farsetia aegyptia				+
Suaeda monoica				++
Crotalaria microphylla				++
Cassia senna				++
Chrozophora sp.				++
Jatropha sp.				++
Blepharis ciliaris				++
Sorghum bicolor				--

* ++ = selective - = accidental

\+ = preferential -- = stray

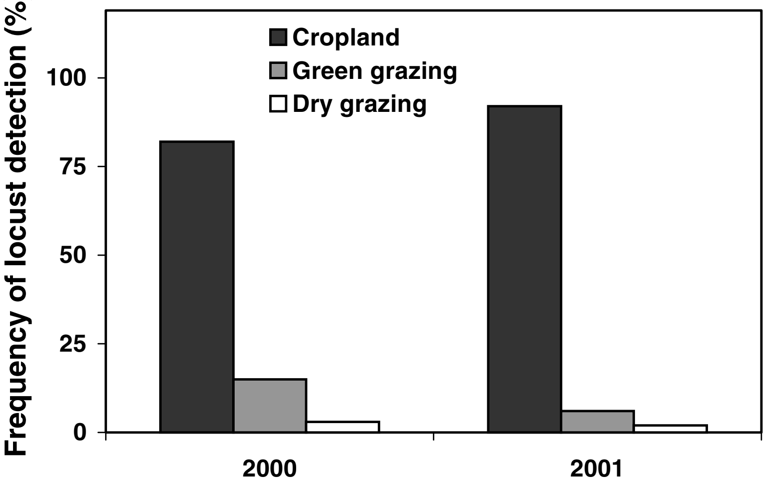

Fig. 9. Frequency of locust occurrence in cultivated wadi croplands, green grazing and dry grazing sites between Halaib and the Tokar delta in the winters of 2000 and 2001.

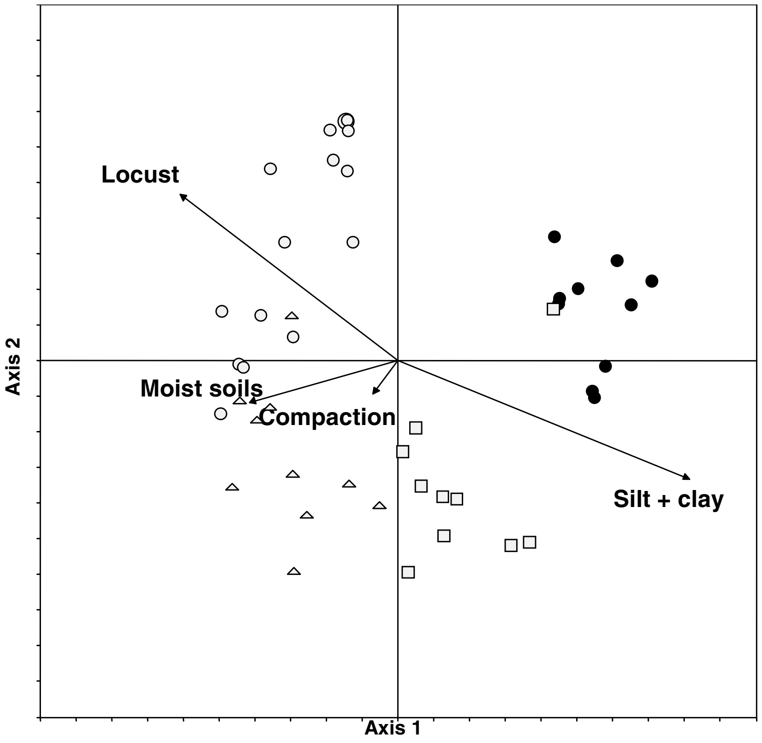

Fig. 10. PCA ordination plot showing the relationship of locust density (number/ha), plant composition (axis 1 and 2) and habitat variables as indicated by arrows in the Tokar delta in 2001. Symbols in the ordination plot indicate plant communities in sample sites: *Dipterygium-Medicago* (o), *Sorghum-Solanum* (Δ), *Brachiaria* (□) and *Prosopis chilensis* (●).

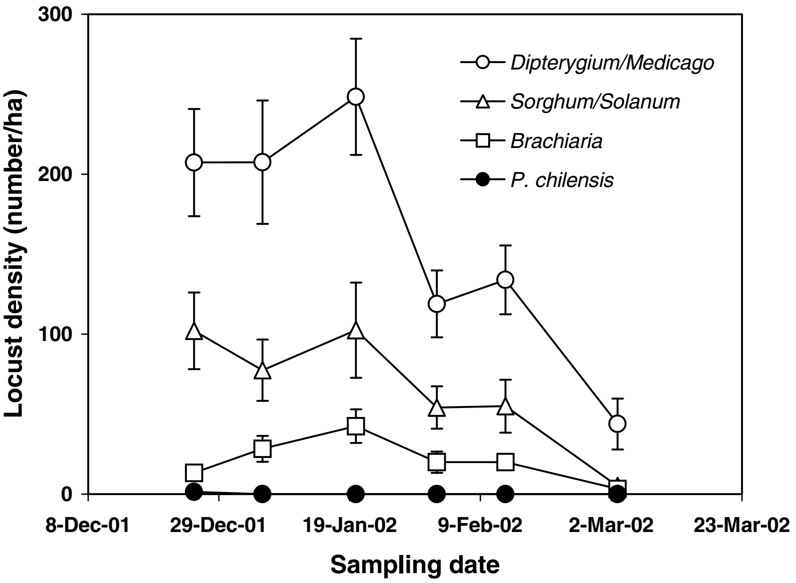

Fig. 11. Locust density (number/ha) in relation to plant communities in the Tokar delta in 2001. Bars indicate standard error of the mean.

preferential species *Sorghum halepense* L., *Solanum dubium* Fres. and *Gossypium barbadense* L., and was mainly found in mixed crop fields on fine sand to silt-clay soils. The *Brachiaria* plant community was characterized by the preferential grass *Brachiaria* sp. (Griseb), and occurred mainly on silt-clay soils cultivated with *Sorghum bicolor* (L.) Moench. The *Prosopis chilensis* plant community was dominated by perennial shrubs such as *P. chilensis* (Molina), *S. monoica* and *Cassia senna* (L).

Locust density in the Tokar delta. Locust density was positively correlated with the first, and to a lesser extent with the second PCA species axis and with soil moisture (Fig. 10, Table 1). The soils in the Tokar delta were dominated by a higher fraction of fine sand and silt plus clay, very different from the soils of the study area between Port Sudan and wadi Siterab. Locust density correlated negatively with the fraction silt plus clay ($r = -0.66$). Locust densities were highest in the *Dipterygium/Medicago* plant community (millet fields) followed by *Sorghum/Solanum*, and almost absent in the *P. chilensis* plant community (Fig. 11). For instance, on 25 December 2001, the number of locusts/ha was 207 ± 33 in the *Dipterygium/Medicago* plant community, 102 ± 24 in the *Sorghum/ Solanum*, 13 ± 3 in the *Brachiaria* sp., and 1 ± 1 in the *P. chilensis* plant community. Consistent differences were observed in desert locust density in the four plant communities until late in the season.

Discussion

In a field study covering three locust-breeding seasons on the coastal plain of Sudan, we found a strong association of the solitarious adult desert locust, *S. gregaria,* with millet growing areas. In most of the study area, the millet cropping areas are characterized by high incidence and density of the wild annual *H. arbainense.* This annual was growing inside the millet crops, on road verges and on large non-cropped areas. In the Tokar delta, which is distinct in soil and seasonal water availability from the rest of the coastal plain, *H. arbainense* was not present, but desert locust was here also associated with millet crops. For most of the plain, the millet growing areas are the sites with the best water availability.

It is difficult to unravel whether a higher density in the millet/*Heliotropium* habitat is caused by preference for suitable host plants or to other favourable conditions, e.g. availability of soils suitable for egg laying, sufficient soil moisture and vegetation development, or to nutrient content in plants. An indication that moisture is not the decisive factor responsible for the association of locusts with the millet agriculture or with the *Heliotropium* community is the finding that the *Heliotropium* community also showed the higher locust densities when the soil at all plant communities was also relatively moist as a result of recent rain, viz. on 22 December 1999 and 31 December 2000. In the Tokar delta, where *Heliotropium* is absent, higher locust densities were found in millet than in sorghum or other plants, even when all the sites were relatively moist. Direct observation indicates that nymphs of desert locust prefer to feed on *Heliotropium,* rather than on millet, and that their density is linearly related to the cover abundance of *Heliotropium* (Chapter 4). An indication that both *Heliotropium* ánd millet may be important indicators for locust-prone habitats, is the finding that *Heliotropium* and millet are both among the best food plants for the desert locust (Abdel Rahman, 1999), giving the highest survival and fecundity in a comparison of 27 food plant species from the Sudanese Red Sea coast. Moreover, Bashir *et al.* (2000) reported that desert locust adults prefer to lay eggs near *Heliotropium* (60%) or millet (40%) rather than near other plants. Finally, host plants in the *Heliotropium*/millet plant community have higher leaf nitrogen content than host plants in adjacent plant communities, which is likely to enhance survival, development rate and reproduction on those habitats (Chapter 6). Thus, the high density of desert locust in the millet and *Heliotropium* areas on the coastal range of Sudan can be ascribed to a complex of favourable factors, including the presence of suitable host plants (*Heliotropium* and/or millet*)*, long(er) duration of green vegetation due to higher soil moisture, and fine sandy soils conducive to egg laying (Pedgley, 1981).

This study is the first to demonstrate an association between the desert locust and plant species or plant communities. In a study in a specific habitat in the Thar desert of India, Chandra (1984a) reported that solitarious locusts were associated with specimens of *P. typhoideum* and *Tribulus terrestris*, but they did not compare distant sites with different plant communities. The latter is needed to show usefulness of locust-plant associations for site selection in survey. Stower and Greathead (1969) noted that gregarizing adults and hoppers were confined to *Heliotropium aegyptiacum* Lehm., in cultivated wadies, and rarely occurred on other plants (e.g., *S. monoica*) in the wadi Wucharo on the Red Sea coastal plain of Eritrea. In the Tamesna area of Niger and Mali, gregarizing locusts were reported to be confined to areas with the host plants *Tribulus ochroleurcus* Maire and *Schouwia purpurea* L., which together occupy less than 10% of the study area (Roffey & Popov, 1968). Isely (1938) and later Anderson (1964) reported a concentration of grasshoppers (Orthoptera: Acrididae) in sites hosting preferred food plants in Texas and Montana, USA. The Australian plague locust (*Chortoicetes terminifera* Walker) is associated with habitats with the host species Mitchell grass, *Astrebla* spp. (Lindl.) (Hunter, 1989; McCulloch & Hunter, 1983). Knowledge of habitat preferences of locusts and grasshoppers may assist in targeting and prioritizing survey operations to monitor population build-up and initiate control timely.

The important point for practical application is that while 17-27% of our sample sites were in the *Heliotropium*/millet plant community, these samples contain 93-100% of the locusts detected. This plant community covers only about 5% of the study area, and it is much more feasible to conduct survey for locust detection if these habitats are prioritized than when survey is targeted at the coastal plain as a whole. Additional work is needed to test and validate the reported findings in other breeding areas of desert locust, including those around the Red Sea.

Chapter 4

Plant species descriptors of the breeding habitat of solitarious desert locust (*Schistocerca gregaria* Forsk.) on the coastal plain of Sudan

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Chapter 4

Plant species descriptors of the breeding habitat of solitarious desert locusts (*Schistocerca gregaria* Forsk.) on the coastal plain of Sudan

Abstract

Systematic field surveys were conducted on the coastal plain of Sudan to delineate breeding habitats of solitarious desert locust (*Schistocerca gregaria* Forsk.) in the winters of 1999, 2000 and 2001. A total of 126, 97 and 97 sample sites, respectively, were visited in the three winter seasons of the study area to score oviposition probing, egg laying and hopper incidence. All of the observed probing and egg laying, and more than 95% of the observed hoppers were located in the *Heliotropium* plant community, which covered 5% of the study area. No probing and egg laying, and only a few hoppers were found in the three other main plant communities on the coastal plain, characterized by *Suaeda monoica* (Forssk.), *Panicum turgidum* (Forssk.) and *Acacia tortilis* (Forssk.), respectively. Within the *Heliotropium* plant community, hopper densities were significantly correlated with cover abundance of *Heliotropium arbainense* (Fresen.). Densities of hoppers were greatest on *H. arbainense*, lower on *Pennisetum typhoideum* (Rich.), and lowest on *S. monoica* and *P. turgidum*. These findings indicate that the *Heliotropium* plant community is the main breeding habitat of solitarious desert locust on the Red Sea coastal plain of Sudan. Here, surveys should be targeted to monitor the population build up of locusts.

Key words: Breeding habitat, hopper incidence, plant community, *Heliotropium*, *Schistocerca gregaria,* survey.

Introduction

Breeding of the desert locust (*Schistocerca gregaria* Forsk.) is associated with the occurrence of rains (more than 20 mm) allowing the development of green vegetation. The green vegetation provides food for larval locusts, called hoppers. In the recession area, locusts occur in the solitary phase for many years (Dempster, 1963; Uvarov, 1957). Build up of the locust population is likely when there is successful breeding of solitarious populations. Solitarious locusts then transform into gregarious ones and an outbreak may develop. An outbreak has been defined as the first generation of an upsurge sequence in which clear gregarious behaviour occurs. This usually takes the form of small aggregations of three and four instar nymphs comprising a few thousand individuals and covering a few square meters, often referred to as 'patches'. The size of the patches will vary but the range is probably between 5 and 20 m^2. The first generations comprise small gregariously behaving groups of hoppers with some very small bands and a few, probably non-persistent swarms of adults; a substantial proportion of the population is, however, 'scattered'. When there is further possibility of breeding, an upsurge sequence develops, which leads to a plague, consisting of a series of generations of successful breeding on widespread rains, linked by migration. As the upsurge develops, the gregariously behaving infestations get larger and more cohesive, and the proportion of the population not behaving gregariously declines. The upsurge will be considered to have become a plague after the first breeding that involves some large parent swarms. These adult swarms or hopper bands threaten crops and pastures by migrating beyond their recession habitat. For example, some valuable fodder herbs on the Red Sea coast failed to recover for about three years after being attacked by gregarious hoppers (Bashir *et al.*, 1998).

To prevent the occurrence of locust outbreaks and subsequent breeding that eventually lead to plagues, teams routinely conduct field surveys in an attempt to detect and prevent the population build-up of locusts. They do so in suspected breeding habitats, areas with 'green vegetation', following rain (Cressman, 1996a; van Huis, 1994). The area of green vegetation to be covered by ground survey teams is very large. Consequently, initial outbreaks may be missed. We hypothesize that knowledge about habitat descriptors, in particular plant communities, may help to define potential breeding sites for solitarious desert locusts. For another locust species, the Australian plague locust (*Chortoicetes terminifera*), it has been found that population build-up is associated with Mitchell grass (*Astrebla* spp.) (Hunter, 1989) and breeding habitat of grasshoppers species such as *Melanoplus sanguinipes* (Fabricius) and *M. bivittatus* (Say) is associated with specific soils and vegetation types (Johnson, 1988; Hewitt, 1985; Isely, 1938). In case of the desert locust, sites dominated by *Heliotropium* spp. and *Pennisetum typhoideum* (Rich.) or cultivated millet plants were mentioned as breeding sites (Maxwell-Darling, 1936, 1937; Stower *et al.*, 1958; Roffey & Popov, 1968; Stower & Greathead, 1969; Roffey & Stower, 1983). These reports are based on reconnaissance surveys not allowing spatially explicit quantitative assessments of locust occurrence in relation to plant communities. The aforementioned published reports focused mainly on gregarious locusts and may not apply to the solitary phase of the species.

On the coastal plain of Sudan, four plant communities were distinguished using multivariate analysis namely, the *Suaeda*, *Heliotropium*, *Panicum*, and *Acacia* plant communities (Chapter 2). In the present study, we tried (1) to identify breeding habitats of the solitarious desert locust population by quantifying oviposition probing, egg deposition and hopper incidence in these four plant communities, and (2) to establish relationships between hoppers and particular host plants within those communities.

Materials and methods

Study area. A 20 × 120 km large study area was chosen between Port Sudan (North) and the Tokar delta (South) on the Red Sea coastal plain of eastern Sudan. The plain is delineated by mountains in the West and the Red Sea in the East. In terms of vegetation, the *Acacia* plant community covers approximately 60% of the study area, *Panicum* 21%, *Suaeda* 14% and *Heliotropium* 5% (Chapter 3). The *Heliotropium* plant community is characterized by the annual herb *Heliotropium arbainense* (Fresen.) and cultivated millet, *P. typhoideum*, and is found mostly at the outflows of the wadies. Sites with the *Panicum*, *Acacia* and *Suaeda* plant communities are grazed during the winter season (Chapter 2).

The study area is characterized by hot summers (min. 28 °C and max. 41 °C) and warm winters (min. 20 °C and max. 33 °C) (Satakopan, 1965). The area receives rain between October to January. The amount of rain during the winter is variable. In 1999/2000, 158 mm of rain fell from October through January; and in 2000/2001, 138 mm from October through January (Table 1). In both winters, most rain fell in December. In 2001/2002, the total rainfall during the winter was only 29 mm which was too low to sustain plant growth. The 1999 winter season, or simply 1999, refers to the period from November of 1999 to March 2000. The same terminology was used to describe the winters of 2000/2001 (‘2000’) and 2001/2002 (‘2001’).

Locust breeding and plant communities. Oviposition probing, egg laying and hopper incidence in time were considered as locust breeding indicators and were recorded in the different plant communities. Before actual egg deposition or laying, adult females probe the soil, inserting the tip of the abdomen into the upper 10 to 15

Table 1. Monthly total rainfall (mm) during the winters of 1999/2000, 2000/2001 and 2001/2002 in Port Sudan.

Winter season	October	November	December	January	Total
1999/2000	22.0	10.6	122.8	2.2	157.6
2000/2001	25.5	42.4	70.3	0	138.1
2001/2002	0	4.9	24.0	0	28.9

cm soil layer to select suitable egg deposition sites. Eggs are normally deposited as egg pods at 5 to 15 cm depth. The tunnel above the egg pod is covered by a shiny and waxy substance called froth. The deposited eggs hatch within 10 to 14 days under the prevailing conditions at the Sudanese Red Sea coast. Hatched nymphs or hoppers can be observed around the egg deposition sites. Solitarious hoppers are green, whereas gregarizing hoppers are yellow.

At the plant community level, probing, egg laying and hopper incidence in time were measured at 120 sample sites, 60 of which were arranged in an approximately 5 × 5 km grid, and 60 in a 1 × 2 km grid within the 5 × 5 km grid used in the winter of 1999. Forty four sample sites were in the *Heliotropium*, 18 in the *Suaeda*, 40 in the *Panicum* and 18 in the *Acacia* plant communities. Data on breeding habitat indicators were taken: 7, 15, 22 and 29 December 1999; 3, 13, 19 and 26 January; and 9 February 2000. In the winter of 2000, the same data were collected at 97 sample sites, 64 of which were in a 5 × 5 km grid, and 33 in a 1 × 2 km grid within the 5 × 5 km grid. Thirty eight of the sample sites were in the *Heliotropium*, 25 in the *Panicum*, 20 in the *Suaeda*, and 14 in the *Acacia* plant community. Occurrence of hoppers was checked: 1, 15, and 31 December 2000; 13 and 27 January; 10 and 24 February; and 10 March 2001. In the winter of 2001, the same sample sites were visited: 10 and 24 November; 8 and 22 December 2001; 5 and 19 January; and 2 and 15 February 2002.

Sampling protocols. At all sample sites, probing, egg laying and hopper incidence were checked on three parallel 400 m transects. Three scouts walked 400 m in the same direction at a distance of 10-20 m from each other (Chapter 3). Presence of probing could be detected by finding the ‘probing holes’, or when females were seen during the act of probing. Deposited egg pods was ascertained by finding the shiny froth at the exit of the probed hole, or when females were seen depositing the eggs. The three scouts flushed the vegetation using a stick within a one meter swath at the three parallels 400 m transects to check the presence of any fifth instar hoppers. Hopper incidence in time was defined as the number of times hoppers were observed at a sample site divided by the number of sampling occasions. The same formula was used for estimating the incidence of probing and egg laying. The position of each sample site was ascertained by Global Positioning (GPS, Garmin 12XL).

Distribution of solitarious hoppers and host plants. In the 1999 winter season, we observed that the occurrence of solitarious hoppers was largely restricted to the *Heliotropium* plant community. Within the *Heliotropium* plant community, the next aim was to search for any associations between solitarious hoppers and host plants to be used as indicators of locust breeding sites. For this study, the Gwob-Gabol area was selected. The *Heliotropium* plant community in this area mainly consisted of *Heliotropium arbainense*, cultivated millet, and some scattered bushes of *S. monoica* and *P. turgidum*. The density of solitarious hoppers was estimated on individual plant species: *H. arbainense*, millet (*P. typhoideum*), *S. monoica* and *P. turgidum* in a 1 × 2 km grid at 28 sample sites. Most of the sample sites consisted of mixture of millet and *H. arbainense* plants, and five samples included *S. monoica*, and four samples *P. turgidum*. Presence of *S. monoica* and *P. turgidum* in the study area was limited due to the replacement of these bushes by millet. *H. arbainense*, a naturally occurring herb, was growing at the fringes of the millet cultivated fields and in less cropped sites.

Hoppers on *H. arbainense* sample sites were counted using 10 quadrats of 30 × 30 cm area and 20 cm height, placed over *Heliotropium* plants. In the case of *S. monoica* and *P. turgidum*, 3-5 individual plants per site were selected, the area of each plant was measured and the number of hoppers per plant was counted. The density of hoppers at each sample site was expressed per unit area of foliage cover of the host plants. The foliage cover of *Heliotropium* in each sample site was estimated to the nearest 5% (Kent & Coker, 1992). Hoppers on millet in the *Heliotropium* plant community were counted on 60 plants per sample site. The area ground cover by the millet plants of one hill was about 1 m^2. Hoppers were counted on 17 and 24 February, and 2, 6 and 12 March 2000.

Further samples were taken using a 50 × 50 m grid, to determine the presence of relationships between the foliage cover of *H. arbainense* and hopper density. Hoppers were counted at 42 sample sites in a 300 × 350 m area in the northern part of Gwob-Gabol. Hopper density was estimated using 10 quadrats per sample site. The foliage cover of *Heliotropium* in each sample site was estimated as in the 1 × 2 km grid on 17 February 2000. The sample sites were visited 18 and 25 February, and 3 March 2000, and the average hopper count per site was used in analysis. In 2000 and 2001, hopper abundance was low and therefore not estimated.

Distribution of gregarious hoppers and host plants. Incipient development of gregarious hoppers was found in a millet field in wadi Ashat in February 2000. The spatial pattern was estimated in a 150 × 700 m area which was subdivided for sampling in 42 plots of 50 × 50 m each. The whole of each plot was searched for presence of hopper patches. If a hopper patch was found, the infested area was estimated and the densities of hoppers were assessed. If hoppers were present in *H. arbainense* vegetation or on *S. monoica*, their density in the foliage was estimated using five quadrats. Foliage cover of *H. arbainense* and *S. monoica* was scored to the nearest of 5%. Hoppers on millet were enumerated per hill. Total hopper numbers per plot were estimated by multiplying estimated densities per unit area (patch, *H.*

arbainense, *S. monoica*) or per hill (millet) with the appropriate patch or host area in the plot. Hill area for millet was taken to be one m^2.

Data analysis. The spatial distribution and association of the average hopper incidence in time and plant communities as well as hopper density and cover abundance of *Heliotropium* plants were mapped using ArcView GIS v3.3 in 1999 and 2000. The strength of the relationship between hopper density and *Heliotropium* cover abundance was estimated by least square regression analysis using SPSS (SPSS, 1999).

Results

Locust breeding sites and plant communities. In the winters of 1999 and 2000, probing and egg laying were observed in the *Heliotropium* plant community only (Figs. 1a and b). In the winter of 2001, no probing or egg deposition was observed in any plant community.

In 1999, about 95% of the hoppers were found in the *Heliotropium* plant community and hardly any in the *Suaeda* and *Acacia* plant communities (Fig. 1c). In 2000, hoppers were found in the *Heliotropium* plant community only. In 2001, when the *Heliotropium* plant community was dry, no hoppers were found in any of the plant communities. Hopper incidence within the *Heliotropium* plant community sites was highest (29%) in 1999, intermediate (10%) in 2000, and nil in 2001. In both 1999 and 2000, the distribution of hopper incidence was confined largely and spatially to the *Heliotropium* plant community (Figs. 2a and b).

Distribution of solitarious hoppers and host plants. In the winter season of 1999, the number of solitarious hoppers, measured per m^2 host plant area, was greater on *H. arbainense* than on millet, *S. monoica*, or *P. turgidum* (Fig. 3). For instance, on 17 February 2000, the average number of hoppers/m^2 area covered was 3.4 ± 1.0 on *H. arbainense*, while no hoppers were found on *S. monoica* or *P. turgidum*. High densities of solitarious hoppers were associated with high cover abundance of *H. arbainense* plants in 1999 (Fig. 4). The results were further analysed by regression indicating significant correlation between area cover with *Heliotropium* and the density of solitarious hoppers at a site (number per m^2 plant area) (Fig. 5).

Distribution of gregarious hoppers and host plants. The densities of gregarious hoppers (number/m^2 host plants) observed on 27 and 28 February 2000 were higher on *H. arbainense* (34 ± 7 hoppers/m^2) than on millet (3 ± 1 hoppers/m^2), or on *S. monoica* (7 ± 4 hoppers/m^2) (Fig. 6). The pattern of gregarious hopper distribution correlates

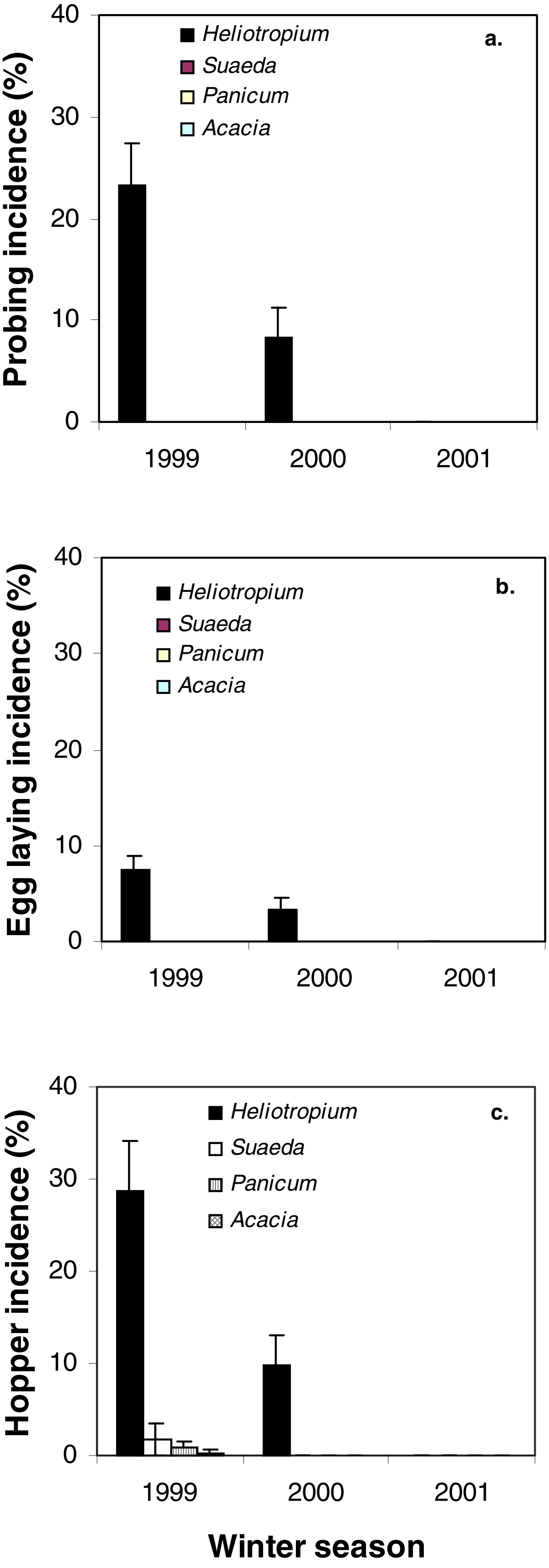

Fig. 1. Incidence of probing (a), egg deposition (b) and hoppers (c) in four plant communities in the winters of 1999, 2000 and 2001.

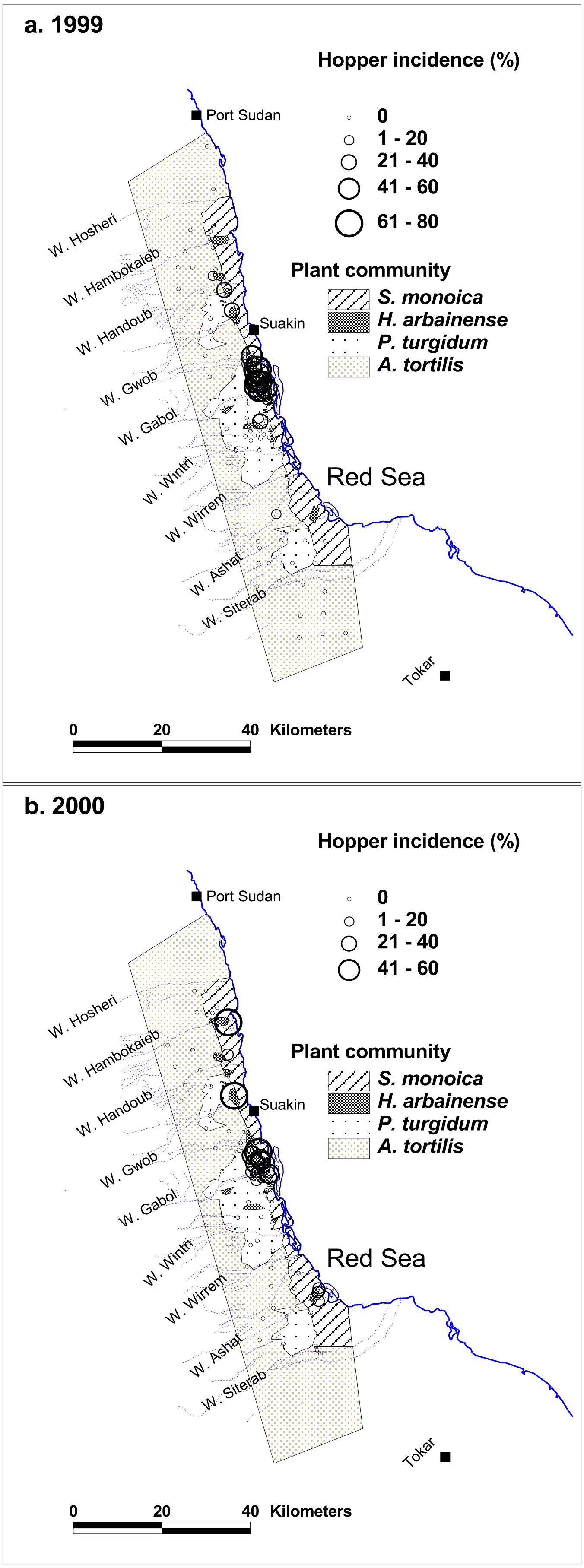

Fig. 2. Distribution map of hopper incidence (%) in relation to plant communities in the winter season of 1999 (a) and 2000 (b). Each circle in the map represents a sample site and its area represents hopper incidence.

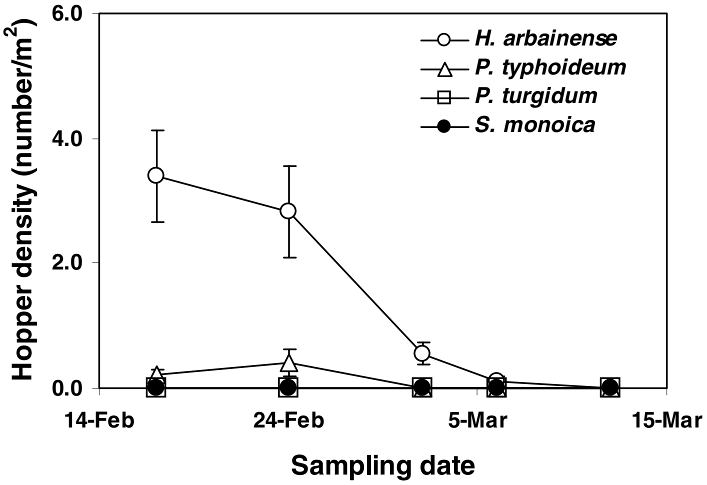

Fig. 3. Density of hoppers (number/m^2 plant cover) on *Heliotropium*, millet (*P. typhoideum*), *S. monoica* and *P. turgidum* plants in solitarious populations (b). Arrow bars indicate standard error of the mean.

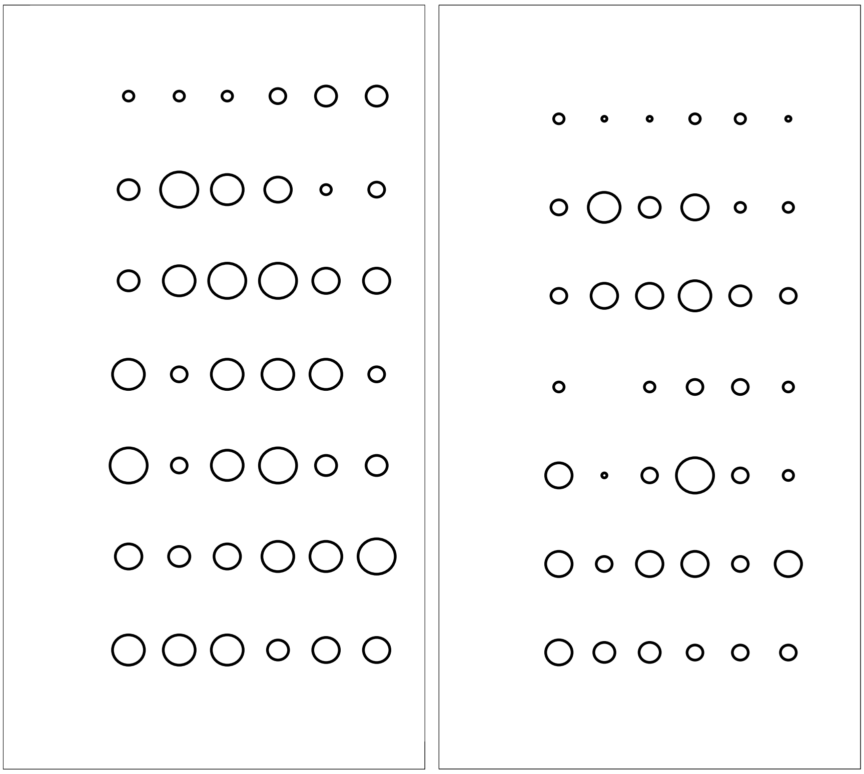

Fig. 4. Distribution maps of cover percentage of *Heliotropium arbainense* (left) and density (number locusts per m^2 plant cover) of solitarious locust hoppers (right) in a 300 × 350 m area of the *Heliotropium* plant community in wadi Gwob-Gabol in the 1999 winter season. Each circle in the map represents a sample site and its area represents *Heliotropium* cover (left) or hopper density (right).

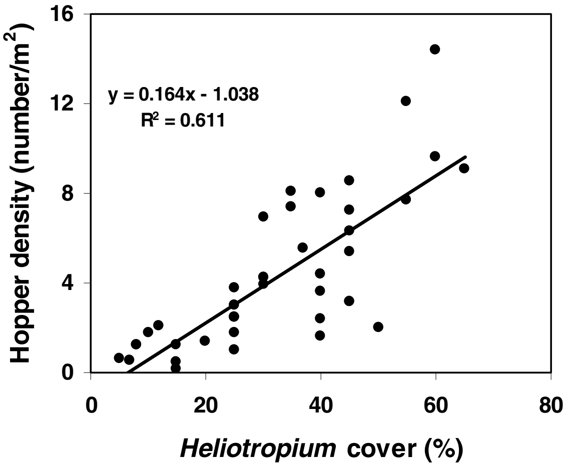

Fig. 5. Relationship between solitarious hopper density and cover abundance of *Heliotropium arbainense*.

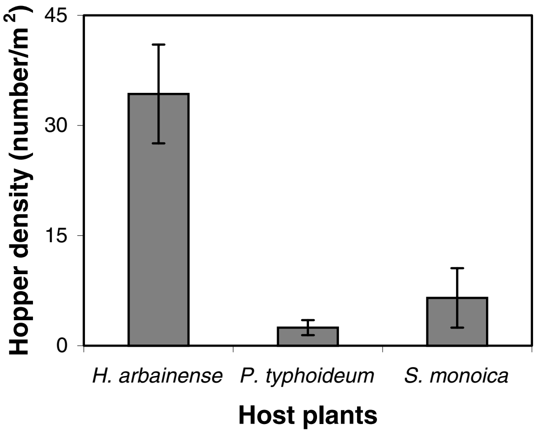

Fig. 6. Density of hoppers (number/m^2 plant cover) on *Heliotropium*, millet and *S. monoica* plants in a gregarious locust populations in wadi Ashat in the 1999 winter season. Arrow bars indicate standard error of the mean.

positively with the cover abundance of *H. arbainense* (Figs. 7 and 8). This shows that per unit of *Heliotropium* cover, the density of hoppers was practically constant (Fig. 8).

Discussion

Probing, egg laying and hopper incidence as indicators of solitarious locust breeding habitats were largely confined to the *Heliotropium* plant community. Hopper density was correlated with ground cover by *H. arbainense*. There are several reasons why the *Heliotropium* plant community may be a preferred breeding habitat of the desert locust.

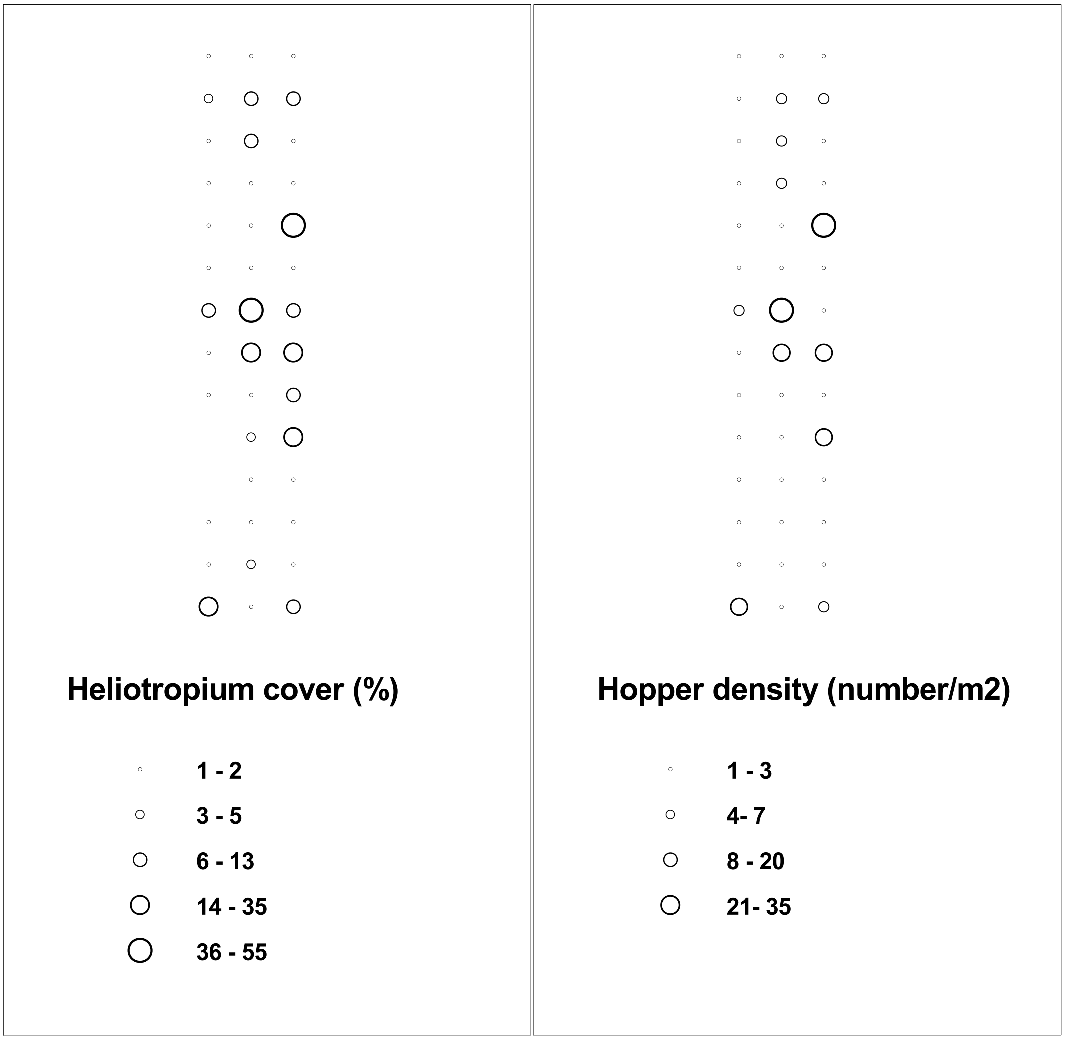

Fig. 7. Distribution maps of cover percentage of *Heliotropium arbainense* (left) and density (number per m^2 soil) of gregarious locust hoppers (right) in a 150 × 700 m area of *Heliotropium* plant community. Each circle in the map represents a sample site and its area represents *Heliotropium* cover or hopper density.

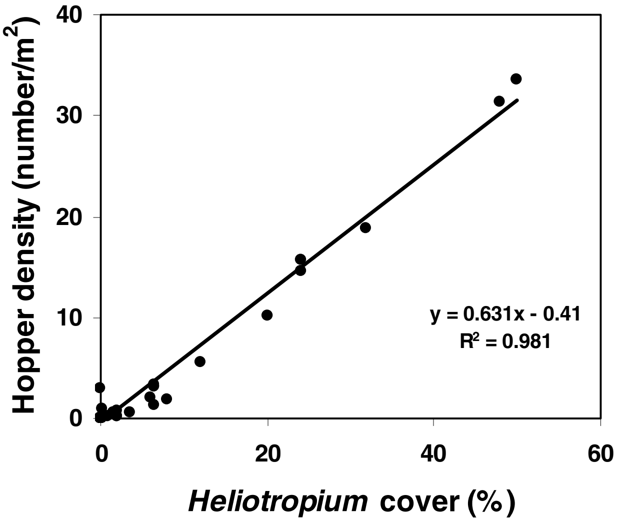

Fig. 8. Relationships between the spatial distribution of the gregarious hopper densities and cover abundance of *Heliotropium* plants at 50 × 50 m grid.

First, the fine soils in the *Heliotropium* sites stay relatively moist for an extended period of time, which renders them more (Chapter 3) suitable for successful egg deposition, development, and hatching than the other plant communities. Second, presence of high quantity and quality host plants or suitable host plants with high leaf nitrogen content may attract adults and hoppers (Chapter 6). Thirdly, the association of hoppers with the *Heliotropium* plant community and *H. arbainense* host plants may be related to a better protection or shelter. Particularly, the patchy green mat of *Heliotropium* plants could be a good protection against natural enemies, mainly the locust-eating birds observed in the area. The *Heliotropium* plant community provides food without competition and disturbance from grazing while the other plant communities were heavily grazed (Chapter 2). Parallel observations on the same sites and season indicate that hoppers prefer to feed on *Heliotropium* and millet compared to other plants (Chapter 6). Similarly, preference of hopper feeding on *Heliotropium* plants was also reported from the coastal plain of Sudan (Bashir *et al.*, 1998), from Mauritania (Culmsee, 2002) and from India (Chandra, 1984a). In the absence of *Heliotropium* plants in the Tokar delta in the 2001 winter season, however, we observed that millet is preferred over other food plants such as sorghum and cotton. The choice of hoppers for *Heliotropium* and millet plants is in line with results of laboratory studies by Abdel Rahman (1999). He found that *Heliotropium* and millet gave the highest survival and fecundity of the desert locust when comparing 27 food plant species from the Sudanese Red Sea coast. Besides, the leaf nitrogen content of host plants within the *Heliotropium* plant community was higher than that of the same plants found in nearby sites in the *Panicum* plant community (Chapter 6).

Locust breeding in 1999 seems more successful than in the other two seasons that led to the development of gregarizing hoppers. This development of gregarizing hoppers occurred in the *Heliotropium* plant community indicating that this plant community is a potential locust breeding site where local outbreaks could develop. These findings indicate that the *Heliotropium* plant community, which covers approximately 5% of the surveyed area is the major breeding habitat for solitarious desert locust. Here, surveys should be targeted to monitor the population build up of locusts. Abundance of *H. arbainense* host plants could be further used as an indicator for desert locust breeding sites to guide surveys. The plant communities at the coasts on both sites of the Red Sea are similar (Chapter 2), and, therefore, it should be verified whether our results are also valid for these areas.

Chapter 5

Spatial variability of solitarious adult desert locust (*Schistocerca gregaria* Forsk.) populations on the coastal plain of Sudan

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Chapter 5

Spatial variability of solitarious adult desert locust (*Schistocerca gregaria* Forsk.) populations on the coastal plain of Sudan

Abstract

The spatial distribution of desert locusts on the southern part of the coastal plain of Sudan was determined using regular sampling grids with up to 126 sample sites throughout the winters of 1999 and 2000. Geostatistical procedures were used to describe the spatial pattern and estimate locust densities at unsampled sites. Sample variograms indicate that 71-90% of the population variance was explained spatially over a range of 5 to 24 km. This range shrunk as dry conditions towards the end of the season concentrated the locusts in the most suitable and still sufficiently humid areas. Locust densities were significantly and positively correlated with cover abundance of the host plants *Heliotropium* and millet. Locust densities at unsampled sites were well estimated and kriging maps delineating the high and low locust sites were produced. The relationship between sampling intensity and kriging variance was explored. Geostatistical methods offer promise for assisting in the optimization of sampling efforts for the desert locust.

Key words: Desert locust, geostatistics, kriging, *Heliotropium*/millet, sampling.

Introduction

The desert locust (*Schistocerca gregaria* Forsk.) usually lives at low densities in the arid and semi-arid areas of Africa, the Middle East and south-west Asia. An outbreak occurs when there is a marked increase in the number of locusts as a result of concentration, multiplication and gregarization. This may eventually lead to upsurges and plagues with marching hopper bands and migrating swarms (Pedgley, 1981). The change from the solitary to the gregarious phase is associated with a profound change in locust physiology and behaviour. Gregarious locusts migrate in swarms and invade areas outside their recession habitat, damaging crops and pastures over a very large area of the arid and semi-arid lands. Monitoring the build-up of solitarious locusts before they lead to upsurges and plagues is difficult because the area to be monitored is huge (van Huis, 1994). Many outbreaks in the past may not have been detected until they had become too large for effective control (Symmons, 1991; van Huis, 1994). An example was the 1986-89 locust plague during which some 65 countries were infested.

Currently, ground surveys are the principal means for monitoring the build-up of solitarious populations (FAO, 1994). In practice, ground survey teams search in the most likely locust habitats, i.e. areas with green vegetation. The Sudanese Red Sea coast is often an important element in the chain of subsequent breeding areas that leads to plagues (Maxwell-Darling, 1936). The locust habitat on the southern part of the coastal range of Sudan was classified and described using site descriptors such as soils and plant community composition, along with the presence of locusts (Chapter 2). Solitarious locust densities within the green habitat appeared to vary greatly in relation to plant communities (Chapter 3). When the distribution of solitarious locusts is variable, it is difficult to obtain reliable density estimates when only a few sites are visited. A fundamental problem in monitoring the build-up of locust populations in a heterogeneous habitat with a patchy locust distribution is how well locust density can be estimated at unvisited sites using data from nearby visited or surveyed sites.

A geostatistical modelling approach was adopted to quantitatively describe the spatial variation in locust density and predict locust density at unsampled locations. Geostatistics was originally developed in earth sciences for describing and modelling earth resources (e.g., Cressie, 1993). It has also been applied in ecology (Robertson, 1987; Rossi *et al.*, 1992), for example, to analyse the spatial distribution of insects (e.g., Schotzko & O'keeffe 1989; Liebhold *et al.*, 1991; Hohn *et al.*, 1993). Kriging or optimum interpolation methods were found superior in estimating attributed values at unsampled locations as compared to Thiessen polygons and trend surface methods (e.g., Tabios & Salas, 1985). Kriged maps of grasshopper distribution were used to delineate zones of high density. These maps were found useful for assisting area wide surveys for grasshoppers in Montana, the USA (Kemp *et al.*, 1989). The kriging variance can be used to ascertain the sampling spacing necessary to achieve a particular accuracy or precision (Burgess *et al.*, 1981; McBratney *et al.*, 1981; van Groenigen *et al.*, 1999). So far, kriging methods have not been applied to estimate locust densities.

The objective of this study was: (1) to describe the spatial pattern of locust density on the coastal plain of Sudan; (2) to determine whether locust densities can be predicted at unsampled locations by means of kriging; and (3) to determine the relationship between kriging variance and sample spacing. We aimed at attaining a better understanding of the mechanisms underlying spatial patterns of locusts and hoped to find clues how scarce sampling resources might be used more efficiently.

Materials and methods

Study sites. The study area is located between Port Sudan and the Tokar delta on the Red Sea coastal plain of eastern Sudan. The area is a narrow plain extending 20 to 40 km between the Red Sea Hills in the west and the Red Sea in the east (Fig. 1). Run-off water towards the sea creates a gradient in the deposition of soil particle size, moisture and the type of vegetation they support. The coarsest particles, gravel, are deposited in the foothills, and are mostly occupied with scattered scrub vegetation, the *Acacia tortilis* plant community (Chapter 2). Coarse sand is deposited further east, and this area is mostly covered with perennial grassland, the *Panicum turgidum* plant community. At the eastern edge of the coarse sand area, fine sand is deposited in wadi outflow zones, which are often cropped with millet. The locust food plant *Heliotropium arbainense* is common in the wadi outflow zones. Wadi outflow areas are relatively moist during the winter season. The most important wadies are Hambokaieb, Gwob, Gabol and Ashat (Fig. 1). Near the sea, where the soil is salty, the succulent shrub *Suaeda monoica* dominates. During the winters of 1999 and 2000 (October-March), rainfall was measured in Port Sudan: 158 mm of rain was recorded from 15 October to 30 December 1999; and 138 mm from 14 October to 19 December 2000. In both seasons, most of the rain fell in December, and none in January, February or March (Chapter 2).

Sampling. In the 1999 winter season, solitarious adult locusts were counted between December 1999 and February 2000. This period will be referred to as the 1999 winter season or simply 1999. The same terminology is used for the winter of 2000/2001 ('2000'). In 1999, locusts were counted at 126 sites, 66 of which were arranged in a 5 × 5 km grid, 60 in a 1 × 2 km grid in cropland, and its adjacent sites in a 5 × 5 km grid (Fig. 1a). Locusts were counted on nine occasions at 1 to 2 week intervals in an area of about 20 km wide east-west and 120 km long north-south. At each sample site, solitarious locusts were counted on a 1 m wide swath by each of three observers walking a 400 m transect. The three parallel transects were spaced approximately 10 m apart. The same sites were revisited using Geographic Positioning (GPS Garmin 12XL). Locust counts were converted to a hectare basis and locust counts/ha were log-transformed before spatial analysis.

***Heliotropium*/millet cover.** During both winters, cover abundance index of the host plants *Heliotropium* and millet was scored in three 10 × 10 m plots at 50 m, 250 m and 350 m, respectively, along one of the three 400 m transects per sample site. Cover abundance was scored using a modified version of the Braun-Blanquet 1-9 point scale (van der Maarel, 1979). The average cover abundance of both plants was taken and correlated with average locust density.

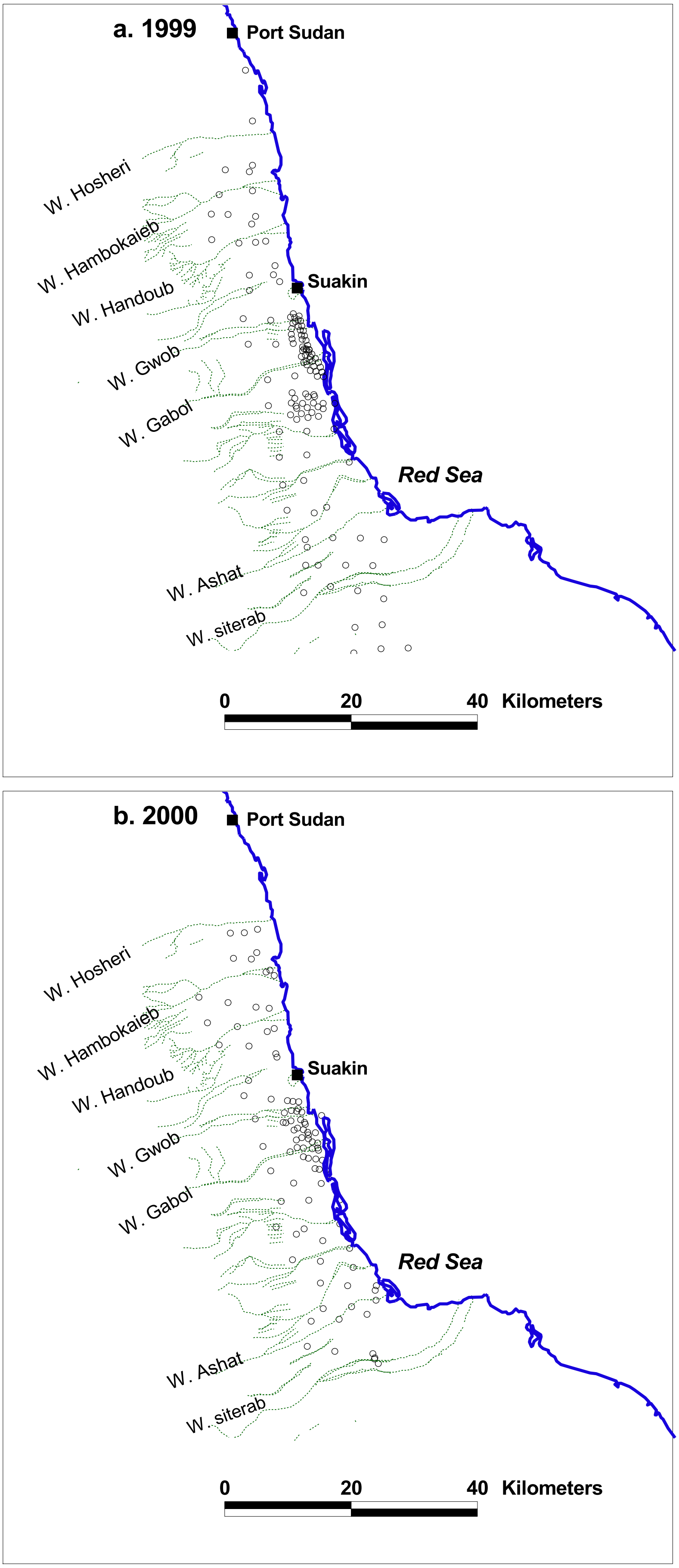

Fig. 1. Map of the study area showing the distribution of sampling sites and major wadies in 1999 (a) and in 2000 (b).

Spatial analysis

A geostatistical analysis was applied in two steps. First, the degree of correlation among sample sites at different distances was characterized by fitting variograms. Second, maps were constructed using kriging or optimum interpolation. Spatial correlation was evaluated by means of the semivariance $\gamma(h)$:

$$\gamma(h) = \frac{1}{2N(h)} \sum_{i=1}^{N(h)} [z\,(x_i) - z\,(x_i+h)]^2$$

where h is distance, $N(h)$ is the total number of sample pairs for the lag interval h, $z(x_i)$ is the log-transformed locust density measured at site x_i; and $z(x_i+h)$ is log-transformed measured locust density at site x_i+h at a distance h from x_i. The shape of the resulting plot of $\gamma(h)$ vs. h describes the spatial dependence. To the empirical variogram data, a spherical and a wave variogram model were fitted.

The spherical model is defined as:

$$\gamma_s(h) = C_0 + C\,[1.5\,(\frac{h}{a}) - 0.5\,(\frac{h}{a})^3] \qquad h \leq a,$$

$$\gamma_s(h) = C_0 + C \qquad h > a$$

$$\gamma_s(0) = 0$$

Here, the parameter a, defines the range, C_0 the 'nugget', i.e., the semivariance at $h = 0$, and $C_0 + C$ the 'sill', i.e. the semivariance for $h \rightarrow \infty$.

The wave model is defined as:

$$\gamma_w(h) = C_0 + C \left[1 - \frac{\sin(\frac{h}{a})}{\frac{h}{a}}\right] \qquad h > 0$$

$$\gamma_w(0) = 0$$

The parameters C_0 and C have the same meaning as in the spherical model, whereas the parameter a is now a combination of a measure of the period length of the sine wave, measured in km and a damping factor.

Both models were fitted across a maximum lag of 30 to 40 km. The relative nugget effect $C_0/(C_0+C)$ was used to quantify the relative importance of spatially unexplained error (C_0; the nugget) with respect to the total variance (C_0+C; the sill). If the ratio of $C_0/(C_0+C)$ approaches zero, apparent spatial dependence is high, i.e., a large proportion of the total sample variance is spatially dependent. If the ratio of $C_0/(C_0+C)$ approaches 1 then the spatial dependence is low, i.e., the data are not spatially correlated.

Kriging. Kriged maps were produced by ordinary kriging with a block size of 1 × 1 km across the area and a 2 × 2 discretization grid within each block (Isaaks & Srivastava, 1989; Robertson, 2000). Geostatistical analysis was made using GS$^+$ version 5.3b (Robertson, 2000) and results were confirmed some test cases in S+ (version 6.0). Kriged log-transformed locust counts were back transformed to original units prior to mapping. The back-transformed locust densities were mapped using ArcView GIS version 3.3.

Cross validation. Cross validation was used to test how well locust densities were estimated using kriging. In cross validation analysis, the locust count at each site was individually removed from the data used for estimating the variogram and its density was estimated via ordinary block kriging. The estimated and observed locust densities were then compared. The mean square error (MSE) was estimated. The MSE should be (considerably) less than the sample variance (s^2) in order to improve upon non-spatial predictions.

Optimal sampling. For survey purposes, a decision on sampling spacing is needed to estimate the locust density within a certain precision or tolerance. A compromise must be reached between sampling effort and precision. For this purpose, optimum sampling as defined by McBratney *et al.* (1981) was applied, based on the property of the kriging variance to be independent of observation values. Using the variogram parameter values and data locations with different sampling spacing, a graph showing the relationship of sample spacing and kriging error was produced. Such a graph yields an optimal sampling spacing given a prescribed level of precision. As a first approximation, a square grid configuration and isotropic variation in locust distribution was assumed.

Results

Locust density and *Heliotropium*/millet cover. In general, the frequency distribution of the locust densities in 1999 (data for single sites and dates, all data pooled) was positively skewed with 75% of the sites having less than 100 locusts/ha, 19% between 101 and 500 locusts/ha, and 6% more than 501 locusts/ha (Fig. 2a). Similar results were observed in the mid (Fig. 2b) and late (Fig. 2c) season of 1999. In 2000, all sites had fewer than 40 locusts/ha (Fig. 2d). The skewed distributions of locusts in both winter seasons indicate that some sites were ‘hot spots’ for high locust densities, where conditions might be more favourable. These spots were characterized by high cover abundance of the host plants *Heliotropium* and millet in the cultivated wadies (Fig. 3).

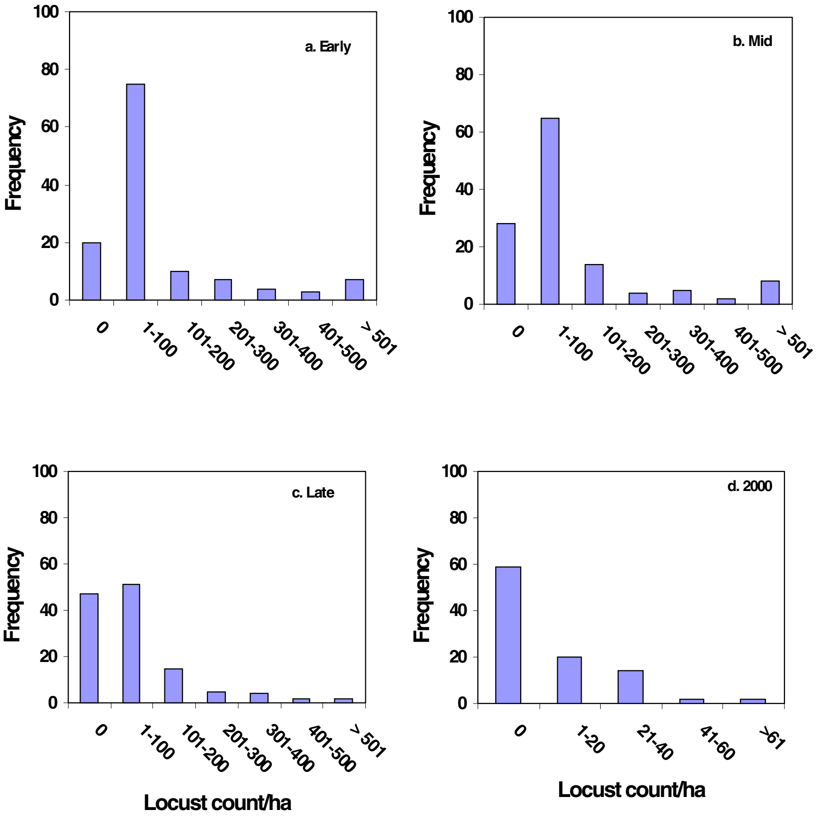

Fig. 2. Frequency distribution for locust density (number/ha): in early (a), mid (b), and late (c) seasons in 1999; and in 2000 (d).

Thus, the locust densities were significantly and positively correlated with the cover abundance of *Heliotropium*/millet in the early season ($r^2 = 0.610$, $p < 0.01$, $n = 126$; Fig. 3a), in the mid season ($r^2 = 0.652$; Fig. 3b), and in the late season ($r^2 = 0.689$; Fig. 3c) of 1999, as well as in 2000 ($r^2 = 0.729$, $p < 0.01$, $n = 97$; Fig. 3d). When the sites with no locusts were removed and refitted, the correlations were still significant during the early ($r^2 = 0.550$, $p < 0.01$, $n = 106$), mid ($r^2 = 0.628$, $p < 0.01$, $n = 98$), and late season in 1999 ($r^2 = 0.643$, $p < 0.01$, $n = 79$), and in 2000 ($r^2 = 0.216$, $p < 0.01$, $n = 38$).

Three phases are distinguished when discussing locust densities observed during the winter season of 1999. During the first phase, which included samples on 7, 15 and 22 December, annuals germinated and vegetation cover increased due to slight rainfall in October (29 mm) and November (13 mm), and good rainfall from 17-20 December (123 mm). During the second phase, which included samples on 29 December 1999, and 3 and 13 January 2000, the vegetation was green. During the third phase, which included samples on 19 and 26 January and 9 February 2000, the vegetation was desiccating because of absence of any rainfall after 30 December 1999. Locust density (mean ± SEM) was 94 ± 14 locusts/ha during the early part of the winter, 103 ± 18 locusts/ha during the mid part, and 62 ± 11 locusts/ha during the late part.

In the winter of 2000, the sequence of greening, maximum, and drying vegetation cover was less clear-cut than in 1999; therefore, the overall locust density at a site, averaged over eight sample occasions, was analysed.

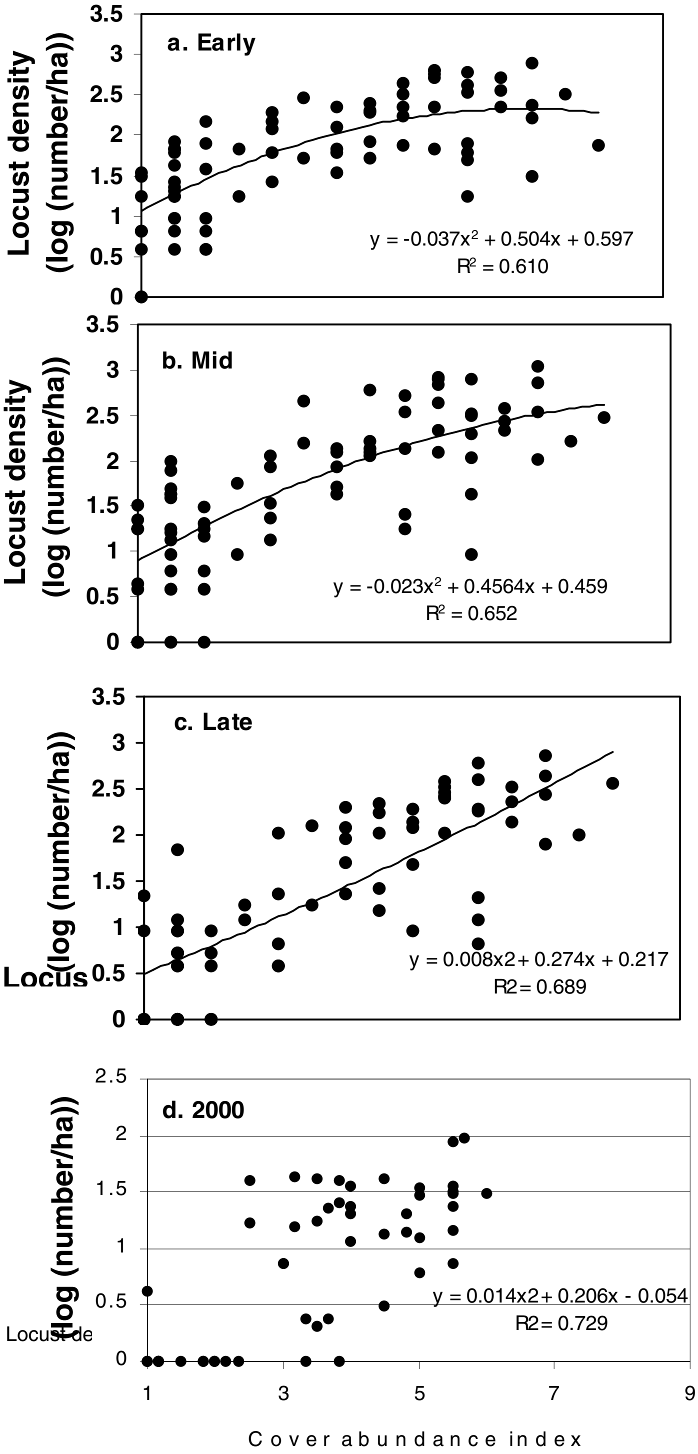

Fig. 3. Relationship of locust density (log (number/ha)) and *Heliotropium*/millet cover abundance: early (a), mid (b), and late (c) season in 1999; and in 2000 (d).

Sample variograms. The spatial correlation of locusts and cover abundance of *Heliotropium*/millet plants was best described using a spherical variogram model. A strong spatial structure was shown in the early, mid and late season of 1999 (Fig. 4). The relative nugget effects of the sample variogram were 10%, 12% and 14%, respectively (Figs. 4a-c), which indicates that 86 to 90% of the total variation was explained spatially. The correlation range was 23, 17 and 11 km for the early, mid and late season, respectively (Figs. 4a, b, c; Table 1). The relative nugget effect of *Heliotropium*/millet cover abundance was 22% and the correlation range was 11 km (Fig. 4d). As in 1999, the spatial distribution of locusts and *Heliotropium*/millet cover abundance in 2000 was best described using the spherical model (Figs. 4e, f). The locust correlation range in this dry season was only 5 km and the relative nugget effect was 29%, which means that 71% of the variation was spatially described, i.e., less than in 1999 (Fig. 4e; Table 1). The *Heliotropium*/millet cover abundance showed a range of 8 km and a relative nugget effect of 40% (Fig. 4f). The decrease in range during the season of 1999 and in 2000 compared to 1999, indicates a 'shrinkage' of the size of suitable habitats for locusts under drier conditions.

Table 1. Parameters of spherical model sample variograms ($\gamma_s(h)$) in early-, mid-, late-season locust density, cover abundance of *Heliotropium*/millet (HM) in 1999, and in 2000, including reduced sum of squares (RSS), mean square error (MSE), and sample variance (s^2).

Data type	Nugget (C_0)	Sill (C_0+C)	Range parameter (*a*) (km)	r^2	RSS	MSE	s^2
1999							
Locust Early season	0.094	0.915	23.040	0.944	0.070	0.233	0.726
Locust Mid season	0.124	1.012	16.620	0.898	0.128	0.288	0.839
Locust Late season	0.132	0.942	10.980	0.631	0.369	0.293	0.844
HM cover	1.350	6.116	11.10	0.808	5.27	1.879	5.583
2000							
Locust	0.126	0.441	5.11	0.542	0.027	0.311	0.424
HM cover	0.922	3.777	8.28	0.785	1.72	2.89	4.009

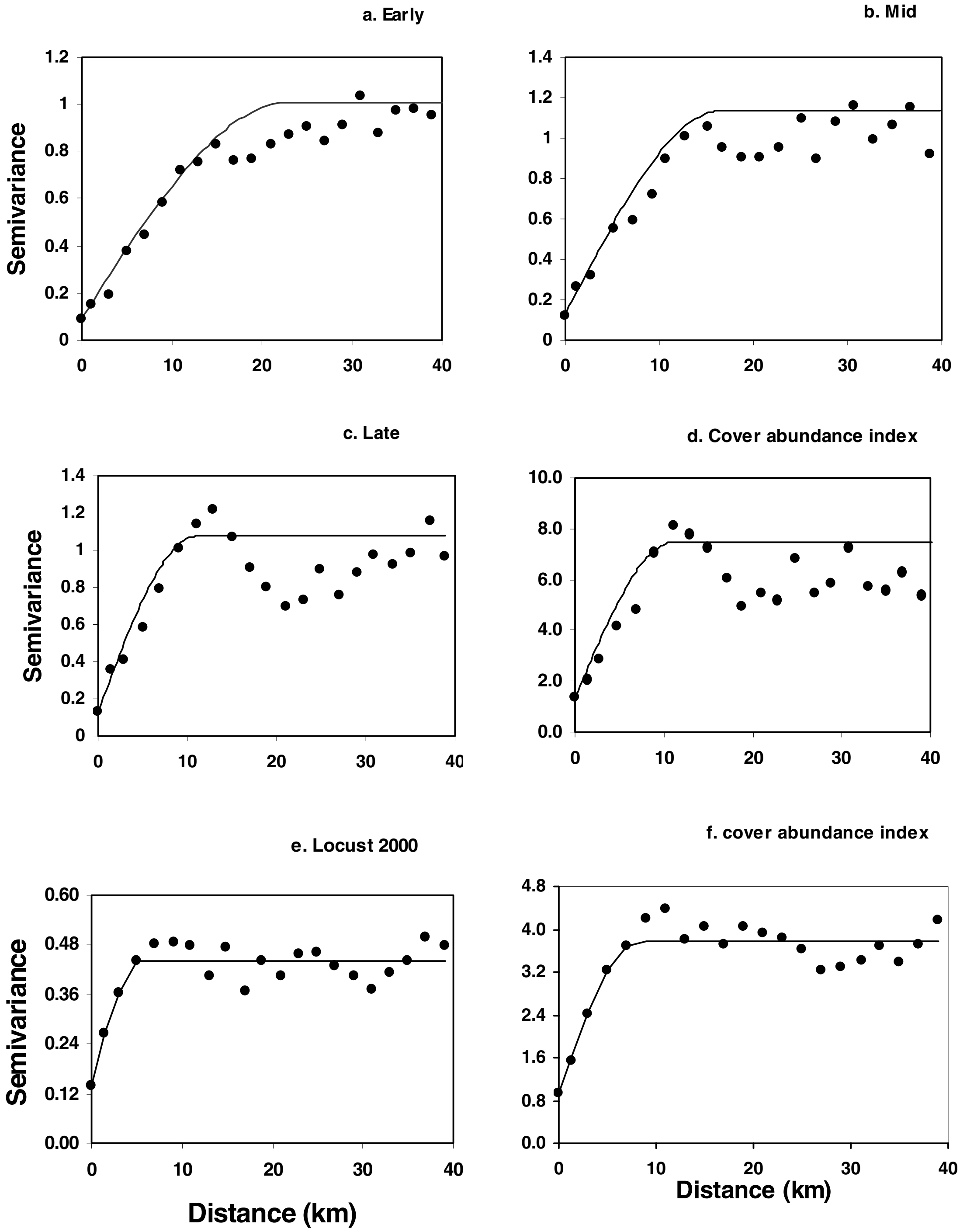

Fig. 4. Sample (•) and fitted variograms (—) for sample variograms of locust density (log (number/ha)): early (a); mid (b), and late (c) season, and *Heliotropium*/millet cover abundance (d and f) in 1999; locust density (log (number/ha)) (e), and *Heliotropium*/millet cover abundance (f) in 2000. All fitted with spherical model.

In 1999, a periodicity in the sample variograms was observed, especially during the late season (Fig. 5a), and also in the *Heliotropium*/millet cover abundance (Fig. 5b). This periodicity was fitted with a wave variogram model. In this model the late season locust variograms had a relative nugget effect of 28% and a period parameter (*a*) of 2.77 km (Fig. 5a; Table 2). For the *Heliotropium*/millet cover abundance, the relative nugget effect was 24% and the period parameter was 2.68 km (Fig. 5b, Table 2).

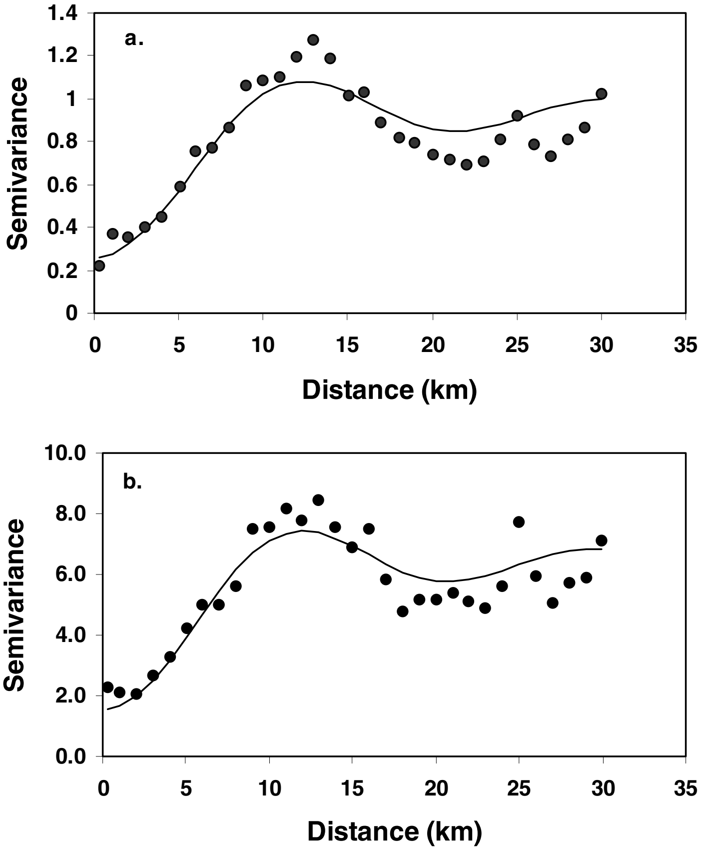

Fig. 5. For late 1999, sample (•) and fitted variograms (—) of locust density (log (number/ha)) fitted with wave model (a), *Heliotropium*/millet cover abundance (b).

Table 2. Parameters of wave model sample variograms ($\gamma_w(h)$) in late season locust density and cover abundance of *Heliotropium*/millet (HM) in 1999 including weighted sum of squares (WSS).

Data type	Nugget (C_0)	Sill (C_0+C)	Range parameter (*a*) (km)	WSS
Locust density	0.262	0.935	2.768	47.3
HM cover	1.555	6.383	2.680	2338.6

Kriged maps. The kriged maps of locust density and *Heliotropium*/millet cover in 1999 show that there was a single hot spot of high locust density in the sampling area, *viz.* in the outflow area of the wadies Gwob and Gabol (Figs. 6a-c), where there was a large cropping area, of maximally 3 km east-west by 10 km north-south, with high cover abundance of *Heliotropium* and millet (Fig. 6d). Similar results were observed in the wadi outflows of Handoub. The greatest extent of the estimated high density area for locusts was reached in the early season (Fig. 6a). During the mid season (Fig. 6b), and especially during the late season (Fig. 6c), the area with high locusts densities contracted. In 2000, the sites with highest kriged estimates of locust density (18-35 locusts/ha) again occurred at the outflows of the wadies Gwob and Gabol followed by the wadi outflows of Ashat and Hambokaieb (Fig. 7a). Again, the highest estimated locust densities coincided with high cover abundance of the *Heliotropium*/millet (Fig. 7b).

Validation. Cross validation indicated a very good correspondence between estimated and observed locust densities (Fig. 8, Table 3). In both winter seasons, the regression coefficients were not significantly different from one (i.e. the slope of the 45 degree line), indicating that the estimated locust density was consistent with the observed locust density (Table 3). The proportion of variation explained by the regression diminished marginally from the early season ($r^2 = 0.679$, $p < 0.01$; Fig. 8a, Table 3) to the mid season ($r^2 = 0.655$, $p < 0.01$; Fig. 8b) to the late season ($r^2 = 0.653$, $p < 0.01$; Fig. 8c). In 2000, the correlation between estimated and observed locust density was low ($r^2 = 0.379$, $p < 0.01$; Fig. 8d). MSE values were lower than the sample variance (s^2) of the observed locust counts in both winter seasons (Table 1) indicating that the spatial predictions do offer useful information, even in 2000.

Optimizing sampling. The relationship between the tolerance level for the standard error of the estimated (kriged) locust density and sample spacing in 1999 and 2000 is shown in Fig. 9. In 1999, the required sample spacing to reach a designated accuracy decreased during the season. For instance, to reach a standard error of six locusts/ha (which corresponds to a variance of 36, approximately 30% of the maximum kriging variance), the required sample spacing was nine km in the early season, five km in the mid season, and two km in the late season (Fig. 9a). Thus, as the season progressed, suitable habitats contracted and locusts became more aggregated, causing the spacing required for sampling to decrease. In 2000, the tolerance level for the standard error of the estimated five locusts/ha (55% of the maximum variance) corresponded to a sampling spacing of about one km (Fig. 9b). Better precision can be obtained at a sampling spacing of less than one km, which would not be feasible in desert locust surveys.

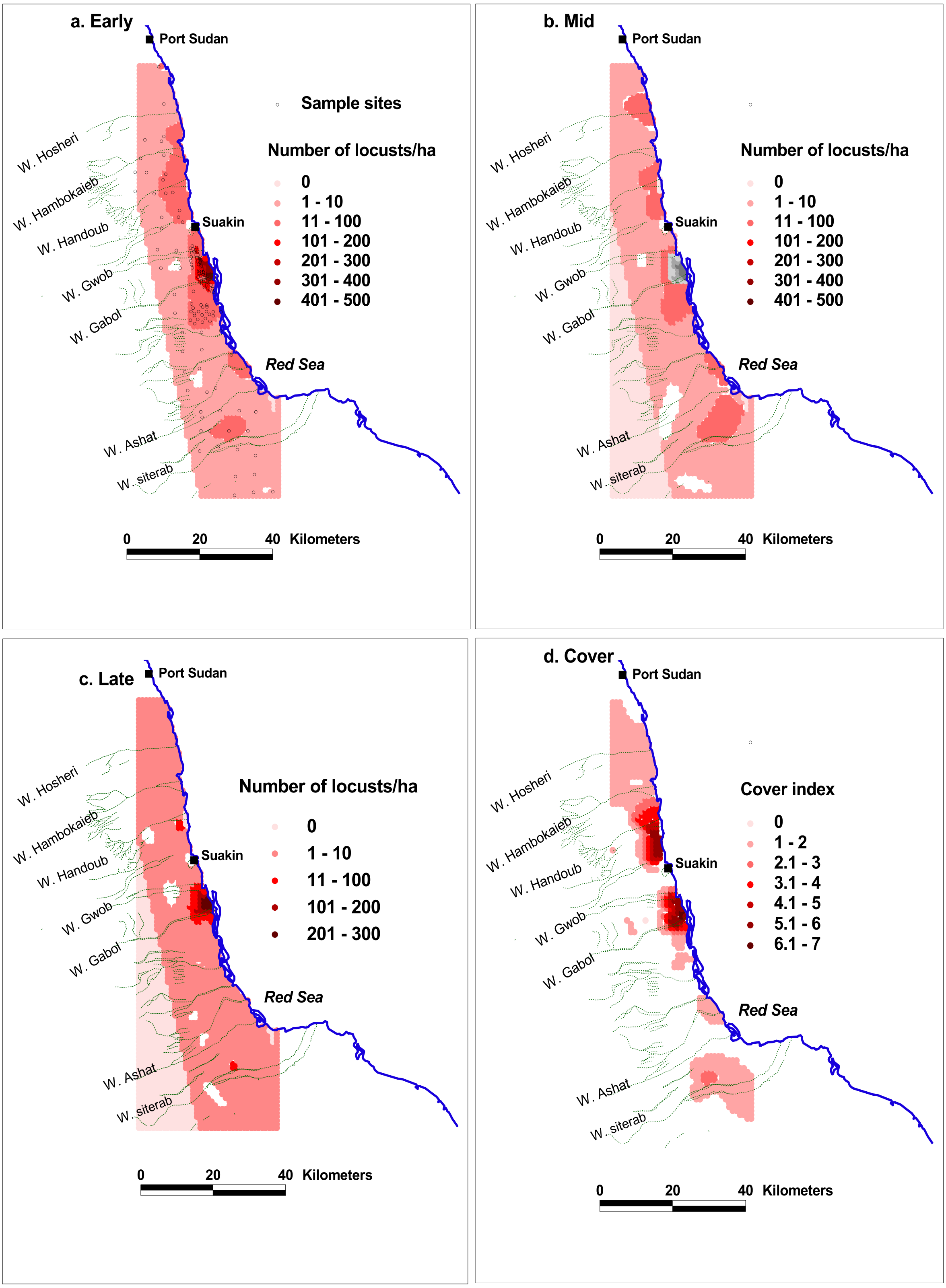

Fig. 6. Kriged maps of locust density estimates (number/ha) across the site: in 1999 winter season for the early (a), mid (b), and late (c) season; and *Heliotropium*/millet cover abundance (d).

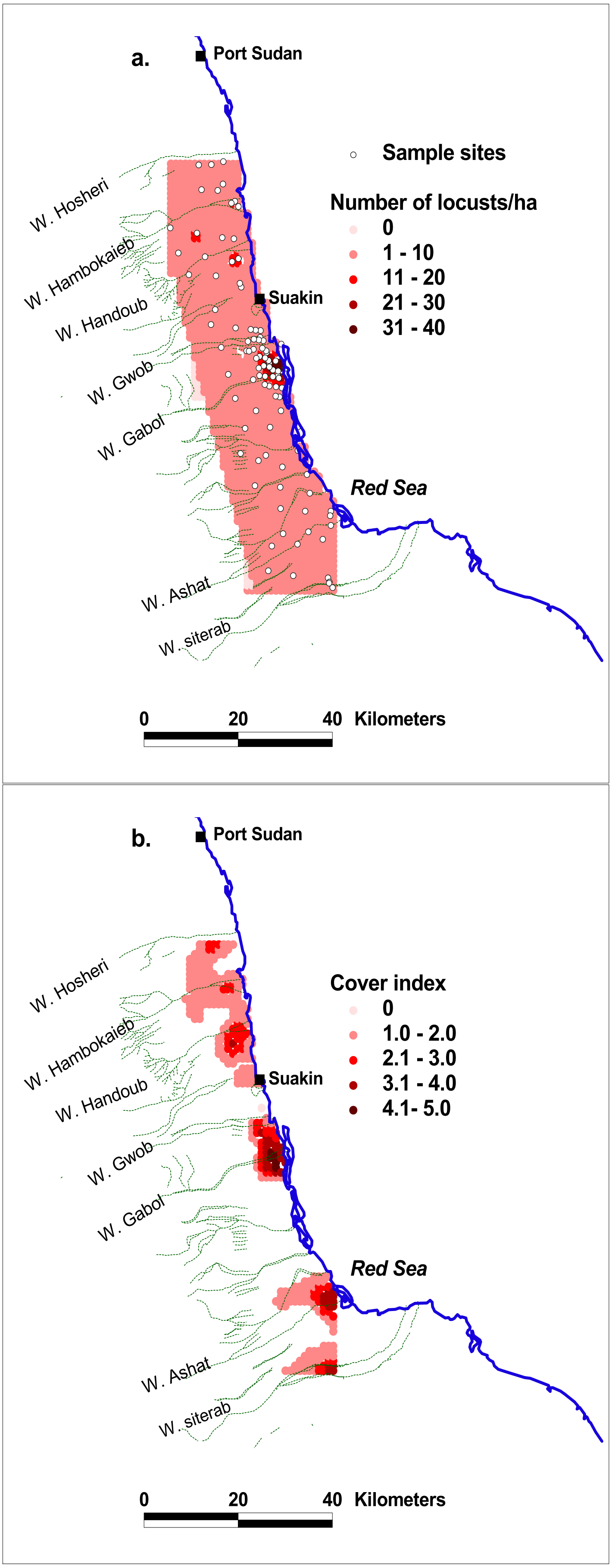

Fig. 7. Kriged maps of locust density estimates (number/ha) across the site in 2000 winter season (a); and *Heliotropium*/millet cover abundance (b).

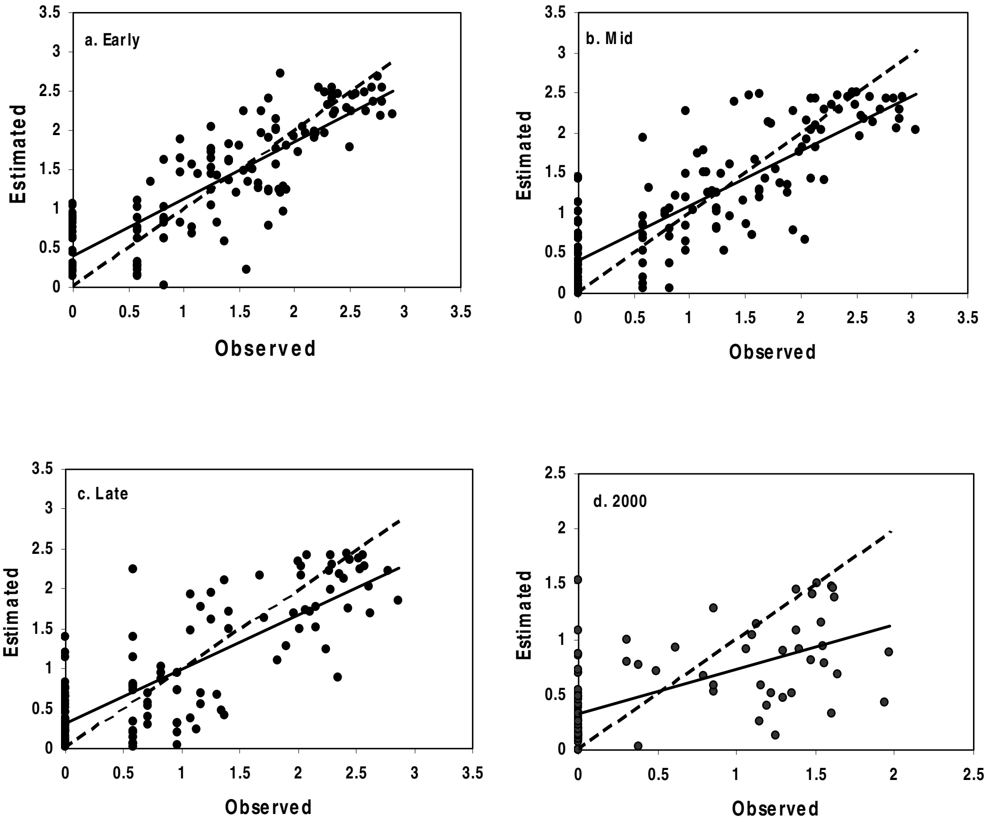

Fig. 8. Plots of estimated against observed locust density (log (number/ha)): early (a), mid (b), and late (c) season in 1999; and in 2000 (d). Comparison of the best-fit line (solid) with the 45 degree line (dotted) (cf. Table 3).

Table 3. Estimated parameters ± SE of simple linear regressions of observed versus estimated values of locust density (log (number/ha)): in 1999 for the early-, mid-, and late-winter season, and in the winter season of 2000 (cf. Fig. 8).

	Intercept	Slope	r^2
1999			
Locust early season	0.048 ± 0.091	0.950 ± 0.059	0.679
Locust mid season	0.027 ± 0.093	0.961 ± 0.063	0.655
Locust late season	0.014 ± 0.077	0.957 ± 0.063	0.653
Heliotropium/millet	0.019 ± 0.188	0.960 ± 0.061	0.665
N*	126	126	126
2000			
Locust	0.139 ± 0.073	0.934 ± 0.123	0.379
Heliotropium/millet	–0.168 ± 0.285	1.012 ± 0.113	0.459
N	97	97	97

[*] N is number of data points.

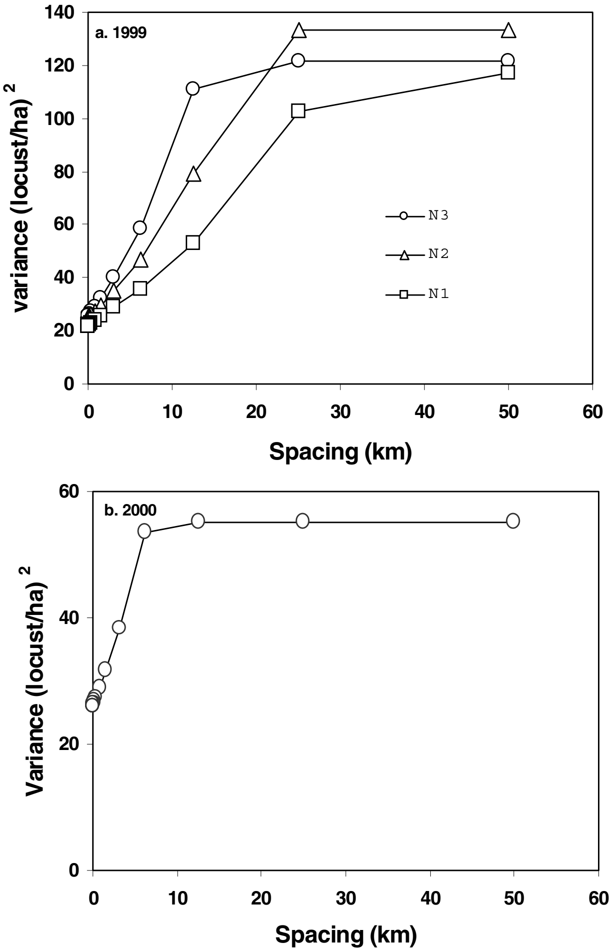

Fig. 9. Graphs showing kriging estimation variance of locust density against sample spacing: early (N_1), mid (N_2) and late (N_3) seasons in 1999 (a), and in 2000 (b).

Discussion

The spatial pattern of the desert locust was geostatistically described using a spherical variogram whereby 86-90% of the variability was explained spatially in 1999 and 71% in 2000. In 1999, the correlation range decreased from 23 km in the early season to 17 km in the mid season and 11 km in the late season. The decreased correlation range is related to the condition of the habitat. In the early season, locusts spread over a relatively large area. In the mid season, under moist and green conditions, when egg deposition was observed, the locust distribution was largely confined to the most suitable breeding sites. As the season progressed, the suitable breeding habitat contracted. The relative nugget effect increased with 20% from the early to the late season. Shrinkage of suitable breeding habitat was the most pronounced in 2000 with a range of five km.

In both winter seasons, the pattern of the locust distribution appeared to be biologically mediated, i.e., locust distribution was largely confined to the sites with a high cover abundance of *Heliotropium* and millet in wadi outflows. Fine texture soils in the wadi outflows absorb water from the run-off and retain moisture for longer period than the other sites dominated by the *S. monoica*, *P. turgidum* and *A. tortilis* communities (Chapter 2). The typically high locust *Heliotropium*/millet sites of the wadies Gwob and Gabol were reported to be the highest receivers of run-off water from the west hills among the wadies (Osman, 1996). The ranges found in this study for desert locust on the coastal plain of Sudan, from five km in 2000 to 23 km in the early season of 1999, are short compared to ranges of 43-112 km found for grasshoppers in three regions of Montana, the USA (Kemp *et al.*, 1989).

Some of the sample variograms indicate non-monotonicity. The wave-like shape of the variogram could be due to variation in plant communities, with the *Heliotropium*/ millet community in wadies alternating with *Panicum* and scrub vegetations in interspersed and comparatively drier areas (Chapter 2). Application of the wave variogram model did not improve the proportion of variance explained, however, and therefore, kriging maps were based on spherical variogram models.

This is the first time that the spatial variability of desert locusts has been described, the kriged locust density estimates mapped, and graphs of sample spacing and kriging estimation variance produced. Under conditions of patchy distribution of locusts, the delineated blocks of high locust areas, 'hot spots', are approximately 5% of the surveyed area. It therefore seems both economical and practical to monitor the build-up of solitarious populations in these hot spots rather than in the whole area at large. This should greatly improve the efficiency of locust monitoring and detection. The strong relationship between solitarious locusts and cover abundance of *Heliotropium*/millet might enable the use of co-kriging to predict locust density, using the cover abundance value of *Heliotropium*/millet as a covariable. It is easier and therefore cheaper to survey plant communities than it is to survey locusts, and moreover, plant communities are consistently in the same place, enabling the reduction of the survey area. Thus, the kriged maps in particular and geostatistical procedures in general, may assist in routine area wide locust survey programmes particularly on the coastal plain of Sudan. The application of the same procedures can be verified and extended to the coastal areas of Eritrea and Saudi Arabia since the ecology of those regions is similar to that of the Sudanese coast (Chapter 2).

Chapter 6

Host plant quality and aggregation of desert locust (*Schistocerca gregaria* Forsk.) on the coastal plain of Sudan

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Chapter 6

Host plant quality and aggregation of desert locust (*Schistocerca gregaria* Forsk.) on the coastal plain of Sudan

Abstract

The desert locust *Schistocerca gregaria* (Forsk.) is much more prevalent in the *Heliotropium* than in the *Panicum* plant community on the Red Sea coastal plain of Sudan. Both plant communities contained suitable host plants. We tested the hypothesis that the difference in aggregation of solitarious desert locust density between the plant communities is related to differences in nitrogen content of host plants. Leaf samples of 9-16 most common plant species were collected in the *Heliotropium* and *Panicum* plant communities during the winters of 1999 and 2000. Leaf nitrogen content in host plants was consistently 0.5 to 1.5 percent higher in *Heliotropium* sites than in *Panicum* sites. In 1999, locust densities (mean ± SE) were higher in the *Heliotropium* plant community (332 ± 56 locusts/ha) than in the *Panicum* plant community (21 ± 5 locusts/ha). Similar results were obtained in 2000, with 56 ± 5 locusts/ha in the *Heliotropium* plant community and no locusts in the *Panicum* plant community. These findings are consistent with the hypothesis that high densities of the desert locust occurred in sites where host plants have a high leaf nitrogen content.

Key words: Leaf nitrogen content, *Heliotropium* plant community, *Panicum* plant community, desert locust, *Schistocerca gregaria*, host plants.

Introduction

In the coastal range of Sudan, four major plant communities occur which are dominated by either *Suaeda monoica* (Forssk.), *Heliotropium arbainense* (Fresen.), *Panicum turgidum* (Forssk.) or *Acacia tortilis* (Forssk.) (Chapter 2). The plant community close to the sea shore is dominated by the scrub *S. monoica,* which reaches a soil cover of not more than 20%. When there is rain of about 100 mm or more during the winter season, there will be substantial undergrowth of annuals such as *Cyperus* spp., *Cenchrus ciliaris* (L.), *Pennisetum* spp., and *Euphorbia* spp. Soils in the *S. monoica* community are generally salty. Further to the west, the plant community is dominated by the perennial grass *P. turgidum*. Here also, soil cover does not exceed 20%. Following rain, there is ample undergrowth of annuals, such as *Amaranthus* spp., *Tribulus* spp., *H. arbainense*, *Trianthema* spp., *Schoenfeldia gracilis* (Kunth), *C. ciliaris* L., *Pennisetum* spp., and *Eragrostis* spp. In the *Panicum* grasslands, nomads herd goats and camels. Soils in this plant community are not salty, and they have a coarser particle size distribution than those in the *S. monoica* community. Yet further to the west, at the foot of a bare rocky mountain range, the 'Red Sea Hills', the vegetation cover becomes sparser, the soil coarser and more gravelly, and water supply more limiting. This is where the *A. tortilis* community occurs. Vegetation cover by perennials here is below 5%. Winter rains here support growth of the following annuals: *Zygophylum simplex* (L.), *Cassia senna* (L.), *Trianthema* spp., *S. gracilis*, and *Pennisetum* spp. The fourth plant community, dominated by the annual *H. arbainense,* occurs at the transition zone between the *P. turgidum* and *S. monoica* areas, especially where wadies originating from the Red Sea Hills provide additional water, and where soils mostly consist of fine sand. There are no important perennials in this community, as naturally occurring plants such as *Calotropis procera* (Aiton.) are removed by farmers.

The area of the *Heliotropium* plant community is extensively used for cropping millet (*Pennisetum typhoideum* Rich.), in as far as the soils are non salty. Solitarious desert locusts (*Schistocerca gregaria* Forsk.) populations are largely aggregated in the *Heliotropium* plant community (Chapter 3). 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 on the southern part of the coastal plain of Sudan, to the immediately adjacent *P. turgidum* and *S. monoica* areas. The reason for the aggregate distribution of desert locust populations associated with the *Heliotropium* plant community is not known. Variation in microhabitat for shelter and egg deposition (Brown, 1947; Husain *et al.*, 1946; Roffey & Popov, 1968; Uvarov, 1977) and host plant quality (Mattson, 1980, McNeill & Southwood, 1978) are mentioned as possible explanations for herbivores to aggregate in selective habitats. The quality of host plants, often measured by leaf nitrogen content, often triggers grasshoppers to choose host plants causing aggregation (Caswell & Reed, 1976; Boutton *et al.*, 1980; Heidorn & Joern, 1987; Lockwood, 1989; White, 1976, 1984, 1993). The protein (27%) or nitrogen (4.5% N) requirement of the desert locust is very high (Dadd, 1960; Hink *et al.*, 1993; Fagan *et al.*, 2002; Raubenheimer & Simpson, 2003). So, when the leaf nitrogen content of host plants is spatially variable, it may induce aggregation of the locust in certain desert habitats (Breman & Uithol, 1984; Breman & de Wit, 1983).

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 a comparatively high leaf nitrogen content. Therefore, our objective was to determine whether differences in nitrogen level of host plants could explain the differences in the aggregation of solitarious desert locust populations in the *Heliotropium* and *Panicum* plant communities.

Materials and methods

Study site. The study site is located between Port Sudan in the North and the Tokar delta in the South, the Red Sea in the East and the Red Sea Hills in the West. The coastal plain has an arid to semi-arid climate, and precipitation occurs in the winter months from October to January (Satakopan, 1965). The amount of rainfall between October 1999 to February 2000 was 158 mm, and from October 2000 to February 2001 it was 138 mm.

Sampling was conducted in the *Heliotropium* and *Panicum* sites during the winter season between December 1999 to February 2000, and referred to as 1999 winter season or simply 1999. The same terminology was used to describe the winter of 2000/2001 ('2000').

Leaf samples in *Heliotropium* and *Panicum* plant community sites. In 1999, leaves were collected from plants 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 on the following dates 18 and 25 December 1999; 8, 18 and 23 January; and 10 and 27 February 2000 (Fig. 1a). Sampling frequency of plant species depended on availability of plants in the sampling sites, in relation to the abundance or frequency of occurrence of plant species and grazing pressure (Table 1). In general, sampling had to be terminated earlier in the *Panicum* sites than in the *Heliotropium* sites because of low moisture in the grassland, causing the plants to senesce earlier.

In the 2000 winter season, leaves were collected from host plants of eight different species in the *Heliotropium*, and of six different species in the *Panicum* sites (Table 1). Leaves were collected at 22 *Heliotropium* sites and at 18 *Panicum* sites (Fig. 1b). Leaves were collected on 6 and 20 December 2000, 3, 15 and 30 January, and 3 March 2001.

In 1999, three to five composite leaf samples were collected for a plant species at any given sample date. Each of those composite samples consisted of leaf material from 12 to 20 individual plants from one or more sample sites. In 2000, the number of composite samples per species and date varied between five and 15. 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 wiremesh. A total of about 850 composite leaf samples in the 1999, and 1200 in the 2000 winter season were analysed

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

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

for their total nitrogen content. The samples were oven-dried at 65 °C until the weight became constant. After drying, the leaf total nitrogen content of each sample was analyzed using Micro-Kjeldahl method, at the Plant Nutrition Unit Sample Analysis Laboratory, Khartoum, Sudan.

Locust count. Locust counts were made in the *H. arbainense* and *P. turgidum* plant community areas at or near the Gwob-Gabol cropland, south of the town of Suakin in the same area where plant samples for nitrogen analysis were collected. In the winter of 1999, locust counts were made at 34 sites in *Heliotropium*, and 22 sites in *Panicum*; and in the winter of 2000, counts were made at 38 sites in *Heliotropium* and 18 sites in *Panicum*. Count dates were 6 and 17 January 2000 for the first winter season, and 6 and 20 January 2001 for the second. Counts were made on three parallel 400 m

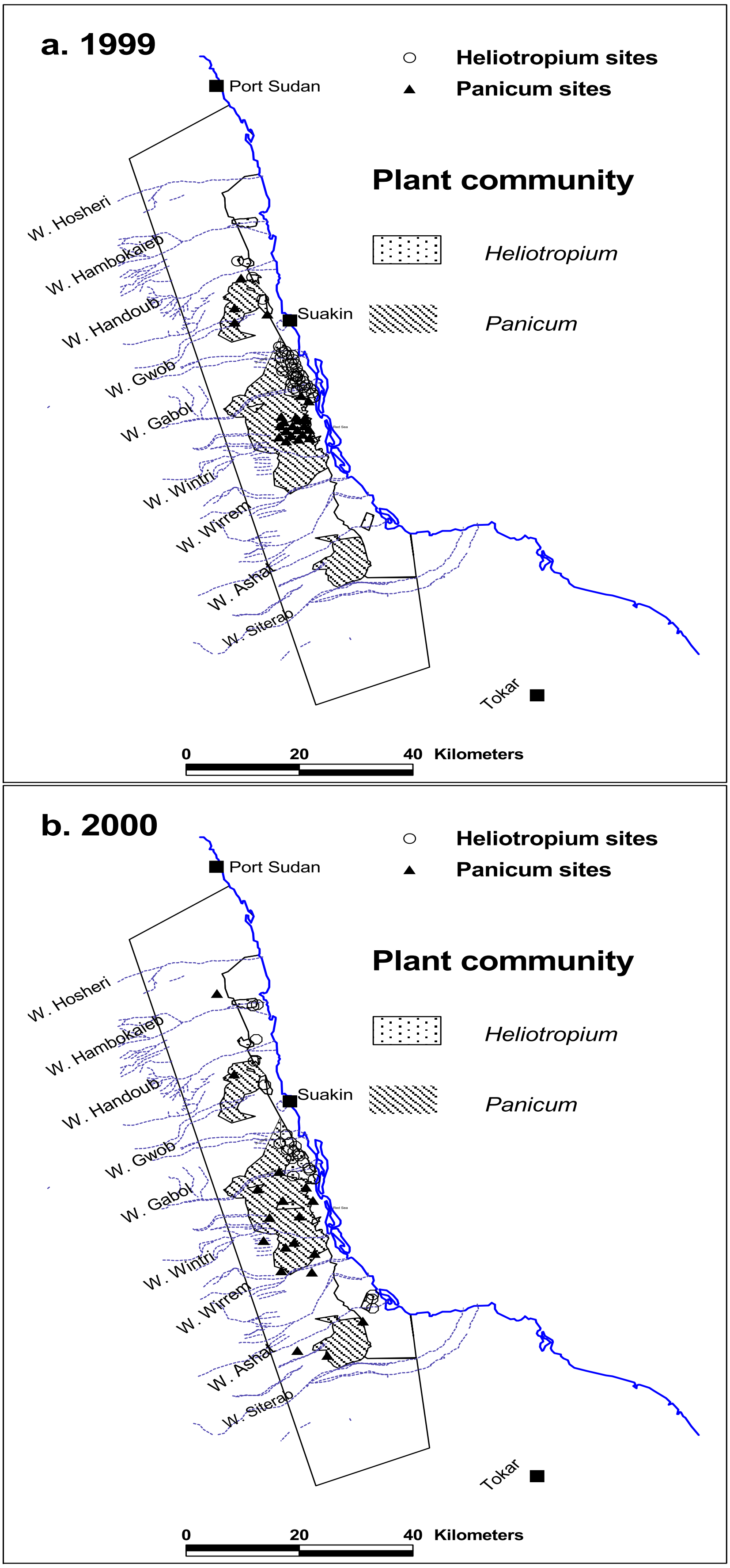

Fig. 1. Location and sample sites in the *Heliotropium* (○) and *Panicum* (▲) plant communities in the winter seasons of 1999 (a) and 2000 (b).

Locust feeding marks. Feeding marks made by hoppers and solitarious adults were scored on individual plant species in the *Heliotropium* sites using a four-point scale. Score 0 – rarely or not fed upon (less than 10% of the plants having feeding marks), 1 – occasionally (11-25%), 2 – commonly (26-50%), and 3 – abundant (> 50%). On 20 February 2000, twenty 50 × 50 m plots in the Gwob-Gabol cropland were haphazardly selected to assess feeding marks by a population of solitarious adults and hoppers. On 26 and 27 February 2000, ten 50 × 50 m plots were selected in the *Heliotropium* area of wadi Ashat to assess feeding of gregarious and solitarious hoppers. The host plants were classified into four groups: grasses (annual and perennial), forbs (herbaceous dicots), legumes, and woody perennials.

Description of the *Heliotropium* and *Panicum* plant community sites. The *Heliotropium* and *Panicum* sites were described using site descriptors such as cover abundance of plant species, soil particle size distribution, soil moisture and grazing pressure (Chapter 2). The correlation between site descriptors such as plant community composition and locust density was estimated using principal component analysis (Jongman *et al.*, 1995). Presence of microbial crusts observed as aggregates of fine soil particles was recorded in *Heliotropium* and *Panicum* sites. Furthermore, soil microbial population, mainly fungi and micro-organisms using mineral and organic forms of nitrogen, such as bacteria and actinomycetes, were quantified in the *Heliotropium* and *Panicum* sites as indicators of soil quality. 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 was estimated by the incubation method (Klute, 1986) in the laboratory of the Department of Biofertilizers, Environment and Nature Research in Khartoum, Sudan.

Results

Leaf total nitrogen (N) content at *Heliotropium* and *Panicum* plant community sites. Leaf N content of host plants at *Panicum* sites was consistently lower than the host plants at *Heliotropium* sites in both seasons (Figs. 2 and 3). During the winter of 1999, nitrogen percentage, pooled over all plant species sampled, was about 2.5% in the *Heliotropium* sites, and decreased to less than 2.0% in February (Fig. 2a). In *Panicum* sites, N percentage was stable around 1.8% until 15 January; after that the vegetation dried and no more samples were taken. The leaf N content of the host plants *H. arbainense* and *T. terrestris* at *Heliotropium* and *Panicum* sites were compared (Figs. 2b and c). In December, the leaf nitrogen content of *H. arbainense* at

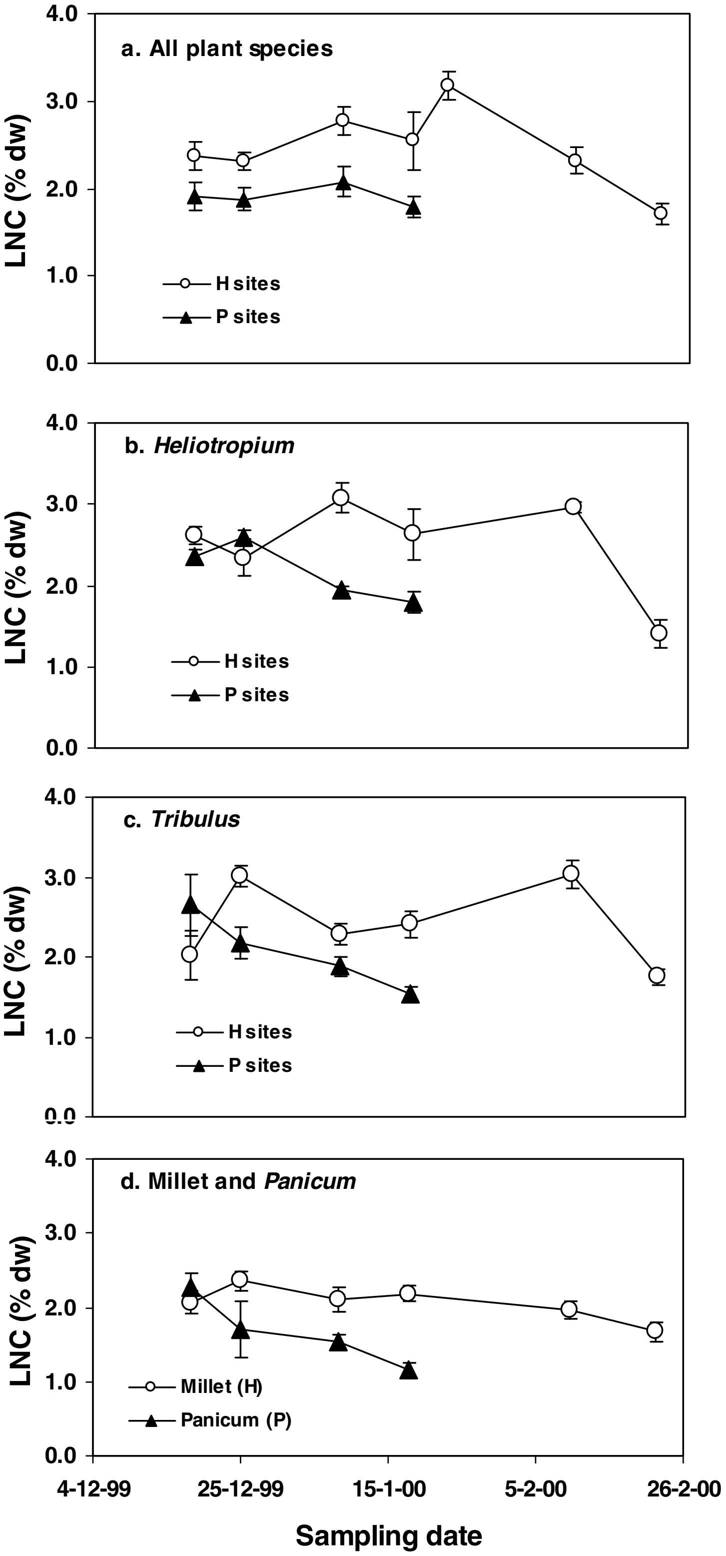

Fig. 2. Leaf total nitrogen content (LNC, % dry weight) of host plants in *Heliotropium* (H) and *Panicum* (P) sites (a), *Heliotropium arbainense* from H and P sites (b) and *Tribulus terrestris* from H and P sites (c), and millet from H and *Panicum turgidum* from P sites (d) in 1999. Bars indicate standard error of the mean.

Heliotropium and *Panicum* sites was similar (Fig. 2b). Thereafter, the leaf N content of the *H. arbainense* at *Heliotropium* sites was about 1% higher than the leaf nitrogen content of the *H. arbainense* at *Panicum* sites. A similar trend was observed in leaf N content of the *T. terrestris* at *Heliotropium* and *Panicum* sites (Fig. 2c). Millet is common and dominant in the *Heliotropium* sites, and *P. turgidum* is the dominant plant in the *Panicum* sites. Both plant species were similar in N content in early December. Thereafter, the N 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% (Fig. 2d).

In December 2000, the pooled N 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% (Fig. 3a). At *Panicum* sites, the nitrogen percentage varied between 2.8 and 3.0%; no green vegetation was available after the end of January. In December and January, the leaf N content of *H. arbainense* and *T. terrestris* at *Heliotropium* sites was higher than the leaf N content of the same host plants at *Panicum* sites (Figs. 3b and c). This difference in leaf N became negligible after January. The leaf N content of the millet at *Heliotropium* sites and the *P. turgidum* at *Panicum* sites were similar in early December and thereafter, the N content declined in both plant species, but in the *P. turgidum* more than in the millet, as in the 1999 winter season (Fig. 3d).

Locust distribution. 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 (Fig. 4). In 1999, locust density amounted to 332 ± 56 individuals/ha (mean ± SEM) in the *Heliotropium* plant community, and 21 ± 5 in the *Panicum* plant community. In 2000, the density was 56 ± 5 locusts/ha in the *Heliotropium* plant community, and no locusts were observed in the *Panicum* plant community (Fig. 4).

Locust feeding marks and host plants. In sites with solitarious hoppers and adult locusts, abundant feeding marks were observed on *H. arbainense* (Table 2). Feeding marks were common also on *T. terrestris*, *P. typhoideum* (millet), *Phaseolus* sp., and *Portulaca oleracea* (L.) plants and occasional or rare on other plants. In sites with gregarizing hoppers and solitarious adult locusts, feeding marks were abundant on *H. arbainense*, *T. terrestris*, and millet (Table 2). In general, feeding marks were observed on forbs, grasses and legumes and rarely on woody plants.

Description of the *Heliotropium* and *Panicum* plant community sites. Ordination using principal component analysis (Jongman *et al.*, 1995) shows an association of

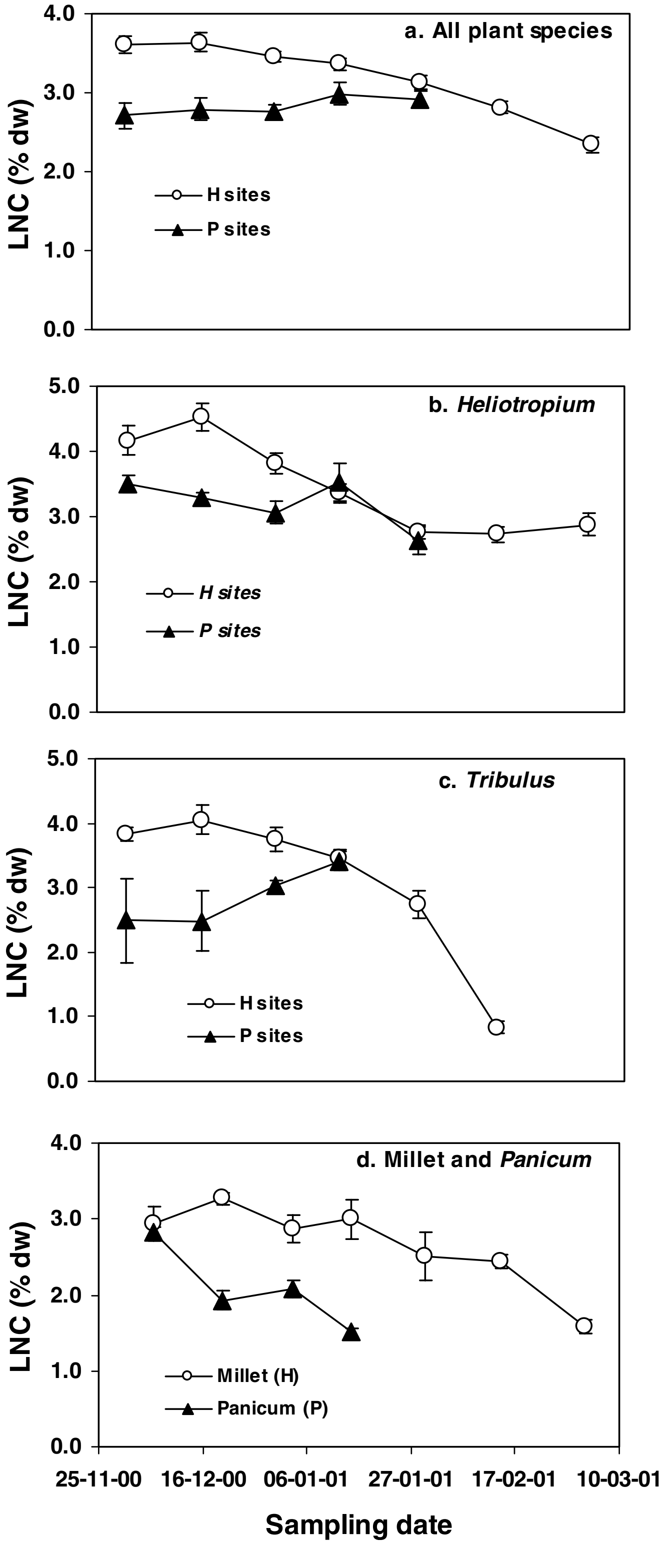

Fig. 3. Leaf total nitrogen content (LNC, % dry weight) of host plants in *Heliotropium* (H) and *Panicum* (P) sites (a), *Heliotropium arbainense* from H and P sites (b) and *Tribulus terrestris* from H and P sites (c), and millet from H and *Panicum turgidum* from P sites (d) in 2000. Bars indicate standard error of the mean.

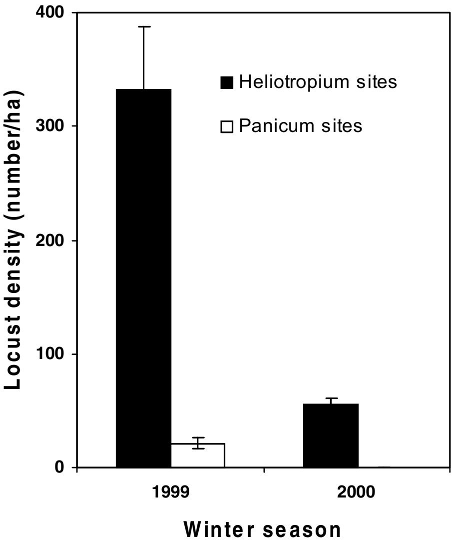

Fig. 4. Density of locusts (number/ha ± SEM) in *Heliotropium* and *Panicum* sites in 1999 and 2000. Bars indicate standard error of the mean.

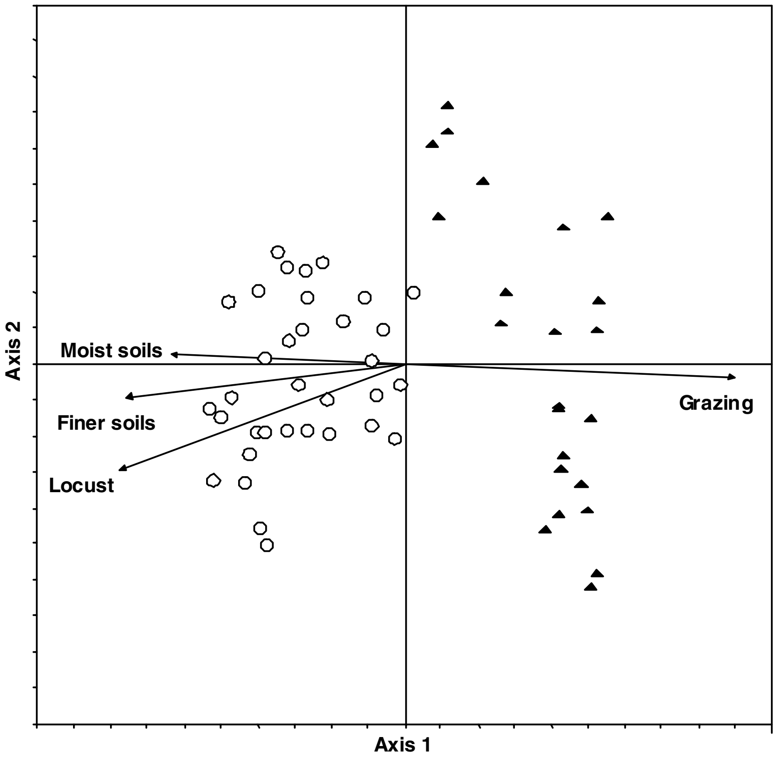

Fig. 5. PCA ordination of sample sites in relation to plant community composition (axes), soil texture, soil moisture, grazing pressure and locust density in 1999. Axes 1 and 2 represent scores of plant communities. Symbols indicate sites in *Heliotropium* (o) and *Panicum* (Δ).

Table 2. Frequency of desert locust feeding marks on leaves of different locust host plant species in the winter season of 1999-2000. Frequency scores of feeding marks: abundant (3), common (2), occasional (1) and rare or absent (0).

Group of host plants	Plant species	Locusts' feeding marks: Solitarious hoppers and adults	Locusts' feeding marks: Gregarious hoppers and solitarious adults
Forbs	*Amaranthus* sp.	1	1
	Caluxya hexagyna	0	0
	Citrullus sp.	0	0
	Dipterygium glaucum	1	2
	Euphorbia sp.	0	0
	Heliotropium arbainense	3	3
	Launaea capitata	2	3
	Portulaca oleracea	2	3
	Trianthema sp.	0	0
	Tribulus terrestris	2	3
	Zygophyllum simplex	0	0
Legumes	*Cassia senna*	0	0
	Crotalaria microphylla	1	2
	Phaseolus sp.	2	2
	Tephrosia sp.	1	2
Grasses	*Cenchrus ciliaris*	0	0
	Cyperus sp.	0	0
	Eleusine sp.	0	1
	Panicum turgidum	0	0
	Pennisetum spp.	0	0
	Pennisetum typhoideum (millet)	2	3
	Schoenfeldia gracilis	0	0
Woody	*Aerva javanica*	0	0
	Acacia tortilis	0	2
	Calotropis procera	0	0
	Prosopis chilensis	0	0
	Ricinus communis	0	0
	Suaeda monoica	0	0

Heliotropium sites with a high fraction of fine soil particles, with presence of moist soil and with low grazing pressure; while *Panicum* sites are associated with coarser soils, relatively dry and highly grazed (Fig. 5). Locust density was correlated positively and significantly with fine soil particle and presence of moist soil, and ordination shows an association with the *Heliotropium* sites (Fig. 5, Table 3). Similar results were found in 2000 (Table 3).

Table 3. PCA correlation matrix (r) between locust density (number/ha), plant species first two PCA axes and habitat variables in the stratified 1 × 2 km grid of the study area in the 1999 and 2000 winter breeding seasons.

Habitat variables	Locust density (number/ha)	
	1999	2000
Axis 1	$+0.772^{**}$	$+0.546^{**}$
Axis 2	-0.293^{*}	-0.105^{NS}
Soil particle size	$+0.787^{**}$	$+0.601^{**}$
Moist soil	$+0.569^{**}$	$+0.483^{**}$
Grazing	-0.631^{**}	-0.424^{**}

Significances: ** $p \leq 0.\,01$, * $p \leq 0.05$, ^{NS} not significant at $p > 0.05$.

Microbial crusts were observed in almost half of the *Heliotropium* sites but rarely found in the *Panicum* sites (data not shown). The median number of colony forming units (CFU) of microbial population was higher in *Heliotropium* sites (427×10^7 CFU/g dry soil) than in *Panicum* sites (9.75×10^7 CFU/g dry soil) (Fig. 6). The microbial population determined in *Heliotropium* sites ranged from 9.6×10^8 to 1.4×10^9 CFU/g dry soil, whereas those of *Panicum* ranged from 1.7×10^7 to 6.2×10^8 CFU/g dry soil. The density of microbial populations in the *Heliotropium* sites was significantly higher than the microbial population in *Panicum* sites (Kolmogorov-Smirnov two-sample test at $p < 0.01$; using SPSS v.11).

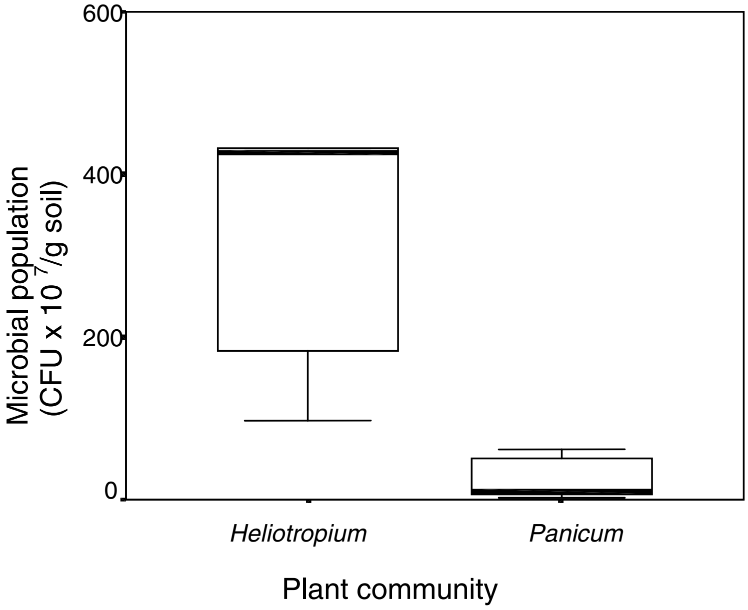

Fig. 6. Estimated microbial population (colony forming units, CFU/g dry soil) in *Heliotropium* and *Panicum* sites. Box plot indicates 25, 50, and 75 percentile and whiskers indicate minimum and maximum values.

Discussion

In both winter seasons, the leaf total 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 population and 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). 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. Microbial crusts consisting of a shallow (1.0 cm) or a thin 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 run-off and retain moisture (Mazor *et al.*, 1996; West, 1990; Fattom & Shilo, 1984). Microbial populations can contribute nitrogen to the soil and thereby to the leaf nitrogen content of the host plants (Belnap & Harper, 1994). For instance, Belnap & Harper (1994) 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 south-eastern Utah, USA. They further indicated that microbial crusts can trap fine soil particles that are more nutrient rich than the coarser sand particles. In our case, the advantages of the microbial crust seems to be in creating a stable fine soil aggregation, protecting the soil against wind erosion, and improving moisture absorption and retention thereby supporting the growth of higher quality host plants.

More desert locust feeding marks are found on host plants where the leaf nitrogen content is high. For instance, feeding marks of the desert locust were associated with high nitrogen host plants (*H. arbainense* and *T. terrestris* and millet), while feeding marks were absent in low nitrogen hosts such as *P. turgidum* plants. This is in line with the findings of Chandra & Williams (1983) indicating that ranking in feeding marks in desert locust matched nutritional ranking. Similarly, Ohabuike (1979) found that *Locusta migratoria* prefers species that support faster rates of growth and development. He attributed this to both higher nutrient concentrations and reduced plant secondary compounds in the favored species. Preferential feeding of solitarious and gregarious hoppers on host plants such as *Heliotropium* sp., *Tribulus* and millet were commonly reported on the coastal plain of Sudan (Bashir *et al.*, 2000), in Mauritania, West Africa (Culmsee, 2002), and in India (Rao, 1942; Chandra, 1984a,

1985) but this was not related to plant quality.

Solitarious desert locusts aggregate in the *Heliotropium* plant community may also be due to the presence of moist and fine sand soils suitable for egg deposition. However, aggregation of desert locust to the *Heliotropium* plant community was also observed when the adjacent *Panicum* plant community was moist as a result of recent rain, viz. on 22 December 1999 and 31 December 2000 (Chapter 3). At the same time, host plants in this plant community have a higher leaf nitrogen content than host plants in adjacent sites with the *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 far below the nitrogen requirement for desert locust (4.5% g N per g dry weight). This means that desert locust populations could choose host plants high in leaf nitrogen content. In both winter seasons, breeding of desert locust populations was largely confined to the *Heliotropium* plant community where the leaf nitrogen of host plants is higher than that in the adjacent *Panicum* plant community (Chapter 3). Thus, our findings are consistent with the hypothesis that desert locusts aggregate in habitats with host plants having a high leaf nitrogen content, i.e. the *Heliotropium* plant community located in areas with relatively moist and fine soil particles.

Chapter 7

Effect of nitrogen content of the host plant millet (*Pennisetum typhoideum*) on fitness of the desert locust (*Schistocerca gregaria* Forsk.)

Kazbek Toleubayev, Gebremedhin Woldewahid, Arnold van Huis & Wopke van der Werf, 2004. Effect of nitrogen content of the host plant millet (*Pennisetum typhoideum*) on fitness of the desert locust (*Schistocerca gregaria* Forsk.). To be submitted.

Chapter 7

Effect of nitrogen content of the host plant millet (*Pennisetum typhoideum*) on fitness of the desert locust (*Schistocerca gregaria* Forsk.)

Abstract

A life table study was made to measure the effect of leaf nitrogen content in the host plant millet (*Pennisetum typhoideum* Rich.), on fitness parameters of the desert locust (*Schistocerca gregaria* Forsk.). Locusts reared on high nitrogen leaves (3.9% g N per g leaf dry weight) developed faster, showed greater synchronization, and reproduced more and earlier than those fed on low nitrogen leaves (1.4% g N per g leaf dry weight). Locusts reared on high nitrogen leaves had higher survival to the adult stage (92% versus 64%) and higher fecundity (mean ± SE) (156 ± 18 versus 92 ± 10 eggs/female) than those reared on low nitrogen leaves. Approximately 75% of the mortality in hoppers reared on low nitrogen leaves was due to cannibalism, while cannibalism was absent in hoppers reared on high nitrogen leaves. Development of hoppers was faster and more synchronized when they were reared on high nitrogen than those reared on low nitrogen leaves. Thus, elevated leaf nitrogen content of host plants increased net reproduction (65 versus 20 female offspring/female) and intrinsic rate of increase (0.072 versus 0.047 day^{-1}), and lowered generation time (58 versus 63 days). The results show that the potential for population increase in the desert locust depends significantly on the nitrogen content of its host plants. Ecological implications are discussed.

Key words: Desert locust, leaf nitrogen content, mortality, cannibalism, fecundity, stage duration, synchronization, life table.

Introduction

The desert locust (*Schistocerca gregaria* Forsk.) lives generally as scattered solitarious individuals at low population densities in arid and semi-arid regions. Observations during three years field study on the coastal plain of Sudan showed a large difference in the density of solitarious locusts between millet cropped areas with the *Heliotropium* plant community and adjacent areas occupied by the *Panicum turgidum* and *Suaeda monoica* plant communities (Chapter 3). Nitrogen content of the host plants in the *Heliotropium* plant community was significantly higher than that of plants in the *Panicum* plant community. Only in these sites, with comparatively elevated nitrogen level in food plants, was breeding successful and gregarizing hoppers were observed.

The desert locust has a high requirement for food nitrogen or protein (Dadd, 1960; Hink *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, or 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 instance, there was a positive correlation between both survivorship and fecundity and N concentration in *Melanoplus mexicanus* fed on wheat with varying N concentration (Smith & Northcott, 1951). In *Melanoplus sanguinipes* fecundity was increased by a diet high in nitrogen (Krishna & Thorsteinson, 1972; Joern & Behmer, 1998) but survival did not (Joern & Behmer, 1998). Similarly, when *Locusta migratoria* females were fed on low protein diet, egg production dropped and terminal eggs were resorbed (McCaffery, 1975). Similar results were reported in the grasshopper *Ageneotettix deorum* 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 elevated leaf nitrogen of the host plants may therefore, assist to the improvement of 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.

Materials and methods

Experimental design and host plants. The host plant used for desert locust food was millet (*Pennisetum typhoideum* Rich.), a staple food crop in semi-arid regions and a suitable host plant of the desert locust (Abdel Rahman, 1999). Millet seeds were obtained from the Gwob-Gabol millet growing area on the Sudanese Red Sea coast. Millet plants were sown weekly over a period of 13 weeks, starting six weeks before the life table study. Six to seven weeks old plants were used to feed the locusts.

Twenty pots and 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 ($Ca(NO_3)_2$, 15.5% N) was applied as solid fertilizer by mixing it with the upper soil of each pot at one week after sowing. Three weeks after sowing, ammonium nitrate (32% N) was applied as liquid fertilizer (2.3 ml/pot). No fertilizer was given to the low nitrogen treatment (N0). Locusts were reared on millet leaves grown with (N1) and without (N0) nitrogen. Daylength in the greenhouse was at least 12h. The daily mean day/night temperature was 28/22 °C. Relative humidity fluctuated between 54 and 70%.

Locust rearing and food supply. The hoppers used for this study came from a gregarious stock, which had been reared at the Laboratory of Entomology, Wageningen University, for more than 10 generations and was originally obtained from the International Center of Insect Physiology and Ecology (ICIPE) field station in Port Sudan. The five replicates of the experiment were started at intervals of 1-3 days. Per replicate 100, 24-48h 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 (1.4 × 2.4 × 2.9 dm) consisted of Poly Vinyl Chloride sides and bottom, a Perspex front and a stainless steel wiremesh on top for aeration. At the rear, a round opening with a sleeve was fixed to manipulate plants and locusts, while two holes with a 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 24h. The other jar was filled with moist sand for egg laying.

Every day, *ad libitum* fresh millet leaves (25-40 cm length), a fresh sponge and water were placed in the water jars, old leaves were removed. Test cages were placed in a controlled climate room kept at a constant temperature of 30 °C, a relative humidity of 46-54%, and a daylight regime of 12L:12D.

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).

Hopper survival. The number of hoppers at each age (n_x) was counted daily. The proportion of hoppers surviving through age x (n_x/n_0) was calculated and a survivorship curve (l_x) was established in both treatments. The number of dead hoppers of each instar was recorded daily in each cage. Mortality due to cannibalism, handling or other causes was recorded separately.

Stage duration and numbers entering a stage. Each day, the number in each stage was counted per cage until all individuals had either completed development or died. The objective was to determine the average duration of each of the stages in both treatments using a life table approach. The average and median duration of life stages, and the standard deviation of the time of recruitment to a stage were estimated from the life table records.

The adult moult in locust is referred to as fledgling, and fledglings are the immatures, i.e. 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 females per cage was assessed by the first egg laying.

Female fecundity. Egg laying jars full of sand (12% water by weight) were placed in each cage from the 10th day after fledging, based on pilot observations. The moisture content of the sand in the egg laying jars was defined experimentally. Every two days, the number of females per cage, the number of egg pods laid and the number of eggs per pod were counted, and the egg laying jars were replaced. Observations on egg laying were continued for four weeks. Egg pods, which were misplaced on the floor of the cage, were cannibalized and were not 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 (Birch, 1948; Keyfitz, 1977; Carey, 1982). The proportion of females in a cage was 0.5. Fecundity was calculated per cage as the ratio between the number of eggs laid and the number of female fledglings.

Morphometrics. Morphometrics (caput width, femur of the third leg and length of first wing (six mature adults per cage: 3 females and 3 males) were measured.

Data analysis. All quantitative characteristics were calculated separately for each cage, resulting in five replicate values per treatment. Significance of difference was assessed by paired t-test (using cages of N0 and N1 started at the same date as a pair) or if the data did not satisfy normality, the Mann-Whitney U test structural analysis were conducted with SPSS 10.0.

Results

Leaf nitrogen content. 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 (t-test, $p \leq 0.05$) in all of the 11 weekly sowings (Fig. 1). On average, the leaf nitrogen content was 3.9 % (2.7-4.9%) in N1 versus 1.4 % (0.9-2.1%) in N0.

Hopper survival to the adult stage. Survivorship was 92 % in hoppers reared on high nitrogen foliage versus 64% in hoppers reared on low nitrogen foliage. Fig. 2 shows survival until average time of fledgling. There were significant differences in mortality between hoppers fed on high and low N leaves in all instars except L5 (Fig. 3). Approximately 75% of the mortality of hopper reared on low N foliage was due to cannibalism, while cannibalism was absent in hoppers reared on high N foliage (Fig. 4). Cannibalism was observed in all instars reared on low N foliage and was the highest in L3 and L4 and least in L5 (Fig. 5). Cannibalism was mostly observed during moulting.

Stage duration and synchronization. L1, L2, L3, and L4 instar hoppers reared on millet leaves with a high leaf nitrogen content (N1) had significantly shorter instar durations ($p \leq 0.05$) than hoppers reared on low nitrogen leaves (N0) (Table 1, Appendices 5 and 6). The greatest difference in instar duration (days, mean ± SE) was

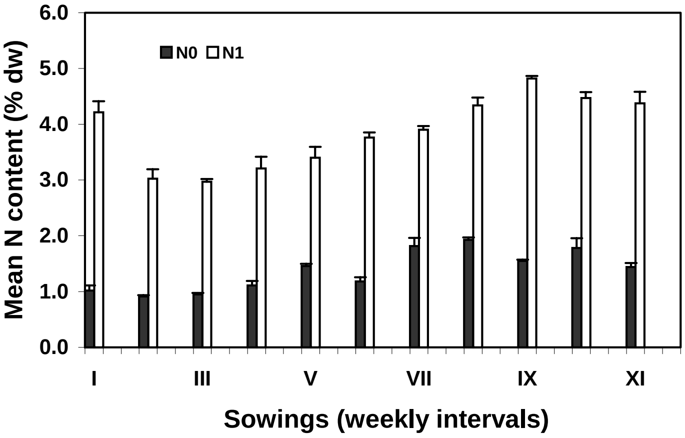

Fig. 1. Leaf nitrogen content of weekly sowings of millet at high (N1) and low (N0) levels of nitrogen in the soil (dw = dry weight; bars represent SE of the mean).

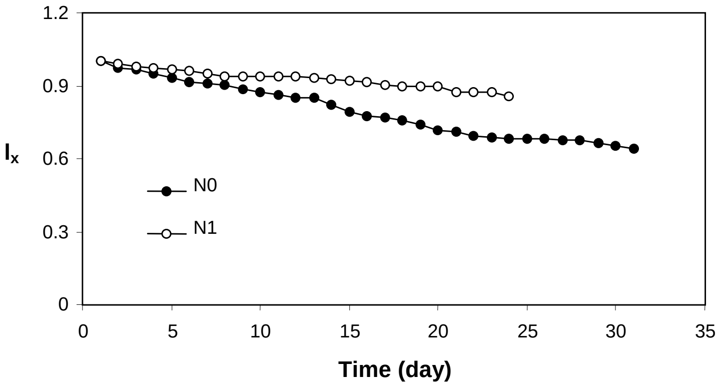

Fig. 2. Survivorship of hoppers (l_x) reared on high (N1) and low (N0) nitrogen content in millet leaves.

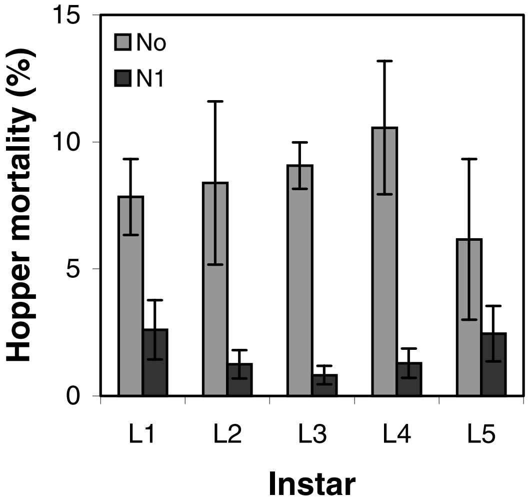

Fig. 3. Mean number of dead hoppers per instar in hoppers reared on high (N1) and low (N0) nitrogen millet leaves. Bars represent standard error of the mean.

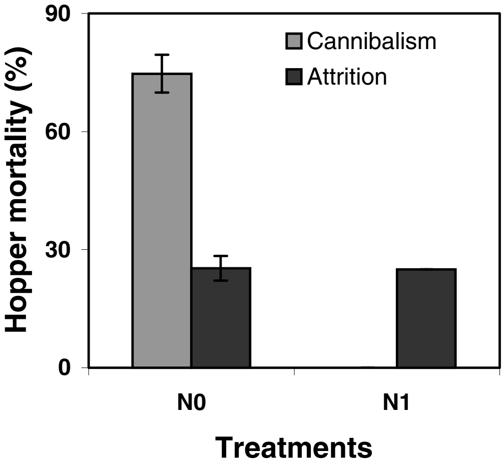

Fig. 4. Mortality (%) due to cannibalism and other causes in hoppers reared on high (N1) and low (N0) nitrogen millet leaves. Bars represent standard error of the mean.

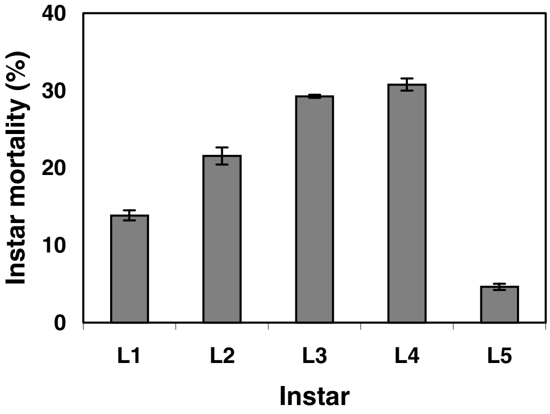

Fig. 5. Mortality due to cannibalism (%) in different hopper instars reared on low nitrogen millet leaves. Bars represent standard error of the mean.

found in the duration of L2 (3.69 ± 0.22 days in N1 versus 4.48 ± 0.15 days in N0) and L3 (4.26 ± 0.20 days in N1 versus 5.15 ± 0.15 days in N0). Recruitment to the next stage of hoppers fed on N1 millet occurred in a more synchronized manner than hoppers fed on N0 millet (Fig. 6; Table 1). A significant difference ($p \leq 0.05$) in time

Table 1. Average stage duration and time range (days, mean ± SE) of recruitment to the next stage of hoppers reared on low (N0) and high (N1) nitrogen foliage.

Stage	Stage duration		Time range of recruitment	
	N0	N1	N0	N1
L1	4.09 ± 0.20	3.24 ± 0.44*	3.2 ± 0.20	2.2 ± 0.20^{NS}
L2	4.48 ± 0.15	3.69 ± 0.22*	3.8 ± 0.20	2.4 ± 0.60*
L3	5.15 ± 0.15	4.26 ± 0.20**	4.0 ± 0.00	2.6 ± 0.68*
L4	5.86 ± 0.10	5.19 ± 0.27*	5.0 ± 0.00	4.0 ± 0.32^{+}
L5	9.25 ± 0.49	9.04 ± 0.41^{NS}	8.7 ± 0.93	7.4 ± 0.24^{NS}

Differences of treatment means of average stage duration within rows are significant: ** $p \leq 0.01$; * $p \leq 0.05$, + $p \leq 0.10$; and ^{NS} not significant ($p > 0.10$) using paired t-test (stage duration) or Mann-Whitney U-test (time range of recruitment).

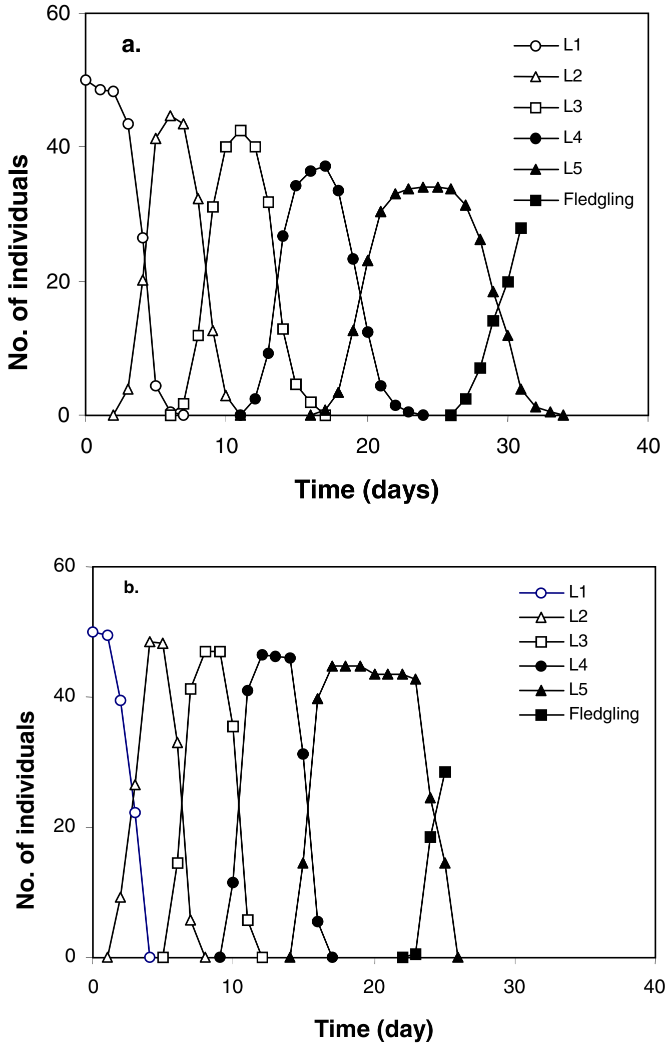

Fig. 6. Stage dynamics in locusts (average of five cages) reared on (a) low (N0) and (b) high (N1) nitrogen millet leaves.

range of recruitment to the next stage was observed in L2 (2.2 ± 0.20 in N1 versus 3.8 ± 0.20 in N0 days) and L3 (2.6 ± 0.68 in N1 versus 4.0 ± 0.00 in N0 days). Similar results were obtained using the standard deviation of the time of recruitment to the next stage and the median duration of recruitment to the next stage (Appendices 5 and 6).

Locusts reared on high nitrogen foliage had a shorter mean time between hatch and first egg laying (48 ± 3 days) than that locusts reared on low nitrogen foliage (56 ± 5 days). The time between adult moult and first egg laying was 21 ± 2 days in locusts reared on high nitrogen foliage and 23 ± 2 days in locusts reared on low nitrogen foliage. The difference was not statistically significant (t-test, $p \leq 0.05$).

Females reared on leaves with a high nitrogen content laid more eggs (156 ± 18 eggs/female) (weakly significant: $p \leq 0.10$) than those reared on leaves with a low nitrogen content (92 ± 10 eggs/female) (Table 2). There was no difference in the number of pods deposited per female (2.2 ± 0.2 vs. 2.1 ± 0. 2) between the two treatments. The mean number of eggs per pod (73 ± 3 versus 42 ± 2), however, was significantly ($p \leq 0.01$) higher in the high nitrogen treatment than in the low nitrogen treatment (Table 2) as were the maximum and minimum number of eggs per pod (Table 2).

Adults (both fledglings and mature ones) reared on high nitrogen millet suffered lower mortality (25 ± 3%) than locusts reared on a low nitrogen millet (46 ± 15%) (Fig. 7a). Cannibalism was a major cause for 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, cannibalism was also observed in the high nitrogen treatment.

The impact of leaf nitrogen content on stage duration, survivorship and fecundity translated into differences between treatment effects on life history parameters (Fig. 7,

Table 2. Fecundity of desert locust reared on low (N0) and high (N1) nitrogen millet (mean ± SE) leaves.

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 ± 0.2^{NS}
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:

Table 3). 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 (Figs. 7b and c). R_0 was three times as high on high nitrogen leaves (65 female offspring/female) than on low nitrogen leaves (20 female offspring/female). The generation time (*T*) was shorter in locusts reared on high nitrogen foliage than in locusts reared on low nitrogen foliage (58 versus 63 days). The intrinsic rate of increase (*r*) was greater on high nitrogen leaves (0.072 day^{-1}) than on low nitrogen leaves (0.047 day^{-1}). Doubling time was 15 days on low nitrogen leaves and 10 days on high nitrogen leaves.

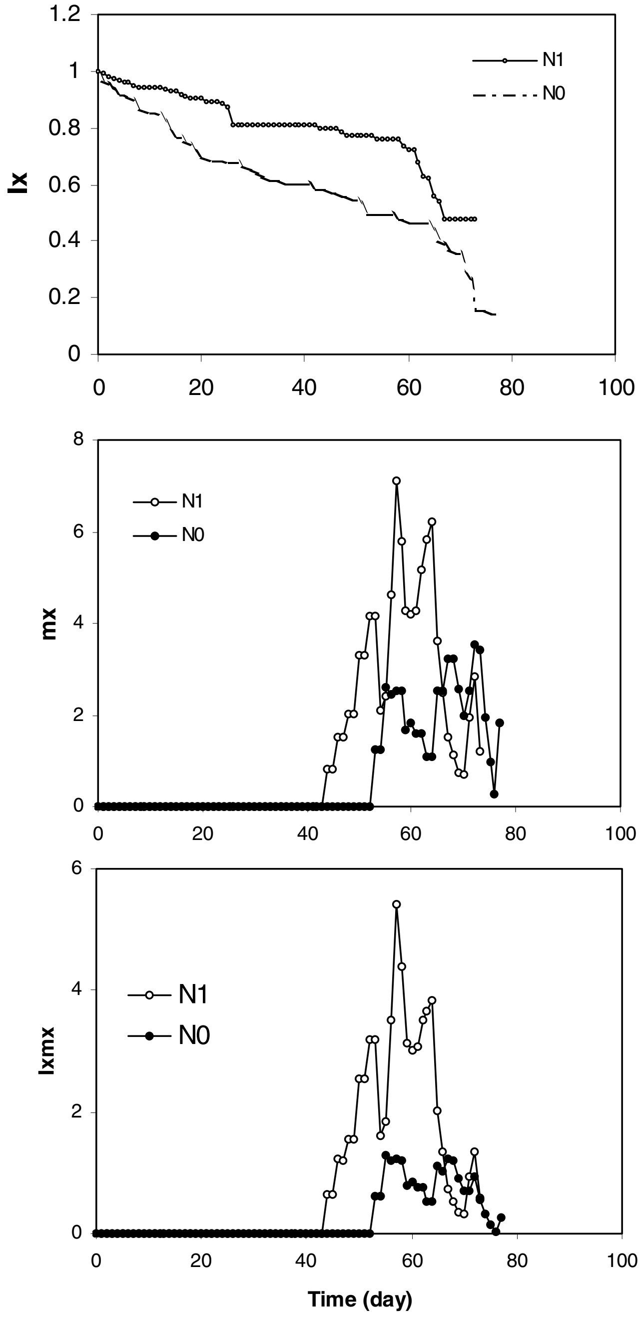

Fig. 7. Survivorship of females (a) and expected number of offspring (b and c) in locusts reared on high (N1) and low (N0) nitrogen millet leaves.

Table 3. Effect of feeding on low (N0) and high (N1) nitrogen millet leaves on life history parameters of the desert locust: 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	19.50	64.82
T	63.22	58.07
r	0.047	0.072
DT	15	10

Table 4. Morphometrics (mm, mean ± SE) of adult desert locust at low (N0) and high (N1) nitrogen content of millet food plants.

	Male		Female	
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 rows are significant at $p \leq 0.01$ using paired t-test.

Adult Morphometrics. The hind femur, caput width and elytron lengths of male and female reared on high leaf nitrogen content (N1) were significantly ($p \leq 0.01$) longer than those of individuals reared on low nitrogen leaves (Table 4).

Discussion

Locusts reared on millet with a high leaf nitrogen content showed better survival, greater synchronization, faster development and higher fecundity than locusts fed on millet with a low nitrogen content. As a result, the potential for population growth, as expressed by the intrinsic rate of natural increase (r) was substantially greater in locusts fed on high nitrogen leaves (r = 0.072 day^{-1}) than in locusts fed on low nitrogen leaves (r = 0.047 day^{-1}). Our results confirm the hypothesis of White (1976) that one of the influences of nitrogen is to enhance the survival of hoppers.

Substantial mortality of hoppers is common in lab and field studies and cannibalism is often an important component in hopper mortality. Abdel Rahman (1999) and Tawfik *et al.* (1971) found up to 100% hopper mortality when comparing different host plants as locust food in the laboratory. In the field, hopper moralities of 40% (Stower & Greathead, 1969) and 76% (Roffey & Stower, 1983) have been reported in the presence of green vegetation. In both cases the causes of mortality were not reported. Ashall & Ellis (1962) found 30-50% hopper mortality in East Africa, due to cannibalism, and Husain *et al.* (1946) reported 50% hopper mortality due to cannibalism in the presence of green vegetation. The hoppers reared at low nitrogen ate their entire casted exuviae whereas casted skins of those reared at high leaf N content were not eaten.

Lack of moisture in the diet has been mentioned as a cause of cannibalism (Uvarov, 1977). Husain *et al.* (1946), however, indicated that hoppers 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. Our results concur with the intensive review and conclusion of White (1993) indicating 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, 1960). 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, 3.9% N in the N1 treatment is in the range of satisfactory N contents mentioned by Dadd (1960). Cannibalism may help the survival of locusts in the low nitrogen leaves. This is because 50% of the cuticle or exuvae in desert locust and grasshoppers is protein (Hinks *et al.*, 1993). In this sense, cannibalism might be a survival mechanism for insects in a nitrogen limited environment (Mattson, 1980; White, 1993).

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 positive correlation between nitrogen content in bulrush millet and the fitness of desert locust indicates that increased leaf nitrogen content of the host plants augments the potential of the desert locust for population increase. Rainfall following an extended drought period in the desert is likely to increase the nitrogen level in the soil and host plants due to stimulated mineralization following dry conditions (Birch, 1960) and the contribution of dry nitrogen deposition from the atmosphere (de Ridder *et al.*, 1982). Desert locust outbreaks were reported following extended drought periods such as the 1986-89 plague following the 1983-85 drought (Hare, 1987; Gruys, 1994). The outbreak records of desert locust in the field might be possibly related to the conditions that improve the leaf nitrogen content of the host plants.

When locusts were fed on leaves with a high nitrogen content, moulting, maturation and egg laying processes were better synchronized than when they were reared on a low nitrogen millet leaves. Synchronization is implicated in the process of gregarization (Collett *et al.*, 1998), but it is not clear whether greater synchronization, found in this study at higher nitrogen levels in the host plant, could enhance gregarization.

Our results demonstrate that increased leaf nitrogen content of the host plants enhanced potential population growth of desert locusts, due largely to a reduction in hopper mortality and an increased and earlier egg laying by the adults. Thus, conditions that allow food plants to attain high protein levels, i.e. high levels of nitrogen in the soil and limited water, in proportion to the available nitrogen, create a risk for locust outbreak.

Chapter 8

General discussion

Chapter 8

General discussion

Desert locust is a migratory pest whose occurrence in space and time is often erratic and difficult to predict at all applicable levels of scale, from the local to the continental. The research presented in this thesis aimed at a better understanding of the spatial distribution of desert locust at the scale levels that are most relevant in field surveys by teams equipped with all terrain vehicles. The smallest resolution at which the data were collected was 50 m (within a locust habitat) while the coarsest resolution was 5 km (in a study area with locust habitats).

Solitarious desert locusts and its habitat

The habitat. The main study was conducted in a 20 × 120 km stretch of the Sudanese Red Sea coast. This area was spatially heterogeneous with four different vegetation zones between the Red Sea Hills in the west and the Red Sea in the east. Four plant communities were distinguished and named after characteristic plant species: *Suaeda monoica*, *Heliotropium* spp., *Panicum turgidum*, and *Acacia tortilis*. These plant communities represent possible habitats for the desert locust. They are an aggregate reflection of the soil texture and moisture, land use and physiography of the land. The physical environment ranges from relatively moist and fine sandy soils at low elevations (37 ± 7 m asl) in the *Heliotropium* plant community to dry, coarse sand and gravel soils at higher elevation (117 ± 13 m asl) in the *A. tortilis* plant community near the Red Sea foothills. The *P. turgidum* plant community occupies grazed territory at intermediate elevation and the *S. monoica* is found on salty and sometimes silty soils close to the sea. The spatial extent of these plant communities was mapped during the winter of 2000/2001. The percentage area covered was about 5% for the *Heliotropium* plant community, 14% for the *S. monoica* plant community, 21% for the *P. turgidum* plant community and 60% for the *A. tortilis* plant community. The separation of the habitat using cover abundance of plant species is less complex and more discernible in the field than the earlier classifications (Hemming, 1961; Kassas, 1957). This separation is useful for studying the spatial distribution of desert locust in relation to plant communities in order to delimit the most likely locust habitats.

Desert locust distribution and plant communities. Nymphs and adults of solitarious desert locust were associated with moist and finely textured soils in the *Heliotropium* plant community (Table 1). This plant community contained 93% of the adult solitarious locusts in 1999/2000 and 100% in 2000/2001, while it had only 17% and 27% of the total number of sample sites in the respective years. Oviposition probing and egg laying was only observed in the *Heliotropium* plant community, also hopper incidence was highest in this community (95%). Similarly, gregarizing hoppers were only detected in the *Heliotropium* plant community at the outflow of the wadi Ashat in the winter of 1999/2000. At the 1 × 2 km scale, the density of desert locust and breeding incidence dropped drastically immediately outside the *Heliotropium* plant community. Association of solitarious desert locusts with millet cultivation at relatively moist locations was confirmed through traverse surveys outside the main study area, between Halaib (near the Egyptian border) and Tokar (near the Eritrean border), and also by a detailed small scale survey in the Tokar delta (Fig. 1). In the whole coastal range of Sudan, with the exception of the Tokar delta, adult desert locusts were associated with millet crops with significant undergrowth of *Heliotropium* spp., and they were scarcely found in other habitats. In the Tokar delta, adult solitarious desert locusts were found predominantly in millet crops and to a much smaller extent in sorghum. In this delta, *Heliotropium* was lacking, possibly as a result of seasonal long-term flooding caused by the wadi Baraka.

Table 1. Characteristics of the habitat according to four plant communities on the Red Sea coastal plain of Sudan.

Parameter	Plant community			
	S. monoica	*H. arbainense*	*H. turgidum*	*A. tortilis*
Total area (%)	14	5	21	60
Elevation	Low	Lowest	Medium	Highest
Soil type and texture	Fine, partly salty	Very fine soil	Coarse sand	Coarse to gravel
Moisture status (relative)	High (salty)	High	Medium	Low
Abundance of suitable host plants	Medium	High	Medium	Low
Leaf quality	*	High	Low	*
Occurrence of solitarious desert locust populations	Low	High	Low	Very low
Egg deposition and hopper incidence	Low	High	Low	Very low
Habitat class	Possible	Most likely	Possible	Unlikely

[*] Not investigated.

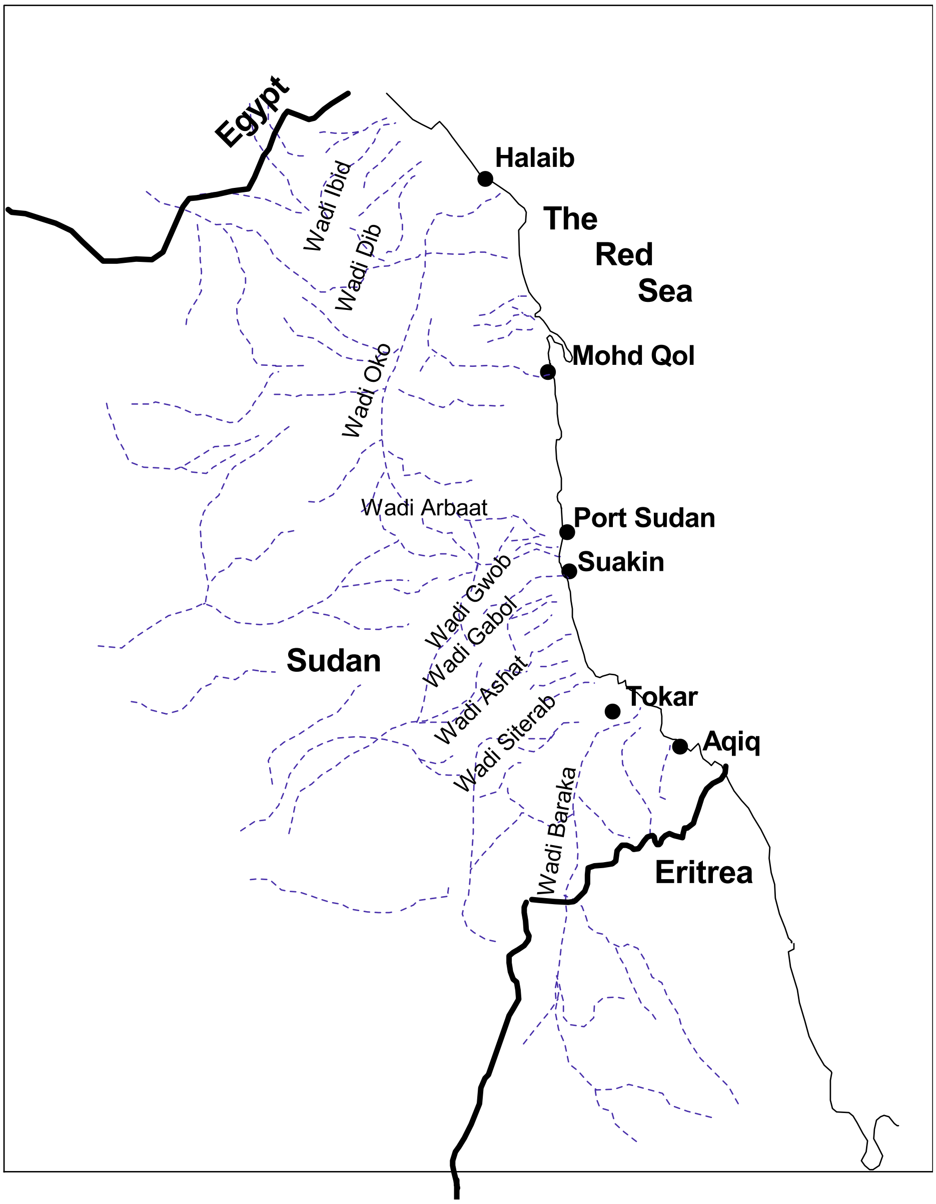

Fig. 1. Distribution of the cultivated wadies on the Red Sea coastal plain of Sudan.

At a more detailed micro scale within the *Heliotropium* plant community, the densities of solitarious and gregarious hoppers were significantly correlated with the cover abundance of *H. arbainense*. The densities of adult locusts were not quantified in millet and *Heliotropium* host plants separately but during field visits we saw adults predominantly in the millet and hoppers in the *Heliotropium* patches. Hoppers might choose the *Heliotropium* patches for quality of food and shelter whereas adults could use the bare soil between millet plants for egg deposition. In the wadi Ashat, Maxwell-Darling (1936) also reported the association of solitarious adults to millet and hoppers to *Heliotropium*. This small scale difference in distribution of hoppers and adults might be important in detection of desert locust during survey operations.

Previously reported preferred habitats of desert locust within the green habitat are 'mosaic habitats', i.e. transition zones between two plant communities (Uvarov, 1957; 1977; Dempster, 1963; Popov, 1997). There are also several reports indicating that within the green habitats on the Red Sea coast of Sudan and Eritrea desert locusts are mostly observed in areas associated with specific host plants such as millet, *Heliotropium* and *Dipterygium* spp. (Stower *et al.*, 1958; Waloff, 1963; Stower & Greathead, 1969; Roffey & Stower, 1983). Similar host plant associations have been reported from Saudi Arabia and Yemen (Maxwell-Darling, 1937; Popov & Zeller, 1963) and India (Rao, 1942). However, the breeding of desert locust has also been reported in *Panicum* grasslands and in scanty and shrubby perennials on the Red Sea coast (Popov & Zeller, 1963) and in Libya (Guichard, 1955), and in association with *Tribulus* and *Schouwia* in West Africa (Roffey & Popov, 1968). The available evidence on locust habitat is based on travel reports and observational visits rather than systematic surveys. Choice of observation of sites during occasional field visits and large area trajectory surveys, such as those by Maxwell-Darling (1936), Waloff (1963) and Popov & Zeller (1963) was selective, and focused on habitats where locusts were expected or reported to be present by local informers. Selective sampling is likely to result in bias (Yates, 1960; Binns *et al.*, 2000).

Much work, therefore, remains to be done to substantiate and quantify the habitat and host plant associations of solitarious desert locust. The present study is only a beginning considering the relative smallness of the study area and the limited number of seasons of study. Further work in other areas and seasons may clarify how generally valid our results are. The current results strongly suggest that on the Red Sea coast of Sudan, sampling for early locust detection should focus on the millet crops and on the *Heliotropium* plant community.

Application of geostatistics in desert locust survey

Geostatistical analysis tools were introduced to describe spatial patterns of adult solitarious desert locust density within the study area, and we investigated whether kriging could be used to estimate the density of locusts at unvisited sites based on samples at nearby locations. Our results indicate that there was a strong spatial dependence in the pattern of desert locust distribution. Approximately 71-90% of the population variance was explained spatially over correlation ranges that varied from five to 24 km in the 1999/2000 and 2000/2001 winter seasons. Using these correlation ranges, locust densities at unvisited sites were estimated by kriging. Blocks with high locust density mainly the *Heliotropium* plant community were delineated from blocks with low desert locust densities dominated by the *S. monoica*, *P. turgidum* and *A. tortilis* plant communities. The pattern of the estimated locust densities over the study area was mapped using GIS. The cross-validation results indicate that the estimated and actual locust densities are significantly correlated. Hence, geostatistical analysis tools can be potentially useful in the survey of desert locust operations and control strategies to delineate potential high locust density zones based on limited sample sites. Moreover, application of geostatistics could be helpful in using spatially referenced indicator values such as presence or absence records of desert locust and plant communities to quickly identify areas with an increased risk of high desert locust densities for further monitoring. Similar to our findings, application of geostatistics was proven to be useful in mapping and forecasting the density of grasshoppers (e.g., Kemp *et al.*, 1989; Johnson, 1989) and gypsy moth (e.g., Hohn *et al.*, 1993; Liebhold *et al.*, 1991). We found that zones of high desert locust density were correlated with high cover abundance of *Heliotropium* and millet. Thus, the use of habitat information in the spatial analysis along with the desert locust counts may further improve the accuracy of prediction in unsampled locations (Kruijer, 2003).

Resources and plant communities

We observed that important links exist between the desert locust and certain plant communities, which probably provided the resources required by the desert locust. When all the sites were relatively moist and green (i.e. suitable for egg deposition and survival) in December of 1999 and 2000, the desert locust largely concentrated in the *Heliotropium* plant community. Explanations are that the millet/*Heliotropium* habitat contained more suitable host plants with higher leaf nitrogen content (Chapter 6) and more appropriate soil conditions for egg laying (Chapter 2), compared to those of adjacent plant communities.

Similar to our results, Chandra & Williams (1983) reported that a ranking of feeding preference of desert locust among host plants matched the nutritional ranking of these host plants. Similarly, *L. migratoria* prefers host plant species that support faster rates of growth and development. This was attributed to higher nutrient concentration and lower secondary compound content in favoured species (Ohabuike, 1979). Thus, our results indicate that the high abundance of suitable host plants with high leaf nitrogen content, among others, may contribute to the concentration of desert locust mainly in the *Heliotropium* plant community.

The role of leaf nitrogen on life table statistics of desert locusts was substantiated by a laboratory experiment in which life cycle parameters of locusts that were reared on millet plants with a high or low leaf nitrogen content were compared. Locusts reared on millet leaves with a high leaf nitrogen content showed a higher survivorship, net reproductive number and intrinsic rate of increase, and lower generation time (T) than locusts reared on millet leaves with a low nitrogen content. This indicates that conditions that allow food plants to attain high nitrogen levels are more likely to attract and increase desert locust populations and may create a risk for locust outbreaks.

Improvement in desert locust survey operations

For practical purposes, the relationship between desert locust and plant community can be simplified into suitable habitat classes based on the occurrence and breeding of the desert locust. Hence, the *Heliotropium* plant community can be considered the most likely, the *S. monoica* and *P. turgidum* plant communities as possible and the *A. tortilis* plant community as unlikely desert locust habitat (Table 1). This means that the area needing regular supervision or survey in the cultivated wadies (5%) during recession periods is very small compared to the total green area that should be surveyed. This tremendously helps in the desert locust preventive strategy adopted by affected countries, donors and FAO. Our findings and recommendations concur with the experiences elsewhere: in India with desert locust, and in Australia with Australian plague locust (*Chortoicetes terminifera* Walk.).

For instance with the Australian plague locust, most of the outbreaks originate in the semi-arid Channel Country of western Queensland (McCulloch & Hunter, 1983; Hunter, 1989). Within the Channel Country, occurrence and breeding of the insect is restricted to habitats with clay plains and Mitchell grass (*Astrebla* spp.) which can remain green for several months after rain. Through monitoring of the restricted breeding habitats, preventive control of Australian plague locust begins when populations are low and before they reach crops. Both monitoring of the restricted breeding habitats and preventive control of the insect is considered successful. For instance, the estimated crop loss of US$103 million without preventive control was reduced to US$5 million with the preventive control in 1984 (Australian Plague Locust Commission; http:\\www.affa.gov.au/content/output.cfn, 25/7/2003). In India, there was no definite information available on the source of periodic infestation of the desert locust prior to 1930 (Rao, 1942). Extensive survey was then conducted between 1932 and 1933 to identify outbreak centers of desert locust populations in India. The results gave a general picture on the distribution of solitarious populations in India. In restricted areas henceforth where solitarious populations had been observed, intensive regional and local surveys were conducted between 1933 and 1939. Accordingly, permanent outbreak centers of desert locust were identified, delimited and put under supervision (Rao, 1942). Consequently, for the first time in the history of desert locust control in India, the swarm cycle of 1940-46 was successfully arrested (Pruthi, 1951). The experiences of India and Australia set an example for the improvement of desert locust survey and control in the Central Region countries. Our research findings concur with the Indian and Australian experience suggesting that the breeding areas of solitarious populations in the green habitat are spatially more restricted than previously thought. This information can be gathered at country level. The defined locust outbreak sites can be mapped and put under regular supervision to reduce the desert locust threat to crops and pasture.

There is also a need to monitor the relationship between the dynamics of leaf quality of host plants (mainly N) and success of desert locust breeding following the seasonal variation of rainfall or run-off in the cultivated wadies. This might be an important input for establishing predictive relationships between quality of host plants and fitness of desert locust as a factor in the initiation of upsurges and plagues.

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Summary

The Red Sea coastal plains of Africa and the Arabian Peninsula are an important breeding area for the desert locust, *Schistocerca gregaria*. This area has been implicated as a source or transit area for locust infestation that threatens agriculture. The spatial distribution of desert locust on southern part of the Red Sea coastal plain of Sudan, between Port Sudan and Tokar, was investigated to establish habitat associations of the desert locust that might help in planning survey and control operations. Systematic field surveys were conducted during the winters of 1999/2000, 2000/2001 and 2001/2002 on a 120 km stretch of Red Sea coastal plain in Sudan. Data on desert locust (adult and hopper counts, egg deposition and hopper incidence) and on habitat factors (cover abundance of plant species, soil texture and moisture, elevation and grazing intensity) were collected in 60-64 sample sites spaced according to a 5 by 5 km grid of sample points. Additional data were also collected at small-scale grids.

Plant communities in the study area, between Port Sudan and Tokar, were described, mapped and classified. Multivariate data analysis resulted in the delineation of four main plant communities, which were named after characteristic plant species: the *Suaeda monoica* scrubland near the coast, the *Acacia tortilis* scrubland near the Red Sea Hills, the *Panicum turgidum* grassland at intermediate location and altitude, and *Heliotropium*/millet, small pockets of cropland (mostly planted with millet) at the transition between the *Panicum* grassland and the *Suaeda* scrub. The spatial extent of these plant communities was 5% for *Heliotropium*, 14% for *S. monoica*, 21% for *P. turgidum* and 60% for *A. tortilis*.

Principal component analysis (PCA) showed that in each of the three winter seasons, high locust densities were associated with the *Heliotropium*/millet plant community, fine soil texture and relatively high moisture availability, and negatively correlated with animal grazing and higher elevation. The *Heliotropium*/millet plant community contained 93% of the locusts found in 1999/2000 and 100% in 2000/2001 while this plant community made up 17% and 27% of our samples in the respective years and covered only 5% of the surveyed area. The localized distribution of locusts in cultivated wadi outflows was confirmed by observations in parts of the coastal zone outside the main study area. In the three seasons of the study, the highest numbers of locusts were found in the season with the greatest rainfall and the longest period of green annual plant growth, while the lowest numbers were found in the driest season.

In the three winter seasons, oviposition probing, egg laying and hopper incidence was scored in the same sample sites. All of the observed probing and egg laying, and more than 95% of the observed hoppers were located in the *Heliotropium* plant

community. No probing or egg laying, and only a few hoppers were found in the three other main plant communities on the coastal plain, characterized by *S. monoica*, *P. turgidum* and *A. tortilis*, respectively. Within the *Heliotropium* plant community, hopper densities were significantly correlated with cover abundance of *Heliotropium arbainense* (Fresen.). Densities of hoppers were greatest on *H. arbainense*, followed by *Pennisetum typhoideum* (Rich.), and lowest on *S. monoica* and *P. turgidum*.

The spatial distribution of desert locusts in the winters of 1999/2000 and 2000/2001 was further analysed with geostatistical methods. Sample variograms indicate that 71-90% of the population variance was explained spatially over a range of 5 to 24 km. This range shrunk as dry conditions towards the end of the season concentrated the locusts in the most suitable and still sufficiently humid areas. Locust densities at unsampled sites were well estimated and kriging maps delineating the high and low locust sites were produced. The relationship between sampling intensity and kriging variance was explored. Geostatistical methods offer promise for assisting in the optimization of sampling efforts for desert locust.

The desert locust *S. gregaria* was much more prevalent in the *Heliotropium* than in the *Panicum* plant community on the Red Sea coastal plain of Sudan, while both contained suitable host plants. We tested the hypothesis that the difference in aggregation of solitary desert locust density between the plant communities is related to differences in nitrogen content in host plants. Leaf samples of common plant species were collected in the *Heliotropium* and *Panicum* plant communities during the winters of 1999/2000 and 2000/2001. Leaf nitrogen content in host plants was consistently 0.5 to 1.5 percent higher in the *Heliotropium* plant community than in the *Panicum* plant community in both winter seasons.

The difference in N content observed in the field is probably ecologically significant, as was demonstrated in a life table study in the laboratory, which compared survival, development and reproduction among gregarious locusts fed on millet leaves with 3.9% or 1.4% N. Locusts reared from hatching onwards on a high nitrogen leaves had higher survival (92% versus 64%) and higher fecundity (156 ± 18 versus 92 ± 10 eggs/female) than those reared on low nitrogen leaves. Hoppers reared on high nitrogen leaves developed faster, were more synchronized, and matured and oviposited earlier than those fed on low nitrogen leaves. Approximately 75% of the mortality in hoppers reared on low nitrogen leaves was due to cannibalism, while cannibalism was absent in hoppers reared on high leaf nitrogen treatment. Thus, elevated leaf nitrogen content of host plants increased net reproduction (65 versus 20 female offspring/female) and intrinsic rate of increase (0.072 versus 0.047 day^{-1}), and lowered generation time (58 versus 63 days). The results show that the potential for population increase in the desert locust increases significantly when the nitrogen content of its host plants is higher.

This study shows a strong relationship between desert locust and the *Heliotropium*/millet plant community in the cultivated croplands on the coastal plain of Sudan. This habitat is characterized by better moisture status of the soil and high leaf nitrogen content in host plants, and contained by far the majority of solitarious locusts in the area. All of the observed locust breeding was in *Heliotropium*/millet croplands. Observations on the other parts of the coastal plain confirmed the results. The *Heliotropium*/millet croplands cover a very restricted portion of the coastal plain (5% of the area), and are relatively easy to survey.

Samenvatting

De kustvlaktes van de Rode Zee op het Afrikaanse continent en het Arabisch Schiereiland vormen een belangrijke plaats voor vermeerdering van populaties van de woestijnsprinkhaan, *Schistocerca gregaria*. Dit gebied wordt beschouwd als een bron of tussenstation voor sprinkhanenplagen die de landbouw in vele landen van Afrika en Azië bedreigen. In het zuidelijke kustgebied van de Rode Zee in Soedan, tussen Port Soedan en Tokar, is de ruimtelijke verdeling van de woestijnsprinkhaanpopulaties bestudeerd in relatie tot de habitat. Meer kennis over de ruimtelijke verdeling van populaties is nodig voor het opzetten van surveys en bestrijdingscampagnes, en geeft nader inzicht in de ecologie van de woestijnsprinkhaan. Het onderzoek werd uitgevoerd gedurende de winterperiodes van 1999/2000, 2000/2001 en 2001/2002. Gegevens over zowel de woestijnsprinkhaan (aanwezigheid en aantallen van larven en adulten, en ei-afzetting) als habitatfactoren (abundantie en bedekkingsgraad per plantensoort, intensiteit van begrazing door vee, textuur en vochtigheid van de bodem, hoogte t.o.v. zeeniveau) werden verzameld op 60 tot 64 plaatsen, die van tevoren waren uitgelegd volgens een 5 × 5 km raster. Aanvullende gegevens werden verzameld op kleinschalige rasters.

Plantengemeenschappen in het onderzoeksgebied tussen Port Soedan en Tokar werden beschreven, geclassificeerd en gekarteerd. Multivariate analyse resulteerde in de beschrijving van vier afzonderlijke plantengemeenschappen, die genoemd werden naar de karakteristieke plantensoorten: de struik *Suaeda monoica*; de boom *Acacia tortilis*, de grassoort *Panicum turgidum*, en de kruipende ruwbladige *Heliotropium arbainense*. Het meest westelijke gedeelte van de kuststrook, aan de voet van een bergketen, is bedekt met de *A. tortilis* plantengemeenschap. De bodem is hier grofzandig of gravel, en de vegetatie heeft een lage bedekkingsgraad. Verder naar het oosten, op grof zand, komen uitgestrekte graslanden van de *P. turgidum* plantengemeenschap voor. De bedekkingsgraad is hier hoger dan in de hoger gelegen *A. tortilis* zone en de vochtvoorziening is marginaal beter. Nomaden gebruiken deze zone om hun vee (geiten en kamelen) te weiden. Nog verder naar het oosten, nabij de Rode Zee en dikwijls op enigszins ziltige bodems vindt men de *S. monoica* plantengemeenschap. Ook deze wordt gebruikt voor beweiding. Rivierbeddingen doorkruisen de kustvlakte van west naar oost en voeren in de winter het regenwater, dat in de bergen valt, af. In de delta's van deze zogenaamde 'khors', op de overgang van de zones met *P. turgidum* en *S. monoica,* vindt men kleine gebieden met een fijnzandige bodem en een relatief goede watervoorziening. Hier komt de *Heliotropium* plantengemeenschap voor. In jaren met voldoende regenval worden deze gebieden door nomaden benut voor de teelt van gierst (*Pennisetum typhoidum*) op kleinschalige veldjes. Het relatieve aandeel van de vier plantengemeenschappen in de oppervlakte van het onderzoeksgebied bedroeg voor *Heliotropium* 5%, voor *S. monoica* 14%, voor *P. turgidum* 21% en voor *A. tortilis* 60%.

Hoge dichtheden van de woestijnsprinkhaan werden uitsluitend aangetroffen in de *Heliotropium*/gierst plantengemeenschap. De *Heliotropum*/gierst plantengemeenschap bevatte 93% van de sprinkhanen gevonden in 1999/2000 en 100% van die gevonden in 2000/2001. Deze plantengemeenschap maakte 17% en 27% uit van de monsters in de respectievelijke seizoenen. Het geconcentreerde voorkomen van sprinkhanen in de khor-delta's, in associatie met de teelt van gierst, werd bevestigd door observaties in andere delen van het kustgebied in Soedan. In de drie seizoenen van deze studie werden de grootste aantallen sprinkhanen gevonden in het seizoen met de meeste regenval, waarin de éénjarige plantengewassen het langst groen bleven; de kleinste aantallen werden gevonden werden in het droogste seizoen. In het droogste seizoen werden substantiële aantallen van de woestijnsprinkhaan uitsluitend aangetroffen in de delta van de Khor Baraka, nabij Tokar, in het zuiden van de kuststrook. Dit gebied heeft een afwijkende bodem en vochtvoorziening doordat de Khor Baraka ontspringt in de hogere gebergtes van Eritrea en Ethiopië en dientengevolge meer water afvoert en klei afzet. Ook hier waren de dichtheden van de woestijnsprinkhaan het hoogst in de gierstakkers.

In de drie winterseizoenen werd op de bemonsteringsplekken ook het testen door sprinkhaanvrouwtjes van potentiële ovipositie-plekken met de legboor, het leggen van eieren en de aanwezigheid van larven bepaald. Het testen van ovipositie-plekken door het vrouwtje en het leggen van eieren werd alleen waargenomen in de *Heliotropium* plantengemeenschap. Ook de waargenomen larven werden voor 95% in deze plantengemeenschap gevonden. In de overige drie plantengemeenschappen, gekarakteriseerd door *S. monoica*, *P. turgidum* en *A. tortilis*, werd het testen van ovipositie-plekken en het leggen van eieren niet waargenomen, maar werden wel enkele larven gevonden. Binnen de *Heliotropium* plantgemeenschap waren de dichtheden van larven significant gecorreleerd met de bedekkingsgraad van *Heliotropium arbainense* (Fresen.). De aantallen waren het hoogst op *H. arbainense*, gevolgd door *Pennisetum typhoideum* (Rich.) en het laagst op *S. monoica* en *P. turgidum*.

De ruimtelijke verdeling van woestijnsprinkhanen in de winters van 1999/2000 en 2000/2001 werd verder geanalyseerd met geostatistische methoden. Variogrammen gaven aan dat 71-90% van de variantie in populatiedichtheid ruimtelijk kon worden verklaard binnen een bereik van 5 tot 24 km. Dit bereik nam af toen droge omstandigheden aan het eind van het regenseizoen resulteerden in een ruimtelijke inkrimping van de gebieden met groene vegetatie. De sprinkhaandichtheden op nietbemonsterde plekken konden goed worden geschat met behulp van de geostatistische interpolatie-methode van ‘kriging’. Hiermee werden kaarten geproduceerd die de gebieden met hoge en lage sprinkhaandichtheden aangaven. De relatie tussen intensiteit van de bemonstering en de kriging-variantie werd gekwantificeerd. De resultaten tonen aan dat geostatistische methoden ondersteunend kunnen zijn bij het ontwerpen van bemonsteringprogramma’s voor de woestijnsprinkhaan.

In de Soedanese kustvlakte aan de Rode Zee was de woestijnsprinkhaan in veel hogere dichtheden te vinden in de *Heliotropium* dan in de *Panicum* plantengemeenschap, hoewel in beide plantengemeenschappen geschikte waardplanten voorkomen. Er werd nagegaan of het verschil in dichtheid van woestijnsprinkhanen tussen de plantengemeenschappen gerelateerd was aan verschillen in de hoeveelheid stikstof in de waardplanten. Bladmonsters van veelvoorkomende plantensoorten werden verzameld in de *Heliotropium* en *Panicum* plantengemeenschappen gedurende de winters van 1999/2000 en 2000/2001. De hoeveelheid stikstof in waardplanten in de *Heliotropium* plantengemeenschap was in beide winterseizoenen consistent hoger (0,5% tot 1,5%) dan die in de *Panicum* plantengemeenschap.

Het verschil in de hoeveelheid stikstof waargenomen in het veld is waarschijnlijk ecologisch relevant, zoals werd gedemonstreerd in een studie naar de biologie van het insect in het laboratorium. De overleving, ontwikkelingsduur en reproductie werden vergeleken tussen sprinkhanen gekweekt op gierstbladeren met 3,9% of 1,4% stikstof. Sprinkhanenlarven die werden gekweekt op bladeren met een hoog stikstofgehalte vertoonden een hogere overleving (92% versus 64%) en een hogere vruchtbaarheid (156 ± 18 versus 92 ± 10 eieren per vrouwelijke sprinkhaan) dan die gekweekt op bladeren met een laag stikstofgehalte. Larven gekweekt op bladeren met een hoog stikstofgehalte ontwikkelden zich sneller en meer synchroon, en produceerden als adult eerder eieren dan larven gekweekt op bladeren met een laag stikstofgehalte. Ongeveer 75% van de sterfte onder de larven gekweekt op gierstbladeren met een laag stikstofgehalte werd veroorzaakt door kannibalisme. Kannibalisme kwam niet voor als de larven gevoed werden met gierstbladeren met een hoog stikstofgehalte. Een hoger stikstofgehalte resulteerde in hogere netto reproductie (65 versus 20 vrouwelijke nakomelingen per vrouwtje), een hogere intrinsieke populatie-groeisnelheid (0,072 versus 0,047 per dag) en een kortere generatieduur (58 versus 63 dagen). De resultaten laten zien dat de potentiële groeisnelheid van een populatie woestijnsprinkhanen positief gerelateerd is aan het stikstofgehalte van de waardplant.

Dit onderzoek toont een sterk verband aan tussen de woestijnsprinkhaan en de *Heliotropium*/gierst plantengemeenschap, die te vinden is op gecultiveerde akkers in de Soedanese kustvlakte van de Rode Zee. Deze habitat, gekarakteriseerd door een geschikte bodemvochtigheid en een relatief hoog stikstofgehalte in waardplanten, bevatte de overgrote meerderheid van solitaire sprinkhanen in het gebied. Uit het gedrag van de woestijnsprinkhaan en het vóórkomen van larven kon worden afgeleid dat de meeste voortplanting plaatsvond in de *Heliotropium*/gierst akkergronden. De *Heliotropium*/gierst akkergronden bedekken slechts een zeer beperkt deel (5%) van de kustvlakte en zijn relatief makkelijk te monitoren. Observaties in andere delen van de Rode Zee kustvlakte bevestigden deze resultaten.

Het onderzoek werd uitgevoerd in samenwerking met de Plantenziektenkundige Dienst van Soedan en de Voedsel en Landbouw Organisatie van de Verenigde Naties (FAO). De Soedanese Plantenziektenkundige Dienst heeft de resultaten van het onderzoek reeds verwerkt in haar operationele surveys.

Appendices

Appendix 1. Cover abundance score of plant species per plot following van der Maarel's scale.

Score	Cover	Abundance
1	<5%	1 individual
2	<5%	2-5 individuals
3	<5%	5-20 individuals
4	<5%	>20 individuals
5	5-12.5%	
6	12.5-25%	
7	25-50%	
8	50-75%	
9	75-100%	

Appendix 2. TWINSPAN classification of relevés (columns) and plant species (records) in the 1999 winter season. Preferential and selective species are printed in bold.

Group	*S. monoica*	*Heliotropium*	*P. turgidum*	*A. tortilis*
Number of relevés	(13)	(10)	(19)	(18)
Citrullus colocynthis	**4--4432223331**	**-243-----2**	**2-2--------43--2--1**	**------------------**
Euphorbia aegyptiaca	**---334333222-**	**-------2--**	**-----------43------**	**32212---------2---**
Euphorbia sp.	**----44434324-**	**----------**	**-----------43------**	**3---2-4-----------**
Tribulus spp.	---342-433332	233-----34	2--3--2-1--44------	------------------
Dactyloctenium aegyptium	---2-2444434-	4---333-42	--------42212------	--21--------------
Chloris virgata	4--4143444-3-	2133243-21	---------4---2-----	--21--------------
Boerhavia repens	-----22-3244-	-4-4------	---4---------------	------------------
Suaeda monoica	**6664456388-36**	**44111-----**	**-3-----62----------**	**5---------5--35-34**
Eragrostis spp.	-----32222232	2--3-44-42	---------2---------	------------------
Aeluropus lagopoides	---------2---	----------	-------------------	------------------
Launaea capitata	----44233----	---4433221	-------------------	------------------
Amaranthus graecizans	**---3---3---3-**	**4324433434**	**2------41----------**	**----1-------------**
Cenchrus ciliaris	--------3----	------24--	-------------------	--------------2---
Tribulus terrestris	--13434434442	4444444444	243---2----44------	---------------24-
Eleusine spp.	4--4223332331	4344444343	-------2-1---------	--43--------------
Caylusea hexagyna	------3-3----	--------33	-------------------	------------4-----
Heliotropium spp.	**4-142-3334322**	**6677656566**	**2-----23-----4-----**	**4--222-3----------**
Pennisetum typhoideum	**-------------**	**--98896566**	**-------------------**	**------------------**
Phaseolus vulgaris	**-------------**	**--44433434**	**2------------------**	**------------------**
Schouwia purpurea	**-------------**	**--34414243**	**-------------------**	**------------------**
Chenopodium murale	**---1-1-------**	**2-44-43333**	**-------------------**	**------------------**
Amaranthus spinosus	**---3---------**	**3-24443322**	**-------------------**	**------------------**
Ricinus communis	**-------------**	**--32333211**	**-------------------**	**------------------**
Ipomoea sinensis	-------4-----	--244-----	----------------4--	------------------
Hypoestes forsskalei	**-------------**	**---43---32**	**---1-------------3-**	**------------------**
Fumaria parviflora	**-------------**	**---22---43**	**-----------------3-**	**------------------**
Cicer sp.	**-------------**	**---433--34**	**-----------------3-**	**------------------**
Sesbania sp.	**-------------**	**---22---22**	**-----------------2-**	**------------------**
Dipterygium glaucum	**-------------**	**--42----3-**	**-------------------**	**------------------**
Sorghum halepense	**-------------**	**--44142-21**	**-------------------**	**------------------**
Sorghum bicolor	**-------------**	**--652-2--1**	**-------------------**	**------------------**
Sesamum indicum	**-------------**	**-----134--**	**-------------------**	**------------------**
Medicago sp.	**---4-2--2----**	**43-3444434**	**-----21------------**	**------------------**
Datura innoxia	**--------2----**	**1122222211**	**-------------------**	**------------------**
Arnebia decumbens	-----3-------	---3----33	-------------------	------------------
Portulaca oleracea	**---3----4----**	**3-34211224**	**-------------------**	**------------------**
Trianthema sp.	**-----3-------**	**---45---33**	**-------------------**	**------------------**
Cucumis melo	**---2---------**	**2-244-----**	**-------------------**	**------------------**
Rumex sp.	---3---------	4---------	-----1-------------	------------------
Cyperus spp.	3--3-----4---	---2244---	-------------------	------------------
Panicum turgidum	**1-2-6812--342**	**43131-2412**	**-447756267665326416**	**23------2-24-3-4-3**
Capparis decidua	**------3---13-**	**--2---2---**	**-1--11-----4443243-**	**------------------**
Prosopis chilensis	--1--13---32-	-2111---22	54---23311---------	----2-2------13-13
Echinochloa colona	---43424-4333	-3-3344-42	-----4334343322234-	----43-------34---
Leptadenia pyrotechnica	-------------	------2443	-45321-------------	-----------444-4--
Salsola spinescens	-52-4------3-	-3--2-----	---343432----------	--3---------------
Solanum dubium	---1-------1-	-1--------	-----1----1--------	-------1-----1-1--
Corchorus olitorius	-----2-------	--------11	---1----1----1---1-	------------------
Cadaba sp.	-----------3-	----------	232----------3---43	----------4-------
Convolvulus sp.	-----------3-	----------	-34----------33--4-	--------2---------
Pennisetum spp.	43-4344444443	34433-4-42	-----43--3444332234	334343444344434---
Tephrosia spp.	--32444234444	2343444344	1-23------333--331-	344242-----3-25-2-
Crotalaria microphylla	--43443334435	3344244254	1-23------333--222-	344232-------33-4-
Calotropis procera	--33233-2-331	-312223424	346353-24----3-244-	-22-3-242--4443445
Zygophyllum simplex	---22-32-3452	24-----544	--45443------52554-	41566654444544-443
Acacia tortilis	23---------3-	--------2-	11-64-45441--4-5552	22-344556544454645
Trianthema crystallina	44---34312---	--233-22-4	-------------------	-2333-42222-------
Schoenfeldia gracilis	44-332-3432-2	3123--3-3-	-4-------244423234-	22324422343324---3
Salvadora persica	**-------4-----**	**----------**	**-4----------5------**	**-2313-45-----3----**
Ochradenus baccatus	**-------------**	**----------**	**---4---------------**	**------2431-----3--**
Indigofera spinosa	-------------	----------	2-----------------4	-----222----------
Lycium shawii	**-1-----------**	**----------**	**-----------------44**	**3----15544434-----**
Fagonia spp.	344----------	-1---212--	---------------12--	444-3---4-43------
Cyphostemma sp.	**-------------**	**----------**	**-------------------**	**1223--34----------**
Cassia senna	33-24--1-3--2	4----1----	--------------233--	--27543644465-----
Aerva javanica	4-1----222-3-	-----222-2	-------------------	4-------4551------

Appendix 3. TWINSPAN classification of relevés (column) and plant species (records) in the 2000 winter season. Preferential and selective species are printed in bold.

Group	*S. monoica*	*Heliotropium*	*P. turgidum*	*A. tortilis*
Number of relevés	(16)	(17)	(17)	(14)
Suaeda monoica	**55-34235-32-2-55**	**4-1------2-----12**	**----------5-----3**	**--------------**
Euphorbia spp.	-3-4----242322--	22312-------4-1--	-1---1---11------	-------------4
Echinochola colona	---425-4412311-3	1--21114241221---	-1------------111	------------14
Dactyloctenium aegyptium	-4141213--------	21213--211-1--1--	---1-----1431----	1-1-2-----11--
Cassia senna	-------1423443--	--1--------1--243	3155-------------	-------------4
Aeluropus lagopoides	--------------3-	-----------------	-----------------	--------------
Halopepis sp.	---------------1	1----------------	-----------------	--------------
Heliotropium spp	-124541143--4---	5235442211-333334	-1--------2-2-421	21-111----1---
Pennisetum typhoideum	**----------------**	***66755665655544434***	**-----------------**	**--------------**
***Eleusine* spp.**	**-----1----------**	**111232322111--1--**	**---1----1111-11--**	**2-1---1---111-**
Eragrostis spp.	-----2------1---	-1---1312131-----	---12---------1--	1---1-1--1--1-
Amaranthus spp.	--23---------1--	--2-1-12122--1---	--------1-1------	----11--------
***Medicago* sp.**	**--2--1----------**	**--11-234-12------**	**--------1---1----**	**----1-1-------**
Aerva javanica	2---------2-----	---21--12121-----	----2-------11---	--------------
Citrullus sp .	------------1---	1--1-111--1------	----------1-----2	----------1---
Cyperus spp.	3------------312	2----1431234-----	-----------------	----1---------
Farsetia eagyptia	----------------	---2-------------	-----------------	--------------
Chenopodum murale	----------------	--1----1---------	-----------------	--------------
Cucumis melo	----------------	---1--1-1--------	-----------------	--------------
Commolina forsskalei	----------------	------1----------	-----------------	--------------
Datura innoxia	----------------	-------12-2------	-----------------	--------------
Portulaca oleracea	----------------	------1----------	-----------------	--------------
Sorghum bicolor	----------------	----------1------	-----------------	--------------
Sorghum helpense	----------------	----------1------	-----------------	--------------
Solanum indicum	----------------3	--11--1-1-2-----	-- --------------	-1--1--------
Chloris virgata	--1-------------	----1-1-21-------	----1------------	--1-----------
Panicum turgidum	**----1-1--11-1---**	**31-1-1----31--12-**	**-2145555553543653**	**-4-214221-1342**
Schoenfeldia gracilis	-211----21------	---111-11--------	--5334443543-313-	34433444443343
Crotalaria microphylla	2344331-4432-2--	411422-1---1-----	--1----4-11-11-1-	42433333221111
Cenchrus ciliaris	**11-4---311------**	**-----------------**	**--32-123134342---**	**--123---------**
Salsola spinescens	--------21------	-----------------	---111-----21-1-1	1-----211--3--
Sesamum indicum	----------------	-----------------	--------2--------	--------------
Corchorus olitorius	**----------------**	**-----------------**	**--------111-1----**	**--------------**
Blepharis ciliaris	**----------------**	**-----------------**	**----12--2---11---**	**--------------**
Heliotropium longiflorum	----------------	-----------------	-----1-1---------	--------------
Crotalaria sp.	----------------	-----------------	----1------------	--------------
Astragallus spp.	----------------	-----------------	--1--------------	--------------
Acacia tortilis	**--------1-------**	**---2-------------**	**232-----3------21**	**-33-32-4354-12**
***Rumex* sp.**	**------1------1--**	**-2---12111-------**	**-------1-------2-**	**1311132121111-**
Cordieus sp.	----------------	-----------------	-----------------	----1---------
Anastatica sp.	----------------	-----------------	-----------------	--11----------
Indigofera spinosa	**----------------**	**-----------------**	**-----------------**	**---111--------**
Cissus spp.	----------------	----------- -----	-----------------	---2----------
***Convolvulus* spp.**	**----------------**	**----------------**	**-- ------1--------**	**-1---1---112-**
Capparis decidua	----------------	-----------------	------1--------1-	--2-2-----2---
Panicum sp.	----------------	----------1------	-----------------	-----------13-
Lycium shawii	----------------	---------21------	-----------------	------11----4-
Pennisetum spp.	1344333444221421	422233424441--21-	--243341313454434	44444244322244
Euphorbia spp.	--123111----41--	11-34211--1--2243.	1-111-34422-13444	3344433321211-
Tephrosia spp.	212132-1121--1--	-3-311221--11--32	---11133443-31314	--33441--2--11
Fagonia spp.	-1433----43-41--	21--111---11--11-	--1212-12-3--2142	123113432244-1
Zygophyllum simplex	--1--43444443-1-	1-1132111353-2231	-1-3223------1-12	1-413255446554
Tribulus terrestris	2-1113----------	-1-----3-11112---	---11-1-111-1--1-	1---1-1--1111-
Launaea capitata	-21---1-2---1---	2-121222212--3---	---11-3-11111-442	1111112--11---
Calotropis procera	-------13---41-2	-1142113313222412	----1-------21--1	21335-43-2-14-
Trianthema spp.	--32311-343--1--	-2233234241------	-------131121141-	1-1-111---1---
Prosopis chilensis	-----1---------4	------12--1------	---------------1-	5---1-----1---
Tribulus sp.	--13-1--31---1--	---1-------2----1	--------3--------	3343----------
Abutilon pannosum	----------------	-------12-1------	----5-1----------	----1---------
Argemone mexicana	---------------4	-1-----3---------	---12-3-1---21---	--------------
Showuia purpurea	----------------	----------2------	-----------------	---------2----
Dipterygium glaucum	----------------	-1---------1-----	-----------------	----1---------
Chrozophora sp.	----------------	-----11--- -----	-----------------	---2--3-------
Trianthema crystallina	---2------------	----1------------	----------2------	--------------
Caylusea hexagyna	--1-------------	----1--1-14------	------3----------	--------------

Appendix 4. TWINSPAN classification of relevés (columns) and plant species (records) in the 2001 winter. Preferential and selective species are printed in bold.

Group	*S. monoica*	*Heliotropium*	*P. turgidum*	*A. tortilis*
Number of relevés	(10)	(14)	(30)	(10)
Suaeda monoica	6644465655	-211786672-526	--------------------3---------	-------1--
Aeluropus lagopoides	-----23---	--------------	------------------------------	----------
Datura innoxia	-----1----	--------------	------------------------------	----------
Halopeplis sp.	------4---	--------------	------------------------------	----------
***Heliotropium* spp.**	**----------**	**3431321441331-**	**--------------1--3---11-------**	**----------**
Ricinus communis	----------	-1---------2--	------------------------------	----------
Pennisetum typhoideum	----------	-4---------4--	------------------------------	----------
Dactyloctenium aegyptium	----------	---------12333	------------------------------	11--------
Amaranthus spp.	----1----1	-4-------2-21-	------------------------------	----------
Portulaca oleracea	----------	-----------1--	------------------------------	----------
Commolina forsskalei	----------	-----------2--	------------------------------	----------
Sesamum indicum	----------	-----------1--	------------------------------	----------
Caylusea hexagyna	----------	------1-----1-	------------------------------	----------
Sesbania sp.	----------	-----------1--	------------------------------	----------
***Eleusine* spp.**	**----------**	**-----11---11--**	**------------------------------**	**----------**
Crotalaria microphylla	----------	------144-2---	------------------------------	-2--------
***Tephrosia* spp.**	**----------**	**-----131424-1-**	**--------------11-1------------**	**----------**
Tribulus spp.	----2-----	-------33111--	------------------------------	-1--------
Citrullus sp.	----------	----11--2-11--	------------------------------	1---------
Euphorbia spp.	----------	-3----3341----	-3----------------------------	--1-------
***Medicago* sp.**	**----------**	**11----1-2-12--**	**------------------------------**	**----------**
***Trianthema* spp.**	**----------**	**11----1-21432-**	**------------------------------**	**----------**
Launaea capitata	**----------**	**13---2-22121--**	**------------------------------**	**2---------**
Eragrostis spp.	----------	---------111-1	--------------1---------------	3---------
Cyperus spp.	-----4----	-2--------12--	------------------------------	----------
Pennisetum spp.	-----1----	1-2--3-331444-	----------1-------------------	323-------
Solanum dubium	--------1-	111--------1--	--------------1-------1-------	--1-------
Cynodon dactylon	----------	-11--------1--	----------------11------------	----------
Cyperus spp.	----------	----------1-1-	---------------------1--------	----------
Chloris virgata	----------	-----1----32-2	--------------1---------------	21-----1--
Schoenfeldia gracilis	-----1----	11---2----24-4	--1---------------------------	344-------
Echinochloa colona	-----2----	--31-2--2-13--	---------------------11-------	322-------
Cenchrus ciliaris	----------	-------------3	------------------------------	-----1----
Xanthium sp.	------1---	--------1-----	------------------------------	----------
Indigofera spinosa	----------	--------------	---------------1--------------	-------4--
Crotalaria sp.	----------	--------------	----1-------------------------	----------
Cordieus sp.	----------	--------------	-------------1----------------	----------
Cissus spp.	----------	--------------	---------------------------2--	----------
Acacia sp.	----------	--------------	---------------------------4--	----------
Hyphaene sp.	---------1	--------------	----------------1-------------	----------
Panicum turgidum	-1---1-332	1---21----11-3	65655416556467363323221--64---	5-13-15452
Calotropis procera	-5-----411	11222----11---	--2221-12321--141243532443553-	1-312-31-2
Salsola spinescens	1-------51	--------------	--3-152434---233--52----------	3252-----3
Capparis decidua	-------2--	----------2---	32622--4-4---------1------45--	4------4--
Leptadenia pyrotechnica	----------	--------------	---2432-1---------------------	-----2----
Prosopis procera	-11-----1-	--1---1--23---	1--1--1---1---1--11--------261	---1-----5
Convolvulus sp.	----------	--------------	1-----------------------------	----------
Ochradenus baccatus	----------	--------------	----111-----------------------	----------
Abutilon pannosum	----------	-----------2--	-52-5--11-------11------------	----------
Cadaba sp.	----------	-------1------	121-11---2--------------------	----------
Aerva javanica	----------	11---1--------	--1-1--41------21-------------	----------
Boscia sp.	----------	--------------	---23-------------------------	-1--------
Arnebia decumbens	----------	--------------	-11---------------------------	--1-------
Argemone mexicana	----------	------1-------	-------153--------------2-----	2---------
Lycium shawii	**--------2-**	**--------------**	**--12-1---------------------2--**	**----21-211**
Zygophyllum simplex	------1---	-----31--1-3--	--2--1-----1--22--------------	--1--1----
Acacia tortilis	**-------21-**	**--------------**	**-33-2--1-1---112------1-------**	**4614554663**
Cassia senna	**-------3--**	**---1-1--------**	**--------------22-----11-------**	**-564-43---**
Fagonia spp.	----------	1----31---1---	--------------1---------------	413---1---
Flaveria trinerva	----------	-----1--------	------------------------------	1-1-------
Ziziphus spina-christi	---------1	--------------	------------------------------	----1-----
Aleo spp.	----------	--------------	---------------1--------------	-----1----
Blepharis ciliaris	---------1	--------------	--1---------2-----------------	3---------
Astragalus sp.	----------	--------------	------------------------------	2---------
Hypoestes forsskalei	----------	--------------	------------------------------	1---------
Cissus spp.	-1--------	--------------	-21-----11--------------------	111-------
Boerhavia repens	----------	------1-------	------------------------------	--3-------
Corchorus spp.	----------	------1---1---	------1-----------------------	-------3--
Jatropha sp.	-1--------	1-------------	1-1---------------------------	-----1-1--
Dipterygium glaucum	----------	1-------------	----------------1-------------	----------

Appendix 5. Average time and standard deviation (SD) of time of recruitment to the next stage for hoppers reared on low (N0) and high (N1) nitrogen millet leaves.

Stage	Average time of recruitment to a stage		SD of the time of recruitment to a stage	
	N0	N1	N0	N1
L2	4.09 ± 0.20	3.24 ± 0.44^{NS}	0.68 ± 0.08	0.42 ± 0.09**
L3	8.57 ± 0.29	6.94 ± 0.62^{NS}	0.72 ± 0.09	0.47 ± 0.07**
L4	13.74 ± 0.33	11.19 ± 0.79^{+}	0.90 ± 0.16	0.50 ± 0.06*
L5	19.60 ± 0.37	16.39 ± 1.05^{+}	1.11 ± 0.11	0.47 ± 0.05**
Fledgling	28.85 ± 0.41	25.43 ± 1.26^{+}	2.63 ± 1.37	0.52 ± 0.04^{NS}

Differences between treatment means are significant:

** $p \leq 0.01$; * $p \leq 0.05$; $^{+}$ $p \leq 0.10$; and ^{NS} not significant at $p > 0.10$ using paired t-test.

Appendix 6. Median duration of stage and median time of recruitment to the next stage for hoppers reared on low (N0) and high (N1) nitrogen millet leaves.

Stage	Median duration of stage		Median time of recruitment to a stage	
	N0	N1	N0	N1
L1	4.34 ± 0.28	4.29 ± 0.59^{NS}		
L2	4.28 ± 0.26	2.06 ± 0.48*	4.34 ± 0.28	4.29 ± 0.59^{NS}
L3	5.19 ± 0.21	4.09 ± 0.12**	8.62 ± 0.39	6.35 ± 0.19*
L4	5.97 ± 0.39	5.42 ± 0.53^{NS}	13.81 ± 0.34	10.45 ± 0.08*
L5	9.21 ± 0.39	8.58 ± 1.03^{NS}	19.78 ± 0.69	15.86 ± 0.57*
Fledgling			28.99 ± 0.71	24.44 ± 0.67*

Differences between treatment means are significant:

** $p \leq 0.01$; * $p \leq 0.05$; and ^{NS} not significant at $p > 0.10$ using paired t-test (stage duration) and Mann-Whitney U-test (median time of recruitment).

Curriculum vitae

Gebremedhin was born on 27 September 1968 in Daero Techli, a village near the town of Adua, Ethiopia. His parents send him to the elementary school which was about 15 km away from his home. After finishing the secondary school (at Adua and Gondar) he studied at the Alemaya University of Agriculture, Ethiopia and obtained a BSc degree in Plant Sciences in 1987. From 1988 to 1993, he worked as a research assistant in field crops (agronomist) at the Institute of Agricultural Research, Ethiopia. From September 1993 to January 1995, he studied Crop Sciences at Wageningen University (WU), The Netherlands, and obtained his MSc degree in Crop Production. In July 1999, he joined the C.T. de Wit Graduate School PE & RC of Wageningen University to conduct a PhD study on the improvement of desert locust survey and control operations. During his PhD period, he visited the Natural Research Institute (NRI) at the Greenwich University in England and the Desert Locust Information Services (DLIS) at FAO in Rome. Moreover, he spent three winter seasons (November-March) conducting field research at the Red Sea coastal plain of Sudan of which the results are included in this thesis.

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