AFRICAN ARMYWORM OUTBREAKS: WHY DO THEY OCCUR AFTER DROUGHT?

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J. A. M. Janssen

Stellingen

1. Om te komen tot een meer betrouwbare, vroegtijdige plaagvoorspelling van de Afrikaanse legerworm in Oost-Afrika dient vooral diens fenologie tijdens de lange droge periode nader bestudeerd te worden.

   Dit proefschrift.

2. Voor een beter begrip van de plaagontwikkeling van de Afrikaanse legerworm dient in daaromtrent te verrichten veldstudies het relatieve belang bepaald te worden van de omgevingsfactoren: waardplantkwaliteit, waardplantleeftijd, regenval en natuurlijke vijanden.

   Dit proefschrift.

3. Uit het oogpunt van opbrengstderving bij maïs, veroorzaakt door de Afrikaanse legerworm, verdient bestudering van het tritrofische systeem 'bodem-plant-herbivoor' de voorkeur boven bestudering van het tritrofische systeem 'plant-herbivoor-natuurlijke vijand'.

   Brown, E.S. & Mohammed, A.K.A. (1972). E. Afr. Agric. For. J. 37: 237-257.

4. Het genereren van hypotheses ter verklaring van droogte-plaag relaties, waarbij ter ondersteuning vervolgens uitsluitend, zonder nadere toetsing, indirect bewijsmateriaal wordt aangedragen, heeft niet geleid tot grotere duidelijkheid wat betreft het mechanisme dat aan deze relaties ten grondslag ligt.

   White, T.C.R. (1976). Oecologia 22: 119-134.
   Mattson, W.J. & Haack, R.A. (1987). In: F. Slansky, J.G. Rodriguez (eds.), Nutritional Ecology of Insects, Mites, Spiders, and Related Invertebrates. John Wiley & Sons, New York: 147-175.

5. Voor effectief gebruik van satellieten in de bestrijding van migrerende plaaginsekten is een gedegen kennis vereist van de ecologie van de betreffende insekten.

   Hielkema, J.U. (1990). Phil. Trans. Roy. Soc. London B328: 705-717.
   Milford, J.R. & Dugdale, G. (1990). Phil. Trans. Roy. Soc. London B328: 689-704.

6. Voor het leggen van relaties tussen onderdelen van het EPG-patroon C en styletpenetratie-activiteit bieden wittevliegen grotere mogelijkheden dan bladluizen.

   Janssen, J.A.M., Tjallingii, W.F. & Lenteren, J.C. van (1989). Entomol. exp. appl. 52: 69-81.

7. Dat kaswittevlieg (*Trialeurodes vaporariorum*) alleen persistente virussen overbrengt is beter te begrijpen wanneer men het styletpenetratiegedrag van dit insekt nauwkeurig kent.

Bird, J. & Maramorosch, K. (1978). Adv. Virus Res. 22: 55-110.
Janssen, J.A.M., Tjallingii, W.F. & Lenteren, J.C. van (1989). Entomol. exp. appl. 52: 69-81.

8. Eigenschappen van de apoplast dichtbij het bladoppervlak spelen een hoofdrol bij de selectie van voedingsplaatsen door kaswittevlieg (*Trialeurodes vaporariorum*).

Janssen, J.A.M., Tjallingii, W.F. & Lenteren, J.C. van (1989). Entomol. exp. appl. 52: 69-81.

9. Voor een optimaal gebruik van de sex ratio bij de beoordeling van de kwaliteit van *Trichogramma* soorten in een massakweek dient de sex ratio in afwezigheid van superparasitering als referentiewaarde genomen te worden.

Bigler, F., Cerutti, F. & Laing, J. (1991). Proc. 5th workshop of the IOBC working group "Quality control of mass reared arthropods": 200-201.

10. De tegenwoordig veelvuldig gebruikelijke korte-termijn financiering van wetenschappelijk onderzoek vertraagt de voortgang op wetenschapsgebieden waar het uitvoeren van langlopende experimenten volstrekt onontbeerlijk is.

11. Het niet accepteren door tijdschriftredacties van wetenschappelijke bijdragen die slechts tot gedeeltelijke verificatie van een hypothese hebben geleid, ondergraaft een gezonde voortgang van wetenschappelijk werk.

12. Het unieke van iemand die Jan Janssen heet berust niet alleen op zijn naam.

Stellingen behorende bij het proefschrift "African armyworm outbreaks: why do they occur after drought?" door J.A.M. Janssen.

Wageningen, 4 juni 1993

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Voor mijn ouders

Voor Karen

In the days that I was close to finishing my biology study, I contacted Prof.Dr. Louis Schoonhoven at the Department of Entomology of the Wageningen Agricultural University to discuss the possibilities of doing research and writing a doctor's thesis. Within a few minutes we were talking about the project here described. I soon realized that the project would offer me an ideal opportunity to gain further knowledge in the field of insect-plant relationships. Moreover, I would be able to extend my knowledge to an essential part of every ecosystem: the soil. Less than a month later I was informed that I would be the man on the job. Louis, thank you for your trust in me. Thank you also for giving me ample space to develop and discuss own ideas and to conduct my research in an independent way. As supervisor you were always available when I needed your valuable help and advice.

Soon after the start of the project I came in contact with Prof.Dr. Günter Findenegg of the Department of Soil Science and Plant Nutrition of the Wageningen Agricultural University. He became my second important supervisor. Günter, thank you for your excellent suggestions throughout the research period and the pleasant discussions during the completion of the thesis.

Of course many more people have generously contributed in one way or another to the completion of this doctoral thesis. At this place I would like to express my sincere thank to all of them. A few I want to name.

Dr.ir. Victor Houba and Dr.ir. Bert Janssen were of great help when I made my first steps in the field of soil science. Their advice profoundly influenced an important part of my work.

In Wageningen the research depended on the assistance of numerous people. Birgit Nübel now knows how difficult it is to culture the African armyworm successfully. Her assistance during some of the laboratory experiments was indispensable. Willeke de Bruin invariably surprised me with her eagerness to prepare the endless numbers of soil and plant samples for analysis. During the actual analysis she was often assisted by Eric Heij, Arie van den Berg, Winnie van Vark and Frans Möller of the Service Laboratory at the Department of Soil Science and Plant Nutrition. Otto van Geffen, Simon Maasland and Willem Menkveld were always more than willing to help with the construction of experimental designs.

During my annual visits to Kenya, I enjoyed the friendship of many

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Summary

The African armyworm, *Spodoptera exempta* (Walker)(Lepidoptera; Noctuidae), feeds almost exclusively on plants of the families Gramineae and Cyperaceae. It is a severe pest of crops, including maize, sorghum and millet, especially on the eastern side of the African continent where a marked seasonal occurrence of outbreaks coincides with the rains. First outbreaks of a season can arise soon after the start of the short rains (October-November) in the so-called primary outbreak areas, which are located in the zone separating the lower desert area to the east from the highlands to the west in Kenya and Tanzania. Adults from these primary outbreaks migrate downwind on the prevailing easterly winds to give rise to subsequent generations further west in secondary outbreak areas. The outbreak season subsequently ends during the long dry season. No further outbreaks are reported, and densities remain very low, until the start of the following short rainy season. Current control aims to destroy, with insecticides, any outbreaks that are critical in terms of their potential to generate upsurges in following generations. Many primary outbreaks are critical in this sense.

Outbreak development of the African armyworm is known to vary greatly between years in eastern Africa: in some years hardly any outbreaks are reported while in others severe infestations occur over very large areas. Drought (below average precipitation) in particular, has often been associated with the most severe outbreak seasons. As outbreaks usually seem to develop on plants which are free of drought stress but that are growing on soils that have previously been subjected to severe drought for a considerable time, the existence of a delayed indirect effect of drought on outbreak development of the African armyworm is postulated. It is hypothesized that:

> *Periods of more severe drought encourage the occurrence of more severe outbreaks by stimulating the mineralization process in the soil when it is remoistened by rainfall as the drought breaks. This results in higher soil nitrate levels and, consequently, higher nitrogen levels in host plants of the African armyworm, thus increasing larval developmental rate and survival (especially of very young larvae) as well as the fecundity of subsequent adults.*

This hypothesis is based on the knowledge that the decomposition of organic material by bacteria in a soil after wetting is correlated with the duration and temperature of the drying period to which the soil has been exposed (the so-called 'Birch-effect'), and that higher nitrogen contents in host plants have often been observed to increase herbivore fitness. The aim of the present study has been to test this hypothesis.

The effect of different climatological conditions on the availability of nitrogen, phosphorus and potassium in soils and correlations with the levels of these minerals in host plants of the African armyworm have been studied in a primary outbreak area during the first month after the start of the short rainy season in the years 1988 to 1991 (Chapter 2). In addition, intraplant variation (in time and space) in the concentration of these minerals as well as in the water content of maize plants has been assessed in the field (Chapter 3). The results show that more intense drought results in soil heating to extreme temperatures towards the end of the long dry season. This stimulates the nitrogen mineralization process during the subsequent short rainy season, especially in soils which are not excessively poor in organic carbon and total nitrogen. The average mineral nitrogen concentration in the soil during the first month of the short rainy season is also influenced by the rainfall pattern: excessive rain (more than 40 mm in a few days) can seriously decrease the nitrate level in the upper 25 cm of soil through leaching. No consistent effect of drought intensity on soil phosphorus and potassium levels has been found. Large differences between years in soil nitrate level, due to different drought intensities and rainfall patterns, result in large differences (up to 2% dry wt.) in the average organic nitrogen content in host plants of the African armyworm; such differences in phosphorus and potassium levels are relatively small. In the primary outbreak area under study, outbreaks of the African armyworm only seem to develop in years in which organic nitrogen concentrations of about 5% or more are found in young grasses.

To relate the fitness of the African armyworm to the nitrogen, phosphorus, potassium and water content of maize leaves, two experimental designs have been used in the laboratory: an excised leaf system (Chapter 4) and a gravel culture system (Chapter 5). Both yield a consistent picture: development, survival and fecundity of the African armyworm are generally only slightly affected by differences in the levels of the four plant constitu-

ents. Fecundity is strongly dependent on adult weight. Only extremely low phosphorus levels (below 0.15% dry wt.) decrease larval growth and survival very significantly. Extremely low nitrogen levels (below 1.5% dry wt.) decrease larval growth slightly and probably affect fecundity negatively, but do not influence larval survival. However, these concentrations rarely occur in the primary outbreak area during the first month after the start of the short rainy season.

Thus, the above mentioned hypothesis is only partly supported by these results. Whilst the observed weather-soil-plant interactions agree with the hypothesis, the assumed plant-armyworm interaction, as studied under laboratory conditions, seems to be incorrect. The observed large differences between years in plant nitrogen level are therefore probably not of key importance in explaining the differences between years in outbreak development of this insect.

This conclusion is further supported by field data from a fertilization experiment with maize plants (Chapter 7). These data also indicate that the nitrogen status of host plants, within the range encountered in the field during the first month of the short rainy season, is not affecting the fitness of young larvae. Moreover, they show that the mortality of young larvae under field conditions is much higher than in the laboratory. Apart from natural enemies, rain and high relative humidity seem to be detrimental to young caterpillars in the field.

The question of how the African armyworm survives the long dry season (Chapter 6) has increased in importance towards the end of the present study as the original hypothesis seemed inadequate to explain the drought-outbreak relationship in this pest species. Furthermore, large differences between years have been observed in the moth numbers caught in the primary outbreak area at the start of the armyworm season. It is important to recognize that the caterpillars preceding these moths have presumably not been able to feed on host plants in the area. This would probably exclude host plant quality as a factor possibly influencing these moth numbers. Thus, the question of survival during the long dry season seems to be of great importance.

Although it can not be excluded with certainty, it seems most unlikely that moths can survive for the duration of the long dry season. While diapause seems not to exist, moths can live for 4 to 5 weeks under certain

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conditions. Such extreme longevity has never been reported before for this insect, but is still insufficient for survival during the entire long dry season. Moths also appear to be capable of delaying their reproductive development to some extent under dry season conditions but this seems, at best, to offer them an improved chance of locating suitable oviposition sites in the eastern African lowlands during this period. These results raise the question of whether this area really is unsuitable for sustaining armyworm larvae throughout the long dry season.

Future studies on the epidemiology of the African armyworm should concentrate on further validation of the laboratory results concerning host-plant quality, obtained in the present study, under field conditions (Chapter 7). Simultaneously, the effects of other, presumably more important, determinants of the fitness of the African armyworm (plant age, rainfall and natural enemies) ought to be assessed. In addition, the dry-season phenology should be subjected to further study. Such field studies will increase our understanding of the observed drought-outbreak relationship of this species and possibly also of other notorious pest species with similar life-history strategies. Until we know the underlying mechanism of this relationship, long-range forecasts of outbreaks are unlikely to be improved. Adequate knowledge on this mechanism should be considered of crucial importance for a more reliable anticipation of the severity of an armyworm season and a further reduction of the area over which control is required.

De Afrikaanse legerworm, *Spodoptera exempta* (Walker)(Lepidoptera; Noctuidae), voedt zich nagenoeg uitsluitend met planten uit de families Gramineae en Cyperaceae. Het insekt kan ernstige plagen veroorzaken in gewassen als maïs, sorghum en millet, met name aan de oostkant van het Afrikaanse continent waar een opmerkelijk seizoensgebonden voorkomen van plagen samenvalt met de regentijden. De eerste plagen van een seizoen ontstaan spoedig na het begin van de korte regentijd (oktober-november) in de zogenaamde primaire plaaggebieden. Deze zijn gelokaliseerd in de zone die het lage, in het oosten gelegen, woestijnachtige gebied scheidt van de meer naar het westen gelegen hooglanden in Kenya en Tanzania. Adulten die voortkomen uit deze primaire plagen migreren westwaarts met de overheersende oostelijke winden mee, om vervolgens nieuwe generaties voort te brengen in verder naar het westen gelegen secundaire plaaggebieden. Het plaagseizoen loopt vervolgens ten einde tijdens de lange droge tijd. Geen plagen worden dan meer waargenomen en dichtheden zijn bijzonder laag tot het begin van de volgende korte regentijd. Momenteel is de bestrijding van het insekt erop gericht om met behulp van insecticiden elke plaag te vernietigen die kritisch is wat betreft zijn potentie tot grotere plaagontwikkeling in volgende generaties. In dit opzicht kunnen vele primaire plagen als kritisch bestempeld worden.

Het is bekend dat de plaagontwikkeling van de Afrikaanse legerworm in Oost-Afrika van jaar tot jaar sterk varieert. Terwijl in sommige jaren nauwelijks plagen worden gerapporteerd, komen in andere jaren ernstige plagen voor over grote oppervlakten. Met name droogte (minder dan gemiddelde neerslag) is vaak met de ernstigste plaagseizoenen in verband gebracht. Plagen lijken gewoonlijk tot ontwikkeling te komen op planten die vrij zijn van droogte-stress, maar die groeien op bodems die daarvoor gedurende een aanzienlijke periode wel bloot hebben gestaan aan intense droogte. Op grond hiervan is het bestaan van een vertraagd, indirect effect van droogte op de plaagontwikkeling van de Afrikaanse legerworm gepostuleerd. Dit heeft geleid tot de formulering van de volgende hypothese:

> *Perioden van intensere droogte bevorderen het voorkomen*
> *van ernstigere plagen door het mineralisatieproces in de*
> *bodem te stimuleren nadat deze is bevochtigd door de regen*

*die de droogte breekt. Dit resulteert in hogere nitraatgehalten
in de bodem en hogere stikstofgehalten in waardplanten van
de Afrikaanse legerworm, met als gevolg een toename van de
ontwikkelingssnelheid en overleving van de larven (met name
van de jongste larven) alsook van de voorplantingscapaciteit
van de adulten.*

Deze hypothese berust op de kennis dat het afbraakproces van organisch
materiaal door bacteriën in een bodem na bevochtiging correleert met de
duur en de temperatuur van de droogperiode waaraan de bodem is blootge-
steld (het zogenaamde 'Birch-effect'), en dat hogere stikstofgehalten in
waardplanten vaak blijken te resulteren in een grotere fitness van herbivoren.
Het doel van de voorliggende studie is geweest deze hypothese te toetsen.

Het effect van verschillende klimatologische condities op de beschik-
baarheid van stikstof, fosfor en kalium in bodems en de correlaties daarvan
met de gehalten van deze mineralen in waardplanten van de Afrikaanse
legerworm zijn bestudeerd in een primair plaaggebied, tijdens de eerste
maand na het begin van de korte regentijd in de jaren 1988 tot 1991 (Hoofd-
stuk 2). Tevens is de intraplant variatie (in tijd en ruimte) in de concentraties
van deze mineralen alsook in het watergehalte bepaald bij maisplanten in het
veld (Hoofdstuk 3). Uit de gegevens blijkt dat intensere droogte extreme
bodemverhitting tegen het einde van de lange droge tijd tot gevolg heeft en
dat deze het stikstofmineralisatieproces tijdens de daarop volgende korte
regentijd stimuleert, vooral in bodems met niet extreem lage gehalten aan
organische koolstof en totaal stikstof. Bovendien blijkt het gemiddelde
minerale stikstofgehalte in de bodem tijdens de eerste maand van de korte
regentijd te worden beïnvloed door het regenvalpatroon: overvloedige regen
(meer dan 40 mm in enkele dagen) kan het nitraatgehalte in de bovenste 25
cm van een bodem sterk doen afnemen door uitspoeling. Er is geen consis-
tent effect van droogte-intensiteit op het fosfor- en kaliumgehalte in de
bodem gevonden. Grote verschillen tussen jaren in het nitraatgehalte van
bodems, als gevolg van fluctuaties in droogte-intensiteit en regenvalpatroon,
blijken te resulteren in eveneens grote verschillen (tot 2% droog gewicht) in
het gemiddelde organische stikstofgehalte in waardplanten van de Afrikaanse
legerworm. Zulke verschillen in fosfor- en kaliumgehalten zijn relatief klein. In
het primaire plaaggebied waar de studie is uitgevoerd, lijken plagen van de
Afrikaanse legerworm zich alleen te ontwikkelen in jaren waarin in jonge

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grassen organische stikstofgehalten van ongeveer 5% worden waargenomen.

Om de fitness van de Afrikaanse legerworm te relateren aan het stikstof-, fosfor-, kalium- en watergehalte van maisbladeren zijn onder laboratoriumcondities twee proefopzetten gebruikt: een afgesneden bladsysteem (Hoofdstuk 4) en een gravelcultuur systeem (Hoofdstuk 5). Beide tonen een consistent beeld: de ontwikkeling, overleving en voortplantingscapaciteit van de Afrikaanse legerworm wordt in het algemeen nauwelijks door verschillen in de gehalten van de vier plantbestanddelen beïnvloed. De voortplantingscapaciteit is sterk afhankelijk van het popgewicht. Alleen extreem lage fosforgehalten (lager dan 0.15% droog gewicht) verminderen de larvale groei en overleving zeer significant. Extreem lage stikstofgehalten (lager dan 1.5% droog gewicht) verminderen de larvale groei enigszins en beïnvloeden waarschijnlijk de voortplantingscapaciteit negatief, maar blijken niet van invloed op de larvale overleving te zijn. Deze gehalten worden echter zelden tijdens de eerste maand na het begin van de korte regentijd in het primaire plaaggebied aangetroffen.

De bovenvermelde hypothese wordt dus slechts gedeeltelijk door deze resultaten ondersteund. Terwijl de waargenomen weer-bodem-plant interacties overeenstemmen met de hypothese, lijkt de veronderstelde plant-legerworm interactie, bestudeerd onder laboratoriumcondities, foutief te zijn. De waargenomen grote verschillen tussen jaren in het stikstofgehalte in waardplanten zijn derhalve waarschijnlijk niet van wezenlijk belang voor het verklaren van de betrokken verschillen in de plaagontwikkeling van dit insekt.

Deze conclusie wordt verder ondersteund door veldgegevens van een bemestingsexperiment met maïsplanten (Hoofdstuk 7). Deze geven ook aan dat het stikstofgehalte van waardplanten, binnen het bereik dat tijdens de eerste maand van de korte regentijd in het veld gevonden is, de fitness van jonge larven niet beïnvloedt. Eveneens is gebleken dat de mortaliteit van jonge larven onder veldomstandigheden veel hoger is dan in het laboratorium. Afgezien van natuurlijke vijanden, lijken regen en een hoge relatieve luchtvochtigheid nadelig te zijn voor jonge rupsen in het veld.

Naarmate de studie vorderde, is de vraag hoe de Afrikaanse legerworm de lange droge tijd overleeft (Hoofdstuk 6) belangrijker geworden omdat de oorspronkelijke hypothese niet in staat leek om de droogte-plaag relatie voor deze plaagsoort te verklaren. Daarbij komt dat grote verschillen tussen jaren

zijn waargenomen in het aantal motten gevangen in het primaire plaaggebied aan het begin van het legerwormseizoen, waarbij het belangrijk is vast te stellen dat de rupsen voorafgaande aan deze motten zich vermoedelijk niet op waardplanten in het gebied hebben kunnen voeden. Dit zou inhouden dat de waargenomen verschillen in waardplantkwaliteit deze motaantallen waarschijnlijk niet hebben kunnen beïnvloeden. Ook daarom lijkt de vraag naar de overleving tijdens de lange droge tijd van groot belang te zijn.

Ofschoon het niet met zekerheid kan worden uitgesloten, lijkt het hoogst onwaarschijnlijk dat motten de duur van de lange droge tijd kunnen overleven. Terwijl het voorkomen van diapauze uitgesloten lijkt, blijken motten onder bepaalde omstandigheden 4 tot 5 weken oud te kunnen worden. Zo'n bijzonder lange levensduur is voor dit insekt nooit eerder gerapporteerd, doch is nog steeds ontoereikend voor overleving van de gehele lange droge tijd. Motten blijken verder hun reproduktieve ontwikkeling enigszins te kunnen vertragen onder condities die voorkomen tijdens droogte, maar dit lijkt hen hooguit betere kansen te geven bij het lokaliseren van een geschikte eilegplaats in de Oostafrikaanse laaglanden tijdens de betroffen periode. De vraag dringt zich op of dit gebied voor overleving van legerwormlarven tijdens de lange droge tijd werkelijk ongeschikt is.

Toekomstig onderzoek betreffende de epidemiologie van de Afrikaanse legerworm zal de nadruk moeten leggen op het verder valideren van de in deze studie verkregen laboratoriumresultaten met betrekking tot waardplantkwaliteit onder veldomstandigheden (Hoofdstuk 7). Daarbij dienen dan gelijktijdig de effecten van andere, vermoedelijk belangrijkere, determinanten van de fitness van de Afrikaanse legerworm (plantleeftijd, regenval en natuurlijke vijanden) gemeten te worden. Voorts moet de fenologie gedurende de lange droge tijd verder bestudeerd worden. Zulke veldstudies zullen ons begrip van de waargenomen droogte-plaag relatie van deze soort, en mogelijk ook van andere notoire plaagsoorten met een vergelijkbare levensgeschiedenis, vergroten. Zolang we het onderliggende mechanisme van deze relatie nog onvoldoende kennen, kan vroegtijdige plaagvoorspelling waarschijnlijk niet verbeterd worden. Adequate kennis omtrent dit mechanisme moet voor een betrouwbare anticipatie van de ernst van een legerwormseizoen en voor een verdere reductie van het gebied waarover bestrijding noodzakelijk is, van groot belang worden geacht.

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Publications resulting from this dissertation

Chapters of this dissertation will be published as the following journal articles:

Chapter 2
Janssen, J.A.M. Soil nutrient availability in a primary outbreak area of the African armyworm in relation to drought intensity and outbreak development. Bull. Entomol. Res., in press.

Chapter 4
Janssen, J.A.M. Effects of the mineral composition and water content of excised leaf sections on the fitness of the African armyworm. Entomol. exp. appl., in press.

Chapter 5
Janssen, J.A.M. Effects of the mineral composition and water content of intact plants on the fitness of the African armyworm. Oecologia, in press.

Chapter 6
Janssen, J.A.M. How does the African armyworm survive the long dry season? Continuous development versus aestivation. Insect Sci. Applic., submitted.

Other publications

The author has also contributed to the following publications in the field of Entomology:

Janssen, J.A.M., Tjallingii, W.F. & Lenteren, J.C. van (1988). Stylet penetration by the greenhouse whitefly. Meded. Fac. Landbouww. Rijksuniv. Gent 53: 1149-1151.

Janssen, J.A.M. (1988). Stylet penetration by the greenhouse whitefly: a comparison with aphids. Neth. J. Zool. 38: 206.

Janssen, J.A.M., Tjallingii, W.F. & Lenteren, J.C. van (1989). Electrical recording and ultrastructure of stylet penetration by the greenhouse whitefly. Entomol. exp. appl. 52: 69-81.

Janssen, J.A.M. & Rose, D.J.W. (1990). The effect of nutrition on outbreaks of the African armyworm, *Spodoptera exempta* (Walker). Symp. Biol. Hung. 39: 481-483.

Janssen, J.A.M. & Rose, D.J.W. (1990). Does the nutritional quality of the larval host plants influence the occurrence of outbreaks of the African armyworm? Meded. Fac. Landbouww. Rijksuniv. Gent 55: 289-295.

Bai, B., Luck, R.F., Forster, L., Stephens, B. & Janssen, J.A.M. (1992). The effect of host size on quality attributes of the egg parasitoid, *Trichogramma pretiosum*. Entomol. exp. appl. 64: 37-48.

Janssen, J.A.M. (1992). Why do droughts often result in devastating insect epidemics? The African armyworm, *Spodoptera exempta* (Walker), as an example. In: S.B.J. Menken, J.H. Visser, P. Harrewijn (eds.), Proc. 8th Int. Symp. Insect-Plant Relationships. Kluwer Academic Publishers, Dordrecht: 49-51.

Janssen, J.A.M. & Luck, R.F. Clutch size and sex allocation by the parasitoid *Trichogramma pretiosum* in the eggs of *Trichoplusia ni*: sex allocation in an uncertain world. Anim. Behav., submitted.

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Species are considered a pest when they occur in such numbers that they have a deleterious influence on human survival and well-being. They might do damage directly to humans or indirectly to their crops or possessions. Pest species occur throughout the spectrum of biological organisms: viruses, bacteria and fungi cause many different diseases, plants are often known as weeds, and animals from mice to mites and from birds to nematodes can be serious pests. Not all species need to occur in large numbers in order to be considered a pest. However, to speak of an outbreak of a pest there must be an explosive increase in the abundance of a particular species over a relatively short period of time (Berryman, 1987).

Outbreaks of pestiferous organisms have plagued mankind from time immemorial. The book Exodus tells us that locusts destroyed crops of the Egyptians in ancient times, and that mosquitoes and blackflies have long annoyed people relentlessly. Because of their serious interference with human affairs, pest outbreaks have drawn the attention of numerous scientists. Though initially the main focus was to record outbreaks and devise means for their control, it was soon realized that the highest ambition must be to foresee and prevent outbreaks. In order to achieve this, a thorough knowledge of the complex interplay of the pest organism with its abiotic and biotic environment is required. This implies that the ecology and phenology of a species should be the focus in research on pest outbreaks.

Herbivore outbreaks: drought as a possible cause

Outbreak development of herbivorous insects can be the result of increased survival and/or fecundity. Both performance parameters depend on genetic, behavioural, and physiological traits of organisms that compromise their adaptive strategies and that are in a very complex way influenced by their abiotic and biotic environments (figure 1-1). In these interactions between organisms and their environment the time factor is of major importance: in general the influence of biotic factors is slow compared with abiotic ones. In the course of evolution organisms have evolved their adaptive strategies to maximize the numbers of their descendents in their habitat which is changing in time and in space (Southwood, 1977).
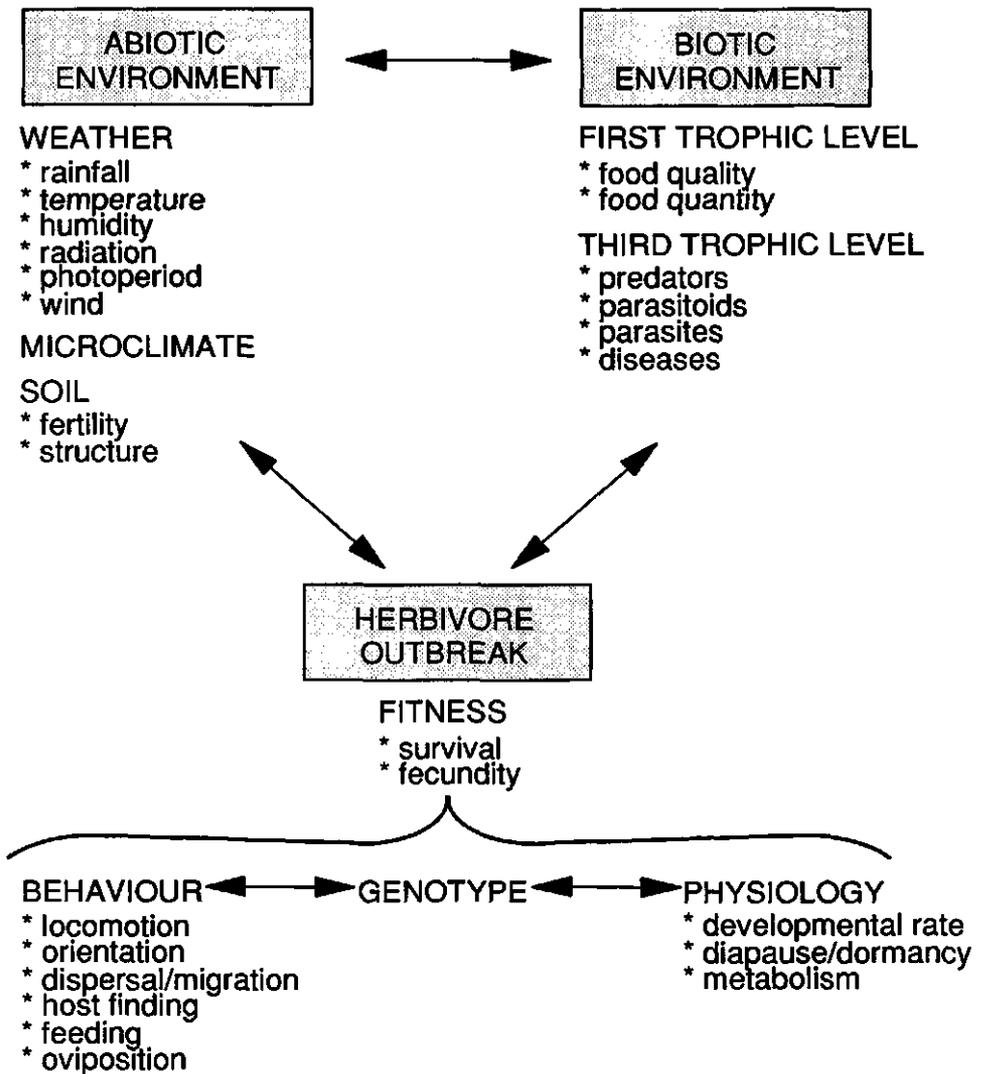
Figure 1-1. The ecological framework in which herbivore outbreaks develop. All factors in an environment interact with each other to a greater or lesser extent. While the abiotic environment strongly affects herbivore outbreaks directly as well as indirectly through its effects on host plants and natural enemies, the biotic environment mainly interacts with herbivore outbreaks and only slightly influences parts of the abiotic environment (microclimate, soil). The effect of the environment on herbivore fitness is dependent on the behavioural, genetic and physiological traits of the herbivore population.

Herbivore outbreaks are rare events in time and space. Usually population size of outbreak species is kept in check by controlling factors like adverse weather conditions, suboptimal microclimatic conditions, poor food quality, predation, parasitism and disease. However, when the controlling factors fail to exert their full influence outbreaks can develop as a result of the tremendous reproductive ability of most insect species. A decrease of as small as 1 per cent in the mortality of some species can result in a 100 per cent increase of the population in the next generation. When looking for explanations for outbreak development, the aim is to identify a key factor or set of key factors in the abiotic and biotic environment. Such factors strongly determine outbreak development because their impact on survival and/or fecundity is large and variable, and therefore have predictive value (Morris, 1959; Varley & Gradwell, 1960). Different key factors can be predominant in different situations in time and space (Barber, 1926; Solomon, 1949). When a key factor fails to control a population at an endemic level, the population is said to be 'released' and an epidemic will develop.

In the past many hypotheses have been formulated as possible causes of herbivore outbreaks (Berryman, 1987), all stressing the importance of another key factor or set of key factors. Probably the most important and all-encompassing environmental variable causing enormous fluctuations in herbivore abundance is weather and its seasonality. As stated by Uvarov (1931) climate, the mean weather during a long period of time, is the ever present factor from which there is no escape for any living organism. He stressed that this does not necessarily mean that weather is always the key factor in determining insect abundance and distribution, but that other environmental conditions are subordinate to it in importance. Clearly, weather by itself cannot regulate population densities of animals because it does not possess the property required to do so: density-dependence (Nicholson, 1933; Klomp, 1962). However, it certainly plays a very important role in determining the level at which regulation occurs and it can act to regulate population densities through its influence on other density-dependent factors, like competition for suitable hiding places (Andrewartha & Birch, 1954; Klomp, 1964).

In many studies weather has been shown to be a main factor in accounting for large changes in herbivore numbers (see references in Andrewartha & Birch, 1954; Mochida et al., 1987; Whitmore, 1991). Because mortality due

to weather is often very difficult to be demonstrated in the field, not in the last place because its effects are extremely difficult to disentangle from other mortality factors, in most studies only a relationship is established between prevailing weather and the occurrence of infestations (e.g. Richards & Waloff, 1954; Greenbank, 1956; van der Laan, 1959; Symmons, 1959; Silver, 1960; Casimir, 1962; Baltensweiler, 1968; White, 1969, 1974, 1976). The mechanisms by which weather factors exert their influence on insect fitness are rarely understood in detail.

Weather can affect herbivore fitness in very different ways. While direct influences of weather factors on insect survival and fecundity have long been recognized (Uvarov, 1931; Andrewartha & Birch, 1954), more recently indirect influences via food plant quality (White, 1974, 1984; Haukioja & Hakala, 1975; Beck & Schoonhoven, 1980; Rhoades, 1983, 1985), food plant quantity (Dempster & Pollard, 1981), natural enemies (Marcovitch, 1957; Debach, 1965) and disease epizootics (Stairs, 1972) have been suggested as well. Good experimental proof for these influences under natural conditions is generally based on circumstantial evidence. Their relative importance is yet unclear and certainly variable among outbreaks of different species, at different times and at different locations (Klomp, 1968). Experimental check methods seem to be the only satisfactory means of rating the efficiency of controlling factors under field conditions. They should involve multiple paired plot comparisons of a suitable size and number in which the different factors with suspected major effects on herbivore fitness can be isolated.

As a particular weather phenomenon drought has long been recognized as a key factor in causing severe outbreaks of tree, grass as well as forb feeding herbivores, among temperate as well as tropical species and in natural as well as agroecosystems (Mattson & Haack, 1987a, 1987b). This widely recognized relation between drought and outbreaks seems to ask for a general underlying, explanatory mechanism. Drought is a meteorological term and can, rather subjectively, be defined as a sustained period of significantly below normal precipitation (Oladipo, 1985). The result is a water deficit stress or drought stress (Levitt, 1980). As a consequence plants might eventually wilt and under severe drought stress partly or fully die.

To indicate the importance of the factor time in drought-outbreak relationships, I propose to distinguish two different situations: one in which

outbreaks develop in an area that is subjected to drought stress, and one in which outbreaks develop in an area free of drought stress but that has previously been subjected to severe drought and was virtually free of the herbivore developing into an outbreak. In both situations outbreak development has been observed.

The first situation occurs wherever rainfall is suboptimal for the existing green plant cover in an area over some time. Severe wilting and death of host plants due to drought are obviously detrimental to most herbivorous insects. Under more moderate drought conditions herbivore outbreaks might develop as a direct result of the generally favourable weather conditions prevailing during drought. Drought is characterized not only by reduced precipitation but generally also by lower relative humidity, higher air and soil temperatures and a higher radiation level than normal. Indirectly, drought can increase herbivore fitness either through the first trophic level by increasing host plant quality (White, 1969, 1974, 1976; Haukioja & Hakala, 1975; Rhoades, 1983, 1985), or through the third trophic level by decoupling natural enemy-herbivore interactions (Price et al., 1980; Risch, 1987). Host plant quality can conceivably be improved by increasing the levels of important nutrients and by decreasing the levels of secondary plant chemicals due to compromised defence mechanisms as a result of drought conditions. Often, however, the concentrations of secondary plant chemicals appear to increase in response to drought stress (Gershenzon, 1984). This led Mattson and Haack (1987a) to hypothesize that drought stress might enhance the effectiveness of the detoxification systems of herbivores via increased nutritional quality of their host plants, resulting in increased fitness.

The second situation is most typical for the tropics where dry and wet seasons alternate. The changes in plants caused by drought generally relax very quickly when sufficient precipitation is received or might even be absent in plants that are known to be quiescent during a drought and become biologically active through germination or regrowth as soon as the drought is broken. Though weather conditions are then generally less favourable than during drought, other factors can still promote survival and fecundity of herbivorous species. When densities of herbivores were greatly reduced by the preceding drought, numbers of natural enemies are likely to be very low and locally they might even be absent. In addition, disease incidence levels may also be reduced. Consequently, natural control is likely to be poor

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during early population buildup of herbivores after drought. Strong selection during drought might also change the genetic composition of a population in such a way that herbivore numbers rapidly increase when conditions become more suitable. However, very little evidence on genetic change associated with outbreaks is available and no conclusive demonstration that such a change influences population growth has been reported so far (Mitter & Schneider, 1987). Finally, plants that have survived drought might be superior hosts for herbivores.

The effect of drought on nitrogen flux

The natural nitrogen supply for plants is generally largely derived from mineralization of the soil organic matter, but also from fixation of atmospheric nitrogen and from nitrogen precipitated by rainfall. During the mineralization process organic matter is decomposed by bacteria and fungi. Nitrogen is released in the form of ammonia (i.e. ammonification) which is held by the soil particles as the ammonium cation. While it can be absorbed by plants as such, under aerobic conditions it is normally rapidly oxidized to nitrite by one group of bacteria and then by another group immediately to nitrate (i.e. nitrification), which is the more usual ion plants absorb to cover their nitrogen need. The rate of the ammonification and nitrification processes and the quantity of nitrate released depend on soil type, its pH and aeration, the amount and nature of organic matter present, and the soil moisture regime and temperature. Nitrogen losses from the topsoil are due to leaching of nitrate, to denitrification of nitrate to atmospheric nitrogen under anaerobic conditions, and to ammonia volatilization. Both leaching and denitrification are enhanced by excessive rain.

When soils are subjected to alternate periods of drying and wetting, they are known to show marked fluctuations in soil nitrate levels (Hagenzieker, 1957; Kabaara, 1964). In laboratory experiments a flush of microbial activity was shown to occur on remoistening a dry soil, resulting in more decomposition of organic material than if the soil was kept continually moist and well aerated (Birch & Friend, 1956; Birch, 1958a, 1958b, 1960a, 1960b). Birch (1959b, 1960b) showed that the magnitude of this flush of decomposition depends on the percentage carbon in the soil and the length and tempera-

ture of the drying period, without necessarily involving a greater degree of drying. He (Birch, 1959a, 1959b, 1960b) indicated that the effect of drying was both an enhanced exposure of organic surface to solution, thus increasing the amount of decomposable organic material going into solution and stimulating microbial processes on the exposed surfaces upon remoistening, as well as an increased killing off of the microflora in the soil, thus providing readily decomposable organic material for a freshly and rapidly developing population of microorganisms after wetting. However, the underlying mechanisms causing the flush and the relative importance of the factors contributing to it are not yet clear (Jenkinson, 1966; Kieft et al., 1987, de Bruin et al., 1989; Singh et al., 1989). The peak in microbial activity is reached within a day from wetting after which a rapid decline occurs, presumably as a consequence of a rapid reduction of the exposed soil surface as a result of swelling of the organic colloids.

From his findings Birch (1958b) concluded that low rainfall, which is generally more intermittent than high rainfall, will be associated with a greater frequency of the drying and wetting cycling and therefore with greater nitrate production. Especially in the tropics where defined dry seasons occur, soil drying should have a marked effect on soil fertility, particularly with regard to nitrogen. Yields of crops planted after the flush is over and the nitrate leached out, have been shown to be considerably lower than yields of crops planted in time to catch the flush (Lebedjantzev, 1924; Hagenzieker, 1957). Particularly in soils low in organic matter (less than 3% carbon) the length of the dry period and the temperature reached can be critical in producing adequate amounts of nitrogen to crops once rains have come (Birch, 1960b).

Thus, more intense heating of soils during drought seems to result in more nitrate production when subsequently rainfall starts. The duration of the enhanced nitrate level in the topsoil is thought to depend primarily on the amount, intensity and distribution of the early rains, as nitrate is readily leached to deeper layers.

The nutritional importance of nitrogen and water

Plant nitrogen and water are often thought to be of key importance in the nutritional ecology of herbivores (Scriber, 1978a, 1979; McNeill &

Southwood, 1978; Scriber & Feeny, 1979; Scriber & Slanski, 1981; Slansky & Scriber, 1985; Mattson & Scriber, 1987), though they are of course not the only nutritional requirements for normal insect development (House, 1974). This is mainly due to their pivotal role in the metabolism of all living organisms. In addition, for nitrogen it is argued that herbivores generally have difficulties in ingesting sufficient amounts of this nutrient because their tissues contain considerably more nitrogen (7-14% dry wt.) than the plant tissues they are feeding on (0.03-7.0% dry wt.)(Mattson, 1980) and because of their very high developmental rates. High levels of both nitrogen and water tend to coincide with low levels of digestibility reducing compounds like structural carbohydrates, lignin, silica and tannins. Therefore, Scriber (1984) argued that nitrogen as well as water content might effectively reflect the nutritional quality of host plants to herbivores.

A survey of the literature indicates that the evidence for this generalization, at least for the nitrogen part, is not unequivocal (see also Scriber, 1984). Though many positive correlations have been found between insect fitness parameters and the nitrogen content of their food (Smith & Northcott, 1951; Fox & Macauley, 1977; Shaw et al., 1978; Taylor, 1984; Manuwoto & Scriber, 1985a, 1985b; Wermelinger et al., 1985; Minkenberg & Ottenheim, 1990; Loader & Damman, 1991; Soldaat, 1991), a number of other studies has shown no (Slansky & Feeny, 1977; Miles et al., 1982; Schroeder, 1986) or even negative (Smirnoff & Bernier, 1973; Jansson & Smilowitz, 1985) correlations as well. This apparent inconsistency might at least partly be explained by the fact that the cited studies represent a wide range of herbivore-plant combinations and vary tremendously in their experimental designs. For example, Jansson & Smilowitz (1985) only created a narrow range of high nitrogen levels in their host plants. The negative correlation they found might just have been the upper part of an optimum curve, a relationship which has actually been shown to exist in several other studies including a wide range of nitrogen levels (Brewer et al., 1985, 1987; Broadway & Duffey, 1986; Karowe & Martin, 1989). The occurrence of an optimum relationship with a range of optimal nitrogen levels, due to compensatory feeding mechanisms of a species (Simpson & Simpson, 1990), might even explain the absence of a correlation when all nitrogen levels fall within the optimum range.

Thus, a valid generalization seems to be that the fitness of herbivores is optimized within a range of nitrogen levels, the width of which depends on the compensatory capacity of a species. While below the optimum fitness is reduced because the nitrogen deficit can not be compensated for anymore by the herbivore, above the optimum excess nitrogen is detrimental either as a consequence of processing costs or increased levels of nitrogen-based secondary plant compounds (Bernays, 1983).

Certainly, not only the quantity but also the quality of nitrogen in host plants (McNeill & Southwood, 1978; van Loon, 1988; Karowe & Martin, 1989; Felton et al., 1989, 1992), or more so the balance of several nutrients, influences herbivore fitness. In addition, secondary plant substances can affect the optimum nitrogen range (Reese, 1979), though the influence of especially qualitative allelochemicals (sensu Feeny, 1975) on adapted herbivores is generally thought to be insignificant at naturally occurring concentrations (Rozenthal & Janzen, 1979). Furthermore, levels of nutrients and allelochemicals are known to show significant diurnal, seasonal and ontogenetic changes, and for any given herbivore-plant relation the optimum relationship will depend on the physiological state of both interacting organisms and the prevailing environmental conditions. Within this very complex framework of physical, nutritional and allelochemical factors shaping the relation between food quality and herbivore fitness, ideally one can only try to identify those factors with major effects on herbivore performance. Field and laboratory studies should be combined to achieve this.

The notion of the importance of nitrogen to herbivores led White (1969, 1974, 1976, 1978, 1984) to postulate the hypothesis that a relative shortage of nitrogen causes high mortality among herbivores, in particular under the rapidly growing young larvae. He suggested that the relative shortage disappears when plants are stressed, especially due to weather extremes. The increased availability of nitrogen in the tissues of stressed plants allows a high proportion of young herbivores to survive and the population to reach outbreak levels. Thus, the concentration of available nitrogen in the food of herbivores is thought to be a key factor driving their population dynamics. It is important to note that White substantiated his hypothesis only with circumstantial evidence. Though the evidence seems quite convincing at first sight, subsequent detailed experimentation has not yielded an unambiguous picture (Miles et al., 1982; Watt, 1986).

In view of this discrepancy, Larsson (1989), while only addressing tree feeding herbivores, proposed a more precise hypothesis by differentiating among the various herbivorous feeding guilds each with their own specific relation of insect fitness to host-tree stress. Based on experimental evidence from the literature he concluded that sucking and mining insects and cambium feeders like bark beetles appear to perform better only under moderate stress levels, while chewing and gall-forming insects never seem to be positively affected by host-plant stress.

The African armyworm:
occurrence, life cycle, field situation, host plant quality and control

The African armyworm, *Spodoptera exempta* (Walker)(Lepidoptera; Noctuidae), occurs throughout tropical Africa, Asia and Australia, but it has not been recorded from the Americas apart from Hawaii (Commonwealth Institute of Entomology, 1972; Haggis, 1986). In his excellent review on this species Brown (1962) stated: '(...) it is best represented in Africa, which appears to be its true home'. Though occasional outbreaks have been reported from elsewhere, it is especially the east side of the African continent where the species is a major agricultural problem. This explains why virtually all work on this pest has been carried out in this area. The larvae periodically reach very high densities causing extensive and severe damage to crops such as maize, sorghum, millet and rice, as well as to pasture and rangeland grasses. In some years infestations might cover more than 20,000 square kilometres in Kenya, Tanzania and Uganda only (Odiyo, 1979). An infestation of this size at 100 larvae per square metre, which is not unusual under outbreak conditions, will consume more than 5 million tonnes of green leaves.

The life cycle of the African armyworm can be completed in as little as one month when temperature and food conditions are optimal (Hattingh, 1941; Brown, 1962; ICIPE, 1974; Persson, 1981). The eggs take about 3 days to hatch. Neonate larvae weigh less than 0.1 mg and are pale green with black heads. They can produce silken threads on which they float in the wind in order to disperse and find suitable host plants. The larvae are oligophagous,

feeding almost exclusively on plants of the families Gramineae and Cyperaceae (Brown, 1962; Brown & Dewhurst, 1975). The basis for this oligophagy of the larvae is thought to be a combination of strong intolerance to chemical feeding inhibitors and a requirement for a well balanced complex of feeding stimulants (Ma, 1976; Ma & Kubo, 1977). Initially, they scrape off cell layers on the underside of leaves resulting in so-called windows. At the third moult their mandibles change so that they are able to chew out leaf edges. It is during the last days of larval development that most damage is done. Plants can be eaten completely except for the stems and tough mid veins of leaves. Normally the larvae pass through six instars in 2 to 3 weeks. When fully developed they may weigh up to 800 mg. They then burrow some 2 cm into the soil where they spin a thinly lined, silken cocoon, and loose about 70 per cent of their weight to become prepupae. Usually within two days from disappearing into the soil pupation takes place, and about eight days later moths emerge which can live up to 14 days. After moth emergence, dispersal and migration take place and subsequent outbreaks may occur hundreds of kilometres away from the previous site (Brown & Swaine, 1966; Rainey & Betts, 1979; Rose et al., 1985). Migration occurs pre-reproductively (Brown & Swaine, 1966). The pre-oviposition period is usually only 2 to 3 days, after which females can lay up to 1000 eggs. They are laid on any kind of substrate; female moths contribute little or nothing to the selection of the food type used by the next larval generation (Hattingh, 1941). Though some reports on diapause have been published (Fonseca Ferrao & Santos, 1965; ICIPE, 1974; Khasimuddin, 1977), diapause or aestivation are generally thought not to occur in this species.

The African armyworm shows a density-dependent polyphenism (Faure, 1943; Matthee, 1946). Whereas uncrowded larvae remain pale and green until pupation, crowded larvae become very conspicuous during development, changing from green to black with yellow stripes, usually at their third moult. These two forms, termed by Faure (1943) *solitaria* and *gregaria* in analogy with locusts, represent the extremes of a continuum; intermediate *transient* forms, brownish in colour, are known as well. Besides the difference in colour, the phases also differ in their biochemical composition, behaviour and physiology (Faure, 1943; Matthee, 1945; Rose, 1979; Khasimuddin, 1981a; Simmonds & Blaney, 1986), and these differences are reflected in the moths as well (Gunn & Gatehouse, 1987; Woodrow et al., 1987). *Gregarious*

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larvae seem to be destined for fast development as a result of their heavy pigmentation and preference for exposed feeding in direct sunlight, thus increasing their body temperature. In addition, *gregarious* moths have a higher abdominal glyceride content, likely to be responsible for their higher migratory capacity. Thus, while the *solitaria* are thought to be the primary form of the insect, the more familiar black *gregaria* supposedly developed as an adaptation to escape from unfavourably high population densities by accelerated larval development, and improved dispersal and migration.

In eastern Africa a marked seasonal occurrence of outbreaks of the African armyworm, coinciding with the seasonal rains that are associated with the inter-tropical convergence zone (ITCZ) in the tropics (Riehl, 1979), has long been recognized (Brown et al., 1969; Haggis, 1986). The importance of rain to outbreak development is not limited to providing the caterpillars with green vegetation. Radar observations have shown that moths rapidly disperse when they move downwind, likely to result in widespread but low-density populations of *solitaria* (Riley et al., 1983; Rose et al., 1985). Therefore, concentration of moths clearly seems to be a prerequisite for outbreak development. Effective concentration is known to occur under the influence of mesoscale meteorological disturbances, especially those associated with convective rainstorms (Pedgley et al., 1982). Additional effects of rain are to induce flying moths to descend (Riley et al., 1983) and to provide the moths with a readily available source of free water which is required by the females for completion of their reproductive maturation (Gunn & Gatehouse, 1985). The often found association between wind convergence, rainstorms and subsequent outbreaks (Brown et al., 1969; Blair, 1972; Rose & Law, 1976; Haggis, 1979; Rose, 1979; Blair et al., 1980; Tucker, 1983; Tucker & Pedgley, 1983; Pedgley et al., 1989) is therefore not surprising.

During the long dry season (June-October in equatorial eastern Africa) population densities are very low, and especially towards the end hardly any armyworms are observed and no outbreaks are reported (Rose, 1979; Odiyo, 1984; Haggis, 1986). This period is called the 'off-season' (Odiyo, 1981). At the beginning of the short rains (October-November) a rapid buildup of the population may occur in the so-called primary outbreak areas due to favourable conditions. These areas are located in the foothill area in Tanzania and Kenya, which is the zone separating the lower desert area to the east from

the highlands to the west, and are generally characterized by low and erratic rainfall. Adults from these primary outbreaks migrate downwind on the prevailing easterly winds, sometimes over large distances, to give rise to subsequent generations further west in secondary outbreak areas (Pedgley et al., 1989). When the ITCZ moves northwards from February onwards, a progression of outbreaks can occur from Tanzania, Kenya and Uganda through Ethiopia and Somalia reaching the Yemen in June (Brown et al., 1969; Betts, 1976; Odiyo, 1987). As yet, however, there is no good evidence for a subsequent return movement from Ethiopia southwards into Kenya, mainly due to the dominant winds being in the wrong direction (Tucker, 1984a; Pedgley et al., 1989). A southwards movement from Tanzania through Malawi and Zimbabwe to South Africa has also been suggested (Blair & Catling, 1974). The occurrence of such extensive migration is supported by the very low genetic diversity among populations in eastern Africa (den Boer, 1978).

Though most moths arising in outbreak areas tend to migrate away, observations have shown that some moths also stay behind and found new populations near the area in which they emerge (Rose, 1975; Khasimuddin, 1981b). This difference in migratory behaviour has been shown to have a genetic basis (Parker & Gatehouse, 1985). However, outbreaks will rarely develop in the same location (Whellan, 1954; Rose, 1975; Khasimuddin & Lubega, 1979; Khasimuddin, 1981b), probably due to decreased food quality and increased mortality from predation, parasites and disease.

It is still not exactly known where the moths come from that appear in the primary outbreak areas. How and where does the African armyworm survive the long dry season? As it has been shown quite clearly that the moths causing these first outbreaks of a season originate from an easterly direction (Tucker, 1984a; Pedgley et al., 1989) and because the vegetation in the area between the primary outbreak locations and the coast is believed to be unsuitable for sustaining armyworm larvae during the long dry season, at present the best answer to this question seems to be that larvae survive at low densities in the coastal regions of eastern Africa (Rose et al., 1987; Pedgley et al., 1989) where sporadic showers fall even during the long dry season. Moths arising from these caterpillars might be blown inland on the easterly winds which dominate around the start of the short rainy season

(Tucker et al., 1982; Pedgley et al., 1989), where they can be concentrated on the first rainstorms to form primary outbreaks.

However, some observations are difficult to understand when this scenario is valid (W.W. Page, unpublished report). The mere absence of moths during the last months of the long dry season, the first catches in pheromone traps coinciding with the very first rains, the subsequent decrease and virtual disappearance in catches during the next two weeks, and the very synchronized larval development in primary outbreak areas, seem illogical when moth activity at the coast is known to be at its minimum around the onset of the short rains and usually builds up to peak two months later. Winds would have to carry moths inland just around and not following the start of the short rains, for which there is no evidence. Page proposed an alternative theory based on moths going into aestivation under dry conditions, but so far only circumstantial evidence is available to support this (Page, 1988). This gap in our knowledge of armyworm epidemiology may appear of crucial importance when accurate predictions have to be made on where primary outbreaks are likely to occur and also on the extent of these outbreaks in a particular year.

Though the importance of host plant quality for outbreak development of the African armyworm has often been recognized (van der Goot, 1931; Hattingh, 1941; Khasimuddin & Lubega, 1979), hardly any experimental work has been done to quantify this relationship (Yarro, 1984a, 1984b, 1985). Host plant quality differs among and within species, in time and in space. While some host plants support outbreak development better than others, within a host plant species young plants seem to be of better quality than old ones. Outbreaks are often reported on Zea mays L. and Cynodon dactylon (L.) Pers., both preferred by the African armyworm and known to be of better quality than other grass species. Especially the presence of young and succulent leaf material is considered to be of major importance for proper establishment of the young larvae. Later instars seem to be less finicky; grasses with hard, fibrous leaves can also suffer severe damage (Bogdan, 1963).

To control a migrant pest like the African armyworm effectively, an international organization is required (Brown, 1972). Currently, a Regional

Armyworm Project is part of the Desert Locust Control Organization for Eastern Africa (DLCO-EA). The main task of the DLCO-EA/EC/NRI Regional Armyworm Project is to operate an information and forecasting service which is designed to control outbreaks in a very early stage throughout the region of the seven countries covered by the DLCO-EA (Djibouti, Ethiopia, Kenya, Somalia, Sudan, Tanzania, Uganda). In addition, research is conducted in cooperation with institutes and universities in the European Community (EC) to come to a better understanding of the epidemiology of armyworm outbreaks, to improve the forecasting service and to control outbreaks in environmentally safer ways. Current control is strongly dependent on the use of insecticides affecting the larvae. Biological control of the African armyworm is generally thought to be unfeasible under conditions that are suitable for outbreak development (Brown, 1962; Merret, 1986), due to the very high fecundity, rapid development and migratory strategy of the species.

In view of the observed progression of major armyworm populations in eastern Africa, it was suggested that spread can be limited by controlling previous outbreaks (Rose et al., 1987). This idea has resulted in the development of a strategic control strategy. The aim of this strategy is to control outbreaks, especially primary ones, that are critical in terms of the potential they have to generate upsurges in following generations. These outbreaks are often small in size compared with subsequent ones, making control more feasible and reducing the adverse impact on the environment. A detailed knowledge of the factors that contribute to the timing, location and successful development of armyworms in areas hosting these outbreaks is likely to improve forecasts and result in more effective control. Currently, testing strategic control is another important objective of the Regional Armyworm Project (Dewhurst, 1991).

The main difficulty in effectively controlling outbreaks of the African armyworm is to begin in time. Outbreaks are often recognized when damage to crops is becoming apparent, leaving only a few days for control before caterpillars pupate. Clearly, a good monitoring network is essential for timely warning of ensuing outbreaks, especially in the zone in which primary outbreaks might develop, both in inhabited as well as more remote areas. At the moment a dense pheromone trap network is the most important tool in predicting outbreaks. Satellite imagery, gathered by Meteosat and indicating where rainstorms might have occurred, gives additional information for

locating areas where outbreaks are likely to occur (Dewhurst, 1991). Finally, historic information available in a computerised database is being used to make forecasts as accurate as possible (Odiyo, 1990). However, it is one thing to make forecasts, and another to ensure that the full advantage is taken of them. Logistic problems, especially related to the remoteness of some locations and the vastness of the area to be covered, are still frustrating control sometimes (Rose, 1985) and add to the fact that control of African armyworms still waits further improvement.

Objective of the present study

The objective of the present project was to test the following hypothesis:

> Periods of more severe drought encourage the occurrence of more severe outbreaks by stimulating the mineralization process in the soil when it is remoistened by rainfall as the drought breaks. This results in higher soil nitrate levels and, consequently, higher nitrogen levels in host plants of herbivores, thus increasing larval developmental rate and survival (especially of very young larvae) as well as the fecundity of subsequent adults (figure 1-2; Janssen & Rose, 1990).

The reasoning behind testing this hypothesis should be obvious from the preceding sections.

The hypothesis was tested for the African armyworm, *Spodoptera exempta* (Walker), a notorious pest for which a drought-outbreak relationship has been established (Brown, 1962; Pedgley et al., 1989). Verification of the hypothesis should improve our understanding of the origin of herbivore outbreaks after drought in general, and in particular for the species under study. When providing an explanation for the enormous differences between years in outbreak development of the African armyworm observed in eastern Africa, this knowledge would be invaluable to further improvement of outbreak forecasts and subsequent control of this species.

more severe drought

↓

higher decomposition of organic material in the
soil upon the onset of the rainy season

↓

higher nitrate level in the soil

↓

higher level of organic nitrogen in the host plants
of the herbivore

↓

increased survival and developmental rate of the
larvae and increased fecundity of the adults

↓

more severe outbreaks
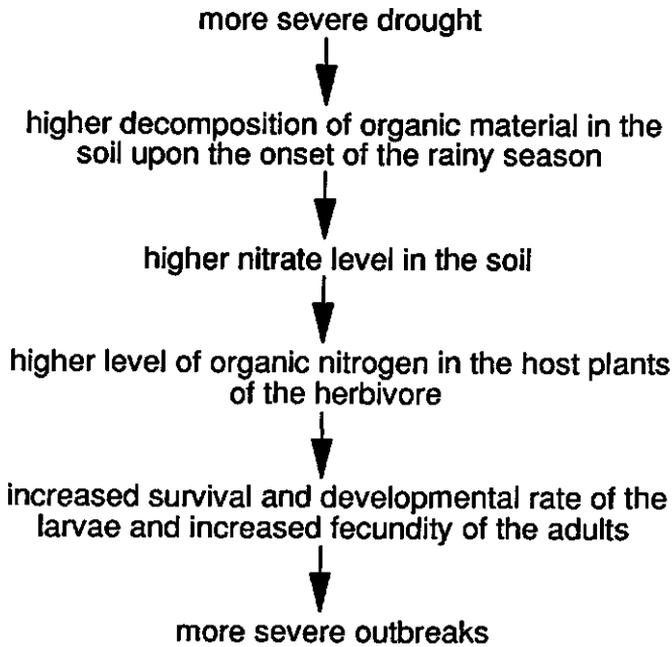
Figure 1-2. The relations hypothesized to explain why severe droughts are frequently followed by severe herbivore outbreaks. For more information see text.

Outline of the research

In order to verify the above mentioned hypothesis, I have addressed the following questions under field conditions:

-    Is the nutrient availability, especially of nitrogen, in soils in a primary outbreak area during the first month after the start of a short rainy season correlated with climatological conditions, especially rainfall and temperature, prevailing during the preceding long dry season? (Chapter 2).

-    Is the level of minerals, especially of nitrogen, in host plants of the African armyworm in a primary outbreak area during the first month after the start of the short rainy season correlated with mineral concentrations in the soil? (Chapter 2).

- Can increased intraplant spatial variation in mineral concentrations in host plants of the African armyworm in a primary outbreak area during the first month after the start of the short rainy season compensate for the overall decrease in these concentrations over time during this period? (Chapter 3).

The relation between the mineral composition and water content of food and armyworm fitness was studied in two systems: an excised leaf system and a gravel culture system. In the first system the naturally occurring variation in mineral composition and water content between different leaf sections within a maize plant was used to confront larvae with various food qualities. In the second system a more natural situation was simulated by using intact maize plants which composition could be manipulated by offering different nitrate solutions to the plants. Thus, the questions addressed with these systems were:

- Are differences in the mineral composition and water content between various leaf sections within a maize plant correlated with the fitness of the African armyworm? (Chapter 4).
- Are differences in the mineral composition and water content between maize plants correlated with the fitness of the African armyworm? (Chapter 5).

In the course of the project the original hypothesis seemed more and more to be partly incorrect. Based on the gained experiences, it was then decided to address the following question as well:

- How does the African armyworm survive the long dry season? (Chapter 6).

The answer to this question might also provide an explanation for the observed large differences between years in outbreak development of the African armyworm in eastern Africa and the generally good correlation of more severe droughts with subsequent more severe outbreaks. The consequences of the results of the present study for strategic control are finally discussed (Chapter 7).

2   *Soil nutrient availability in a primary outbreak area of the African armyworm in relation to drought intensity and outbreak development* [1]

Abstract

To explain differences between years in outbreak development of the African armyworm in eastern Africa, the availability to host plants of soil nitrogen, phosphorus and potassium was studied in a primary outbreak area during the first month after the start of the short rainy season in relation to the drought intensity during the preceding year. The weather-soil-plant interactions observed during four subsequent years (1988-1991) indicated that nitrate levels, especially in soils not extremely poor in organic carbon and total nitrogen, can greatly differ between years in response to differences in drought intensity and rainfall pattern, resulting in large differences (i.e. up to 2.0% dry wt.) in organic nitrogen levels in leaves of host plants of the African armyworm. Phosphorus and potassium levels in soils and host plants showed no consistent relation with the weather pattern over the years and in general their differences between years were relatively small. Armyworm occurrence during the first two months after the start of the short rainy season was well associated with plant nitrogen levels in the primary outbreak area; outbreaks only developed in years with at some locations organic nitrogen concentrations of almost 5% in young grasses. If armyworm fitness is strongly dependent on the organic nitrogen content of its food within the range encountered in this study, weather conditions during the long dry season might indirectly explain the observed

differences in subsequent outbreak development of the African armyworm via their delayed effect on host plant nitrogen levels.

Introduction

In eastern Africa a marked seasonal occurrence of outbreaks of the African armyworm coincides with the seasonal rains that are associated with the inter-tropical convergence zone (ITCZ) in the tropics (Brown et al., 1969; Haggis, 1986). During the long dry season (June-October in equatorial eastern Africa) population densities are very low, and especially towards the end hardly any armyworms are observed and no outbreaks are reported (Rose, 1979; Odiyo, 1984; Haggis, 1986). This period is called the 'off-season' (Odiyo, 1981). At the beginning of the short rains (October-November) a rapid increase in armyworm numbers may occur in the so-called primary outbreak areas due to favourable conditions. These areas are located in the foothill area in Kenya and Tanzania, which is the zone separating the lower desert area to the east from the highlands to the west, and are generally characterized by low and erratic rainfall. Adults from these primary outbreaks migrate downwind on the prevailing easterly winds, sometimes over large distances, to give rise to subsequent generations further west in secondary outbreak areas (Pedgley et al., 1989).

Outbreak development of the African armyworm is known to vary greatly between years in eastern Africa; while in some years hardly any outbreaks are reported, in others severe infestations occur over very large areas (Odiyo, 1979). Like locusts, the African armyworm shows a density-dependent polyphenism (Faure, 1943; Matthee, 1946). Between outbreaks caterpillars are hardly ever observed, because their densities are very low and their solitaria form is very inconspicuous. During outbreaks, however, densities of up to 1,000 caterpillars per square metre may occur (Odiyo, 1981) and damage can be so severe that replanting of crops is required.

Much has been written regarding factors that might be responsible for these tremendous fluctuations in numbers. Mostly weather conditions, operating as a direct factor, have been thought to be of major importance. Hattingh (1941) showed that armyworm fitness is strongly influenced by

temperature. He concluded that outbreaks are unlikely to occur at low temperatures; high temperatures and a sufficient supply of young and succulent grasses are required. The latter is provided by rainfall after a period of drought. The importance of rain to outbreak development is not limited to providing the caterpillars with green vegetation. Reconcentration of dispersed moths on rainstorms (Pedgley et al.,1982), induction of flying moths to descend and land (Riley et al., 1983) and provision of a source of water to moths, which is required by the females for proper reproductive maturation (Gunn & Gatehouse, 1985), are important as well and contribute to the often found association between wind convergence, rainstorms and subsequent outbreaks (e.g. Brown et al., 1969; Rose, 1979; Tucker & Pedgley, 1983; Pedgley et al., 1989).

While rainfall clearly is a prerequisite for outbreak development, poor rainfall has often been associated with the severity of armyworm seasons. Tucker (1984b) found a negative correlation between the amount of early season rainfall (October-December) and the number of outbreaks during the rest of the season. Similarly, Hattingh (1941) observed that widespread infestations in South Africa were often related to delays in the onset of the summer rains. This importance of drought, i.e. below normal precipitation, to outbreak development was in accordance with the popular belief of farmers that drought caused armyworm outbreaks (Hattingh, 1941).

The year 1984 was an exception to the correlation found by Tucker (1984b); in that year one of the most severe armyworm seasons on record developed in Kenya and Tanzania (Pedgley et al., 1989) despite of the fact that the short rains started early and were rich in rain. However, the association with drought was still apparent as these outbreaks followed a very serious drought situation in eastern Africa which had prevailed for one and a half years during which rainfall had been far below normal in three subsequent rainy seasons. Likewise, the very severe outbreaks of 1961 occurred after a year of drought (Graham, 1971; Dewhurst, 1985).

Though drought-outbreak relationships have been observed for many other herbivorous insect species (e.g. van der Laan, 1959; Casimir, 1962; White, 1969, 1974; McDonald et al., 1990), the biological mechanisms underlying these relationships are often poorly understood and still open to speculation (Marcovitch, 1957; White 1976; Rhoades, 1985; Mattson & Haack, 1987a). White (1969, 1974, 1976) hypothesized that periods of

drought increase the level of available nitrogen (amino acids) in host plants of herbivores, thus relaxing the relative shortage of nitrogen that normally causes high mortality among herbivores, in particular the rapidly growing young larvae. However, an indirect effect of drought on host plant quality would better explain outbreak development of the African armyworm, which usually occurs on plants free of any apparent instantaneous drought stress, but that have been exposed to drought prior to the outbreak. Consequently, Janssen & Rose (1990) hypothesized that host plant quality might also be influenced by drought via its effect on the nitrogen mineralization process in the soil.

Almost all nitrogen in soils is present in complex organic compounds that are not available to plants. During the process of mineralization, organic nitrogen is mineralized by bacteria to ammonium which is usually rapidly converted to nitrate, the main form of soil nitrogen available to plants. When soils are subjected to alternate periods of drying and wetting, soil nitrate levels are known to show marked fluctuations (Hagenzieker, 1957; Kabaara, 1964). In laboratory experiments a flush of microbial activity has been shown to occur on remoistening a dry soil, resulting in more decomposition of organic material than if the soil had been kept continuously moist and well aerated (Birch & Friend, 1956; Birch, 1958a, 1958b, 1960a, 1960b). The peak in microbial activity is reached within a day from wetting, after which a rapid decline occurs. Birch (1959b, 1960b) showed that the magnitude of this flush of decomposition depends on the percentage of carbon in the soil and the duration and temperature of the drying period, without necessarily involving a greater degree of drying. Especially in the tropics, where defined dry seasons occur, soil heating should have a marked effect on soil fertility, particularly with regard to nitrogen. Under the assumption that armyworm fitness is strongly dependent on the nitrogen content of its food, differences in heating intensity of soils during dry seasons between years might well explain the large differences in outbreak development of this insect observed between years.

The aim of this study was to test the weather-soil-plant interactions underlying the hypothesis proposed by Janssen & Rose (1990): more severe drought conditions during the long dry season stimulate the mineralization process in soils upon remoistening during the short rainy season, resulting in higher soil nitrate levels and higher nitrogen levels in host plants of the

African armyworm. The interactions as well as armyworm occurrence were monitored under field conditions in Kitui District, one of the most important primary outbreak areas of the African armyworm in Kenya, during four consecutive years (1988-1991). In addition to nitrogen, phosphorus and potassium levels were also considered.

Materials and methods

WEATHER AND VEGETATION INDEX

For the period January 1987 to February 1992 daily meteorological data were obtained from the Kenya Meteorological Department for the Makindu weather station, situated about 50 km south of the area in Kitui District where the soil and plant samples were collected (figure 2-1). In addition, monthly rainfall data were obtained for the period 1961 to 1986. A rain gauge was present at or near all sampling areas for the duration of the sampling period.

Soil temperatures at a depth of 5 cm were thought to be most relevant to the mineralization process, as most mineral nitrogen is normally produced in the surface soil layers (Lebedjantzev, 1924; Hagenzieker, 1957). They were recorded at 8.00, 12.00 and 16.00 hr. As the thermometers employed could not register temperatures above 40°C, these were all set to 40°C. They were only reached at the 16.00 hr observation time. While the soil temperature at 12.00 hr was used to compare the absolute level of soil heating between years, the increase in soil temperature between 8.00 and 16.00 hr provided a measure of the daily temperature variation.

For the sampling areas the short rainy season normally starts in the last two weeks of October or the first two weeks of November; the long rainy season, which is less reliable and usually poorer in rain, tends to start in March. As the main objective of this study was to associate weather conditions preceding a short rainy season with soil and plant mineral levels during the subsequent first month of rain, it was most appropriate to set the start of each year to the start of the short rainy season. Thus, years were not necessarily 365 days long, but always enclosed one short and one long rainy season. Based on observations of the start of the short rainy seasons during the four years of field work, the start of both rainy seasons was set to the
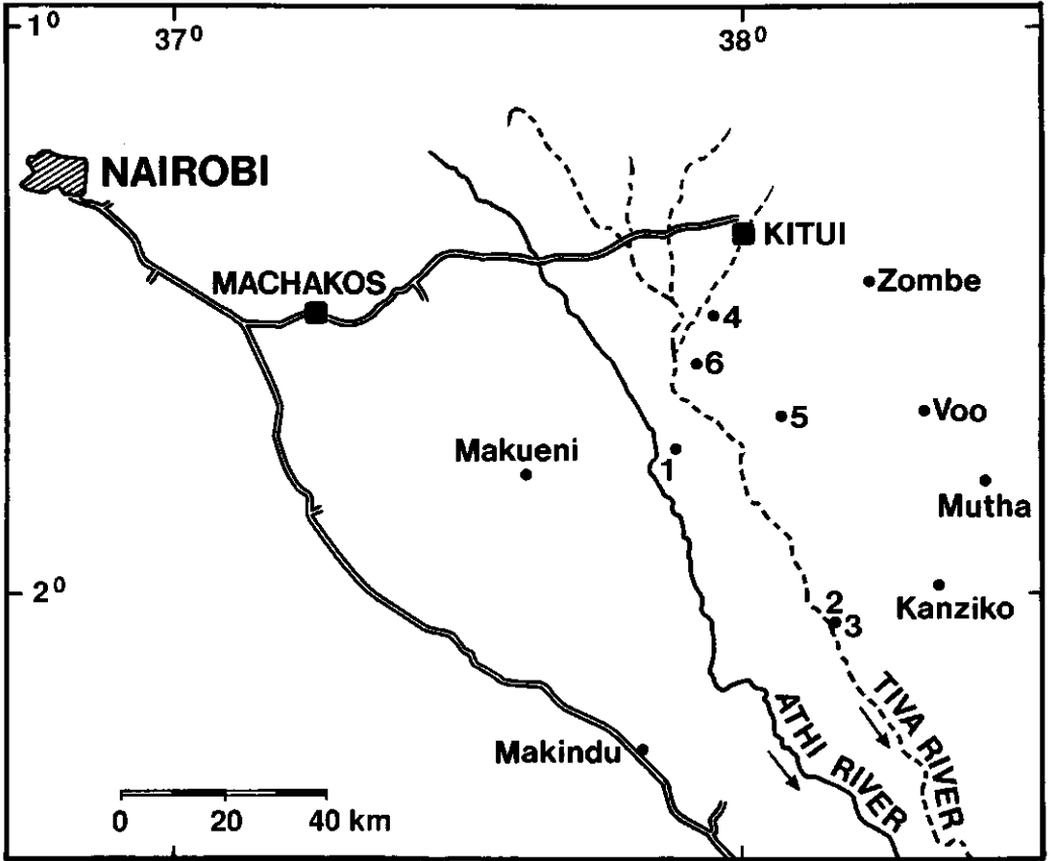
Figure 2-1. The location of the sampling areas in Kitui District of Kenya. **1.** Kanyangi (alt. 1040 m), **2.** Ikutha-1 (alt. 700 m), **3.** Ikutha-2 (alt. 700 m), **4.** Katulani (alt. 1035 m), **5.** Ikanga (alt. 860 m), and **6.** Maliku (alt. 940 m). The Makindu weather station (alt. 1000 m) and some other places are indicated as well.

first day with more than 15 mm of rain, while the day had to be part of a pentade with a total of more than 25 mm of rain. This was enough to start and maintain vegetation development and to make maize seeds germinate. The day preceding the start of the short rainy season (last day of the long dry season) was set to day 0. To compare drought intensities of the long dry

season between years, the last 90 days preceding the start of the short rainy season were selected.

The end of the growing period of the long rainy season could be estimated for the first three years based on decadal ARTEMIS normalized difference vegetation index (NDVI) data (Hielkema, 1990), which were obtained for Makindu, Kanyangi, Ikutha, Ikanga and Maliku (figure 2-1). Gaps in the NDVI data were smoothed according to Bonifacio et al. (1991). This vegetation index correlates well with green vegetation biomass (Hatfield et al., 1984) and has previously been used to set the beginning and end of a growing period (Henricksen & Durkin, 1986).

Here the end of the growing period of the long rainy season was set by the 0.2 NDVI value of the linear regression through the NDVI data from the peak during the long rainy season to when it subsequently fell for the first time below 0.2 (figure 2-4). Because NDVI data can be confounded by a variety of atmospheric influences (e.g. Tarpley et al., 1984), this procedure which usually includes 8 NDVI data points was thought to be more accurate than the method used by Henrickson & Durkin (1986) in which only 2 NDVI data points are included. The 0.2 NDVI value was chosen because it is known to correspond with a dry vegetation cover (Hatfield et al., 1984; Huete et al., 1985). Though field observations might indicate that a higher value is more appropriate, it would not affect the comparisons between years as performed in this study.

SOIL
Soil samples were collected at six locations in Kitui District (figure 2-1). In 1988 sampling was started at only two locations (Kanyangi and Ikutha-1). In subsequent years more sampling areas were added to represent a greater variety of the soils encountered in Kitui District. To observe differences in the soil mineralization process in identical soils between years, samplings in later years were shifted away as little as possible from those in previous years. A shift of 0.2 km between 1988 and 1989 in Ikutha already resulted in large differences in soil characteristics which should be more or less constant over time at one location. Consequently, these sampling areas had to be considered separately (Ikutha-1 and Ikutha-2). Only at Kanyangi samples were collected in all four years. In 1990 and 1991 samples were collected at all sampling areas.

Per sampling area 9 or 18 soil samples were taken on every sampling date, each composed of 6 subsamples of the upper 25 cm. While the locations of the subsamples were 1 m apart, the sampling sites of the soil samples were separated by 6 m. After a maximum of two dry season samplings, sampling was continued immediately upon the start of the short rainy season; it was usually performed daily during the first week and once every 3 to 4 days thereafter up to day 28. Subsequent samplings in time within one year were separated by 0.2 m. Samples were taken with a Riverside auger during the dry season and with an Edelman auger (Eijkelkamp Agrisearch Equipment) after the start of the short rainy season. Soil samples were dried in a thin layer at air temperature (25-35°C) and sieved over a 2 mm grid prior to analysis.

Organic carbon (C) was determined according to Kurmies (see Mebius, 1960), total nitrogen (N_{tot}) and total phosphorus (P_{tot}) after Novozamsky et al. (1983). Nitrate nitrogen (NO_3-N), ammonium nitrogen (NH_4-N), soluble nitrogen (N_{sol}), soluble phosphorus (P_{sol}), soluble potassium (K_{sol}) and pH were determined after Houba et al. (1986). Mineral nitrogen ($N_{mineral}$) is the total of nitrate and ammonium nitrogen. Soluble organic nitrogen (N_{solorg}) is the difference between soluble and mineral nitrogen.

Equal portions of 9 soil samples taken at the same sampling area at day 28 were lumped each year to analyse for the texture of the soils. Organic carbon, pH, total nitrogen and total phosphorus were all constant over time and therefore determined in a selection of the soil samples taken at one sampling site. All other soil characteristics were measured in all soil samples. When comparing years or sampling areas, variation in a soil characteristic over time within a year was excluded by averaging the values of all soil samples taken at the same sampling site during that year.

PLANTS

Plant samples were collected at the same locations as the soil samples, except for Maliku. As the African armyworm feeds almost exclusively on leaves of plants of the families Gramineae and Cyperaceae (Brown, 1962; Brown & Dewhurst, 1975), plant samples contained only leaves of two of the most common grasses in Kitui District: *Digitaria milanjiana* (Rendle) Stapf was sampled at Kanyangi, *Eleusine indica* (L.) Gaertn. at all other sampling areas. Among the wild grasses, annuals are much more common in Kitui

District than perennials. This is mainly due to the fact that large areas are in use as agricultural fields, on which maize is by far the most common crop grown during the short rainy season. Vegetations which have never been disturbed by human activity are rare and tend to consist mainly of perennial grasses. While the perennial grasses react immediately to the start of the short rainy season, taking only 1 to 2 days to produce their first leaf, the annual grasses take almost a week for germination. Vegetation cover of the soil is initially very sparse, but rapidly increases, usually becoming complete within three weeks from the start of the short rainy season.

Plant samples were taken just around the sampling sites of the soil samples. Sampling normally started as soon as enough plant material (more than 1.5 g dry wt.) could be collected and was usually continued once every 3 to 4 days thereafter up to day 28. Plant samples were dried in a stove at 70°C and ground prior to analysis.

Nitrate (NO_3) was extracted by shaking with distilled water for 30 min, and analysed by Technicon AutoAnalyser after reduction to nitrite. Total nitrogen (N), phosphorus (P) and potassium (K) were determined after Novozamsky et al. (1983). Organic nitrogen (N_{org}) was calculated by subtracting nitrate nitrogen from total nitrogen. All characteristics were measured in all plant samples. When comparing years or sampling areas, a similar procedure was applied as for soils. For each year identical sampling periods were considered when calculating the average values of the plant samples taken at the same sampling site.

ARMYWORMS

Armyworm occurrence was observed during the first two months after the start of the short rainy season. A dense network of pheromone traps (Cork et al., 1989) in Kitui District and surrounding areas gave detailed information on male moth activity. Outbreak reports were obtained from farmers, Agricultural Officers and from the Armyworm Forecasting -Service. Outbreaks near the sampling areas were visited for examination. To estimate larval duration from observations of moths arrival dates and subsequent larval pupation dates, peak larval hatch was assumed to occur 6 days after moth arrival (Pedgley et al., 1989).

Results

WEATHER AND VEGETATION INDEX

In the semi-arid zone where Makindu as well as the sampling areas are situated, rain usually falls at night and in heavy downpours of more than 10 mm (figure 2-2). The annual rainfall at Makindu averaged 630 mm over the period 1961 to 1991; the long and short rainy seasons received an average of 220 mm and 410 mm of rain respectively. In spite of the fact that the short rainy season usually lasts longer than the long rainy season in Kitui District, it has been called 'short' in accordance with the situation in other parts of Kenya. The short dry season in January and February is shorter and wetter than the long dry season. This lasts from May to the end of October, a period during which rainfall is almost completely absent, the total averaging 10 mm over the period 1961 to 1991.

After both rainy seasons in 1987 had received far below average amounts of rain (i.e. long rains 142 mm, short rains 208 mm), rainfall was above average during the first five and below average during the last three rainy seasons in the period 1988 to 1991 at Makindu (figure 2-2). Thus, the years preceding the short rainy seasons of 1988 and 1991 received below average amounts of rain, while they were far above average in rain for 1989 and 1990 (table 2-1). Average daily sunshine hours, soil temperature and soil temperature increase were negatively correlated with rainfall over the four years.

When only the last 90 days of the long dry seasons are considered, a similar pattern of high averages for daily sunshine hours, soil temperatures and soil temperature increases in 1988 and 1991 and low averages for these variables in 1989 and 1990 is found (table 2-1). While the soil temperatures recorded at 16.00 hr exceeded 40°C almost daily during the last month of the long dry seasons in 1988 and 1991, this was not the case in 1989 and 1990 (figure 2-3). Soil temperatures dropped sharply as soon as a rainy season started.

During the first 28 days of the short rainy season, the period during which the soil and plant samples were collected, the total amount of rainfall hardly differed between years at Makindu (table 2-1). This was observed at all sampling areas except for Ikutha, where rain was excessive in 1989 and poor in 1991. At Makindu, the clear pattern in the other weather variables
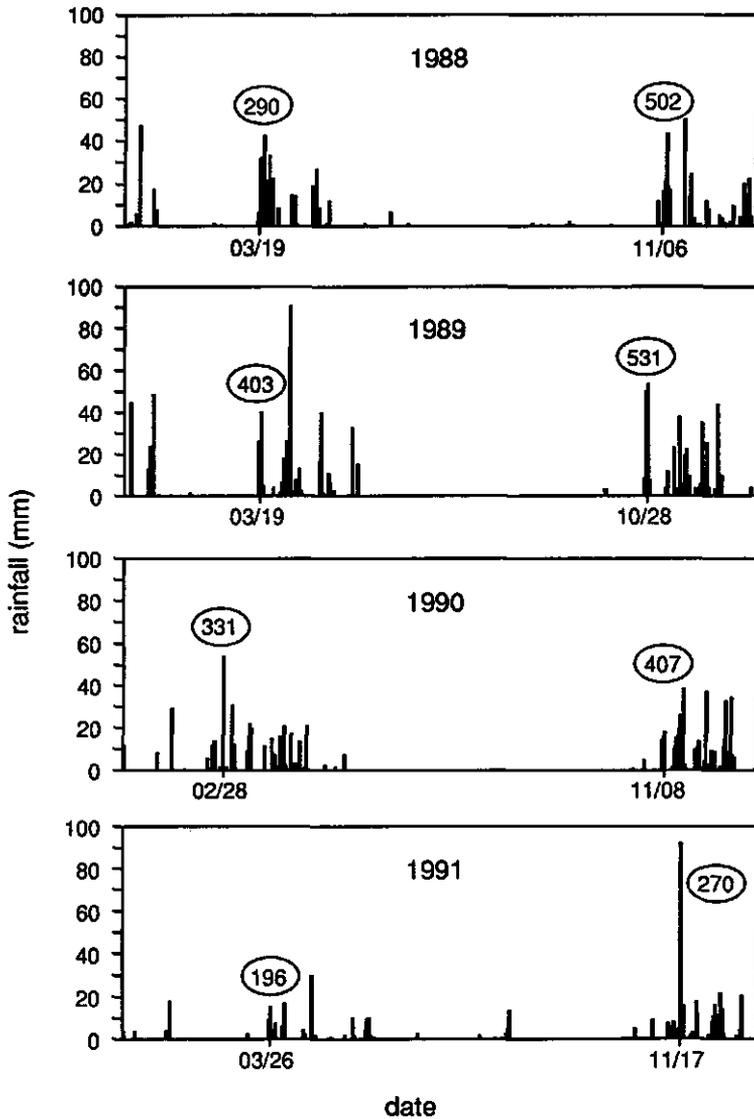
Figure 2-2. Rainfall patterns of daily totals for Makindu during the years 1988 to 1991. The dates indicate the start of the rainy seasons. The total amount of rainfall between two subsequent starts has been indicated in circle above the first of two starts.
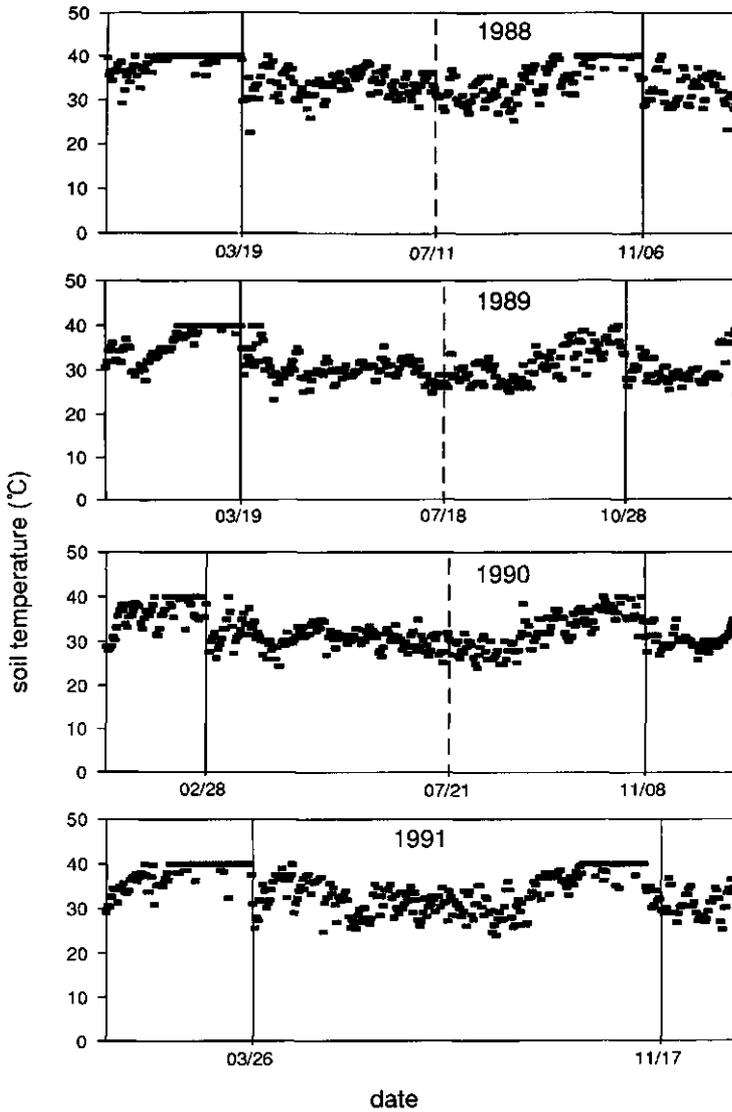
Figure 2-3. Patterns of soil temperature recorded at a depth of 5 cm at 16.00 hr for Makindu during the years 1988 to 1991. Soil temperatures of over 40°C could not be registered and are all set at 40°C. The solid vertical lines indicate the start of the rainy seasons, the dashed vertical lines the end of the growing period of the long rainy seasons (see figure 2-4).
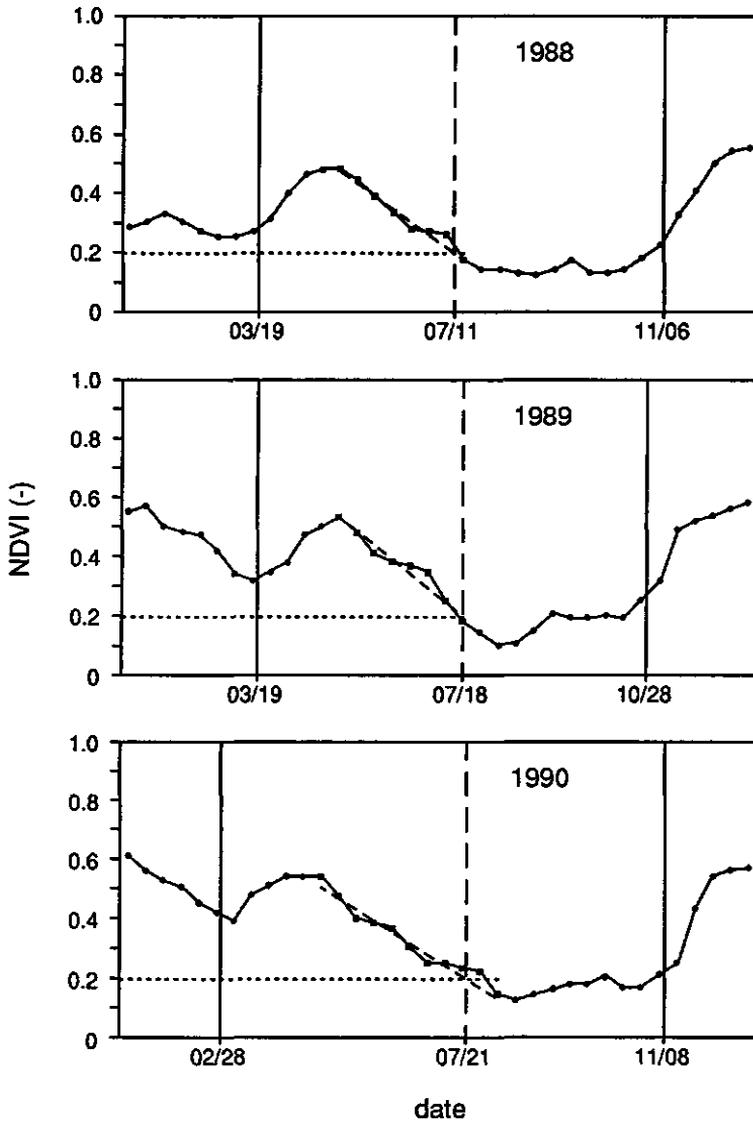
Figure 2-4. NDVI patterns for Makindu during the years 1988 to 1990. The solid vertical lines indicate the start of the rainy seasons, the dashed vertical lines the end of the growing period of the long rainy seasons. Linear regression lines through the NDVI data from the peak during the long rainy seasons to when they fell for the first time below 0.2 (indicated by squares instead of circles) are shown as dashed lines. The intersections of the regression lines with the dotted lines, representing the 0.2 NDVI values, set the end the growing period of the long rainy seasons and the start of the subsequent long dry season. For more information see text.

Table 2-1. Total amount of rainfall, average daily sunshine hours, average soil temperature at 12.00 hr, average soil temperature increase between 8.00 and 16.00 hr, and average NDVI during the whole year (running from start to start of subsequent short rainy seasons), the last 90 days of the long dry season and the first 28 days of the short rainy season for 1988 to 1991 at Makindu.

YEAR	1988	1989	1990	1991
■WHOLE YEAR, preceding short rainy season in year indicated				
Rainfall (mm)	498	905	862	602
Daily sunshine hours (h)	7.5	7.1	7.2	7.5
Soil temperature (°C)	29.4	27.2	27.1	28.6
Soil temperature increase (°C)	10.5	8.8	9.0	10.2
NDVI	0.27	0.35	0.37	NR[1]
■LONG DRY SEASON, last 90 days only				
Rainfall (mm)	16	16	20	46
Daily sunshine hours (h)	7.4	6.0	6.9	7.7
Soil temperature (°C)	29.6	27.0	28.6	29.7
Soil temperature increase (°C)	11.3	8.6	9.7	12.1
NDVI	0.15	0.18	0.17	NR
■SHORT RAINY SEASON, first 28 days only				
Rainfall (mm)	228	251	221	225
Daily sunshine hours (h)	8.2	7.8	9.0	6.8
Soil temperature (°C)	27.7	25.7	27.3	26.6
Soil temperature increase (°C)	9.1	7.1	7.7	7.8
NDVI	0.37	0.41	0.41	NR

[1] Not recorded.

between the four years, observed previously to the short rainy seasons, also disappeared during this period.

The NDVI data indicate that more vegetation was supported in the wetter years, not only at Makindu (table 2-1) but throughout Kitui District (table 2-2). The pattern in time shows a strong increase in NDVI around the start of a rainy season and a more or less linear decrease subsequent to a peak (figure 2-4). Compared to the short dry season, parching of the vegetation was clearly more complete during the long dry season when NDVI

Table 2-2. Average length of the long dry season for five locations in Kitui District and their average NDVI during the whole year (running from start to start of subsequent short rainy seasons), the last 90 days of the long dry season and the first 28 days of the short rainy season in the years 1988 to 1990. Standard errors are given in brackets.

	1988	1989	1990	P
■LENGTH (days)				
Long dry season	123	96	95	
	(2)	(2)	(4)	
■NDVI				
Whole year	0.29 a	0.35 b	0.38 b	***
	(0.00)	(0.00)	(0.01)	
Long dry season	0.16 a	0.17 ab	0.19 b	*
	(0.01)	(0.01)	(0.01)	
Short rainy season	0.39 a	0.42 a	0.44 a	n.s.
	(0.02)	(0.03)	(0.03)	

Data were analysed by oneway ANOVA (n.s.: $P>0.05$; *: $P<0.05$; ***: $P<0.001$) followed by Tukey's multiple range test. Different letters within a horizontal row indicate significant differences ($P<0.05$).

values of 0.2 were reached in all years. While differences in NDVI during the last 90 days of the long dry season and the first 28 days of the short rainy season were small or absent between years, the long dry season was four weeks longer in 1988 compared to 1989 and 1990 (table 2-2).

SOIL
Based on their texture (table 2-3), the soils at the six sampling areas could be classified into three soil types: sandy loam (SL) for Ikutha-2 and Katulani, sandy clay loam (SCL) for Kanyangi, Ikutha-1 and Ikanga, and clay loam (CL) for Maliku. When we also consider the other soil characteristics that were constant over time, no two sampling areas were identical. The two SL soils were quite similar except for their total phosphorus content. Of the SCL soils, Ikutha-1 had a high pH and high levels of total nitrogen and phosphorus, while Kanyangi and Ikanga differed considerably in pH and total

Table 2-3. Average values of soil characteristics that were constant over time at six sampling areas in Kitui District.

AREA	Kanyangi	Ikutha-1	Ikutha-2	Katulani	Ikanga	Maliku
Soil type[1]	SCL	SCL	SL	SL	SCL	CL
∎No. of replicates	6	3	3	2	3	3
Clay (% <2 µm)	20	20	12	12	22	27
Silt (% 2-50 µm)	25	19	17	15	14	43
Sand (% >50 µm)	55	61	71	73	64	30
∎No. of replicates	54	27	27	18	27	27
C (%)	1.05	0.95	0.48	0.65	0.75	1.81
pH_{CaCl2}	5.4	7.2	6.1	5.9	6.0	7.8
N_{tot} (mg/kg)	716	915	499	443	535	1604
P_{tot} (mg/kg)	248	707	491	733	207	410

[1] SL = sandy loam; SCL = sandy clay loam; CL = clay loam.

nitrogen level. The CL soil of Maliku was very different from all other soils; it had a higher pH and much higher levels of organic carbon and total nitrogen.

Of all soil characteristics measured, only nitrate nitrogen showed a consistently large variation in concentration over time during the first 28 days after the start of a short rainy season. At Kanyangi its concentration always peaked on day 1, within 24 hours after the upper 20-25 cm of the soil had been wetted well by rain (figure 2-5A). The peak was highest in 1988, decreased in the two subsequent years to reach its lowest level in 1990, and increased again in 1991. While very low levels of nitrate nitrogen were reached within a few days from the peak in 1989 and 1990, relatively high levels occurred especially throughout the first two weeks after the start of the short rainy seasons in 1988 and 1991. A similar pattern of an early peak and usually strong decrease before the end of the sampling period in nitrate nitrogen concentrations was observed in the soil at all sampling areas in all years.

Based on 1990 and 1991, significant differences also existed between the sampling areas in the average concentrations of all soluble soil fractions

Table 2-4. Average concentrations of soil and plant characteristics at six sampling areas in Kitui District during the first month of the short rainy season in 1990 and 1991 combined. Standard errors are indicated in brackets.

AREA	Kanyangi	Ikutha-1	Ikutha-2	Katulani	Ikanga	Maliku	P[1]
SOILS							
Soil type[2]	SCL	SCL	SL	SL	SCL	CL	
■No. of replicates	36	18	18	18	27	18	
NO_3-N (mg/kg)	2.5 a	7.2 b	4.0 ab	3.8 ab	4.3 ab	16.8 c	***
	(0.4)	(0.9)	(0.2)	(0.4)	(0.2)	(1.9)	
NH_4-N (mg/kg)	4.5 c	0.8 a	0.9 a	1.1 a	1.2 a	3.7 b	***
	(0.2)	(0.1)	(0.0)	(0.1)	(0.1)	(0.1)	
$N_{mineral}$ (mg/kg)	7.0 a	8.0 a	4.9 a	5.0 a	5.7 a	19.0 b	***
	(0.5)	(0.8)	(0.3)	(0.5)	(0.3)	(1.4)	
N_{solorg} (mg/kg)	2.2 c	1.4 b	1.1 ab	0.8 a	1.5 b	3.4 d	***
	(0.1)	(0.2)	(0.1)	(0.1)	(0.1)	(0.1)	
P_{sol} (mg/kg)	0.1 a	0.3 ab	0.9 b	2.7 c	0.1 ab	0.1 ab	***
	(0.0)	(0.1)	(0.1)	(0.6)	(0.0)	(0.0)	
K_{sol} (mg/kg)	178 c	140 b	141 b	169 bc	212 d	70 a	***
	(4)	(11)	(5)	(10)	(7)	(4)	
PLANTS							
Plant type[3]	PER	ANN	ANN	ANN	ANN		
Sampling period[4]	6-28	24-28	13-28	19-28	24-28		
■No. replicates	36	18	18	18	27	0	
NO_3 (% dry wt.)	0.06 a	0.98 c	0.59 bc	0.25 ab	0.46 b		***
	(0.01)	(0.22)	(0.04)	(0.06)	(0.09)		
N_{org} (% dry wt.)	2.97 a	3.47 c	3.43 c	2.29 a	3.04 b		***
	(0.08)	(0.17)	(0.03)	(0.06)	(0.05)		
P (% dry wt.)	0.25 a	0.46 b	0.45 b	0.47 b	0.28 a		***
	(0.00)	(0.03)	(0.01)	(0.02)	(0.01)		
K (% dry wt.)	3.20 a	3.31 a	3.87 b	3.26 a	3.70 b		***
	(0.02)	(0.10)	(0.04)	(0.05)	(0.05)		

[1] Data were analysed by oneway ANOVA (***: $P<0.001$) followed by Tukey's multiple range test. Different letters within a horizontal row indicate significant differences ($P<0.05$).

[2] SL = sandy loam; SCL = sandy clay loam; CL = clay loam.

[3] PER = perennial grass; ANN = annual grass.

[4] Sampling period, in days from the start of the short rainy season, considered when calculating the average concentrations of the plant characteristics.
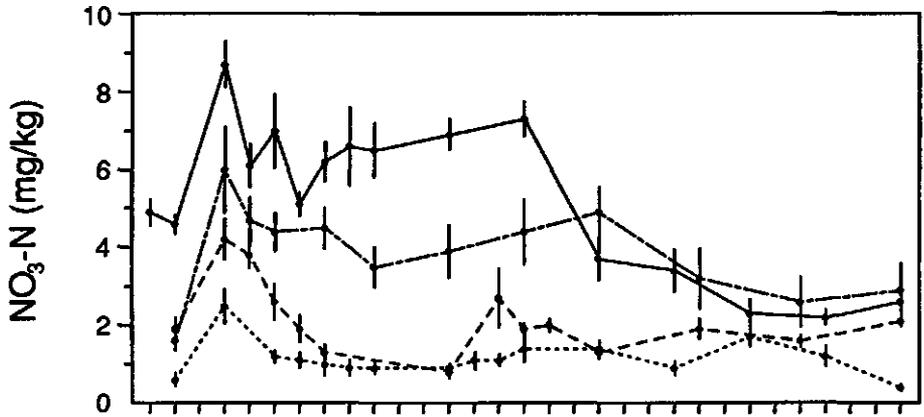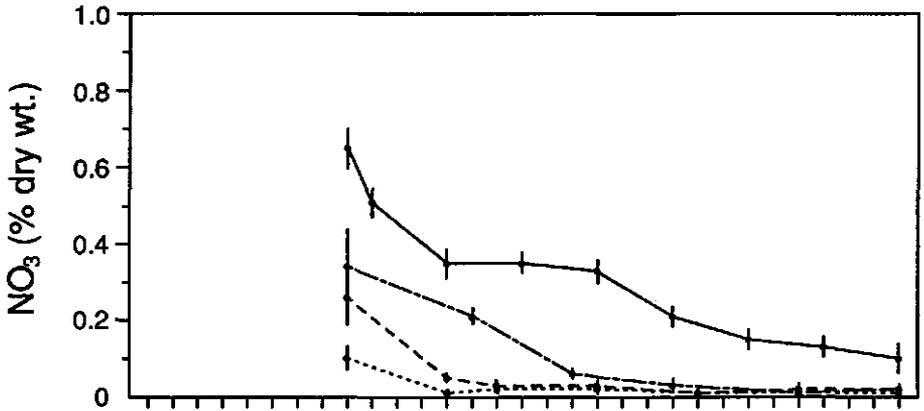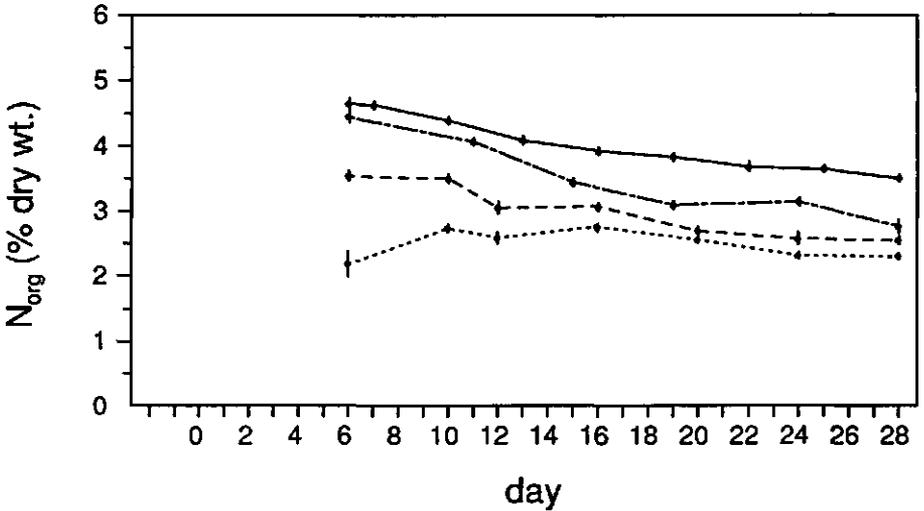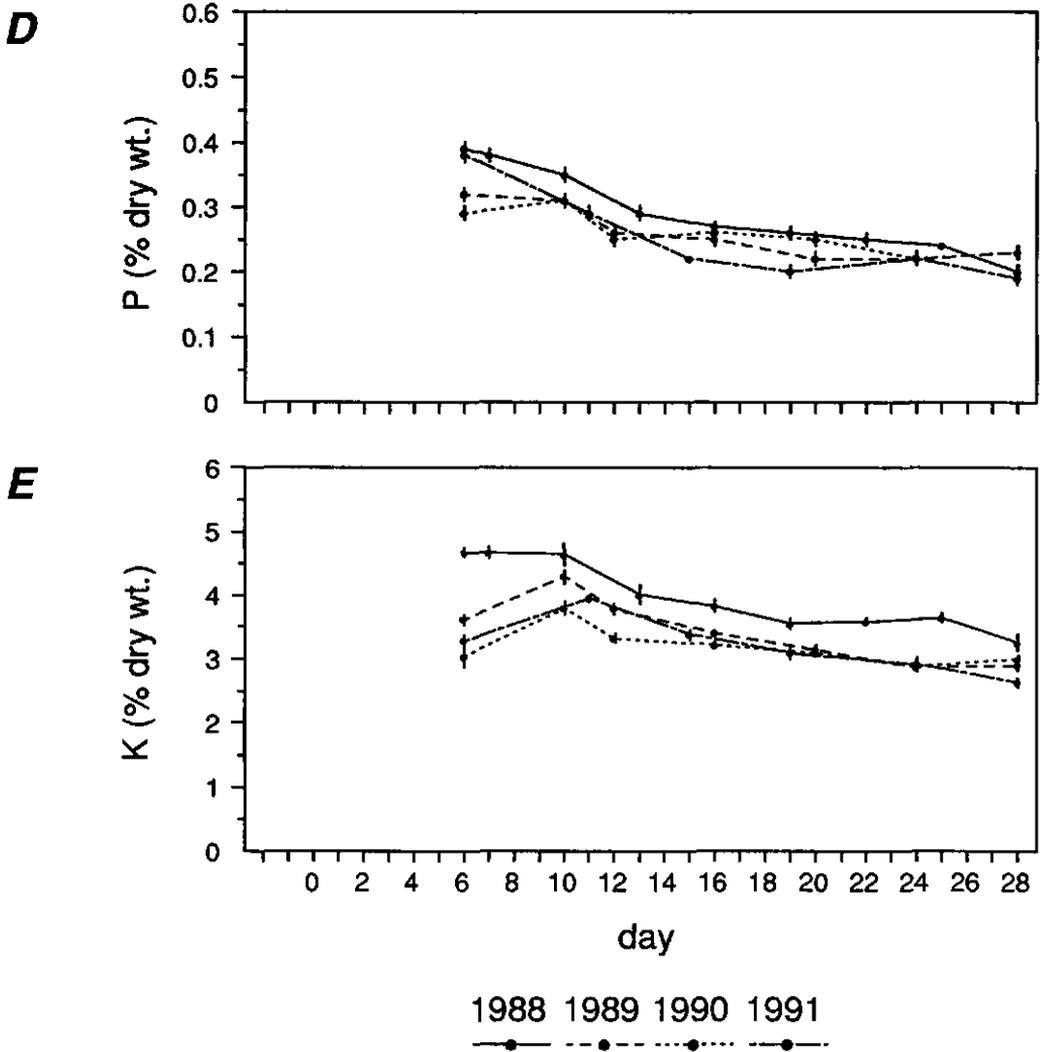
Figure 2-5. Concentrations of **A.** nitrate nitrogen in the soil, and **B.** nitrate, **C.** organic nitrogen, **D.** total phosphorus and **E.** total potassium in the perennial grass at Kanyangi during the first four weeks after the start of the short rainy seasons in the years 1988 to 1991. Vertical lines represent standard errors.

Table 2-5. Average concentration of mineral nitrogen at day 1, and of mineral nitrogen, soluble organic nitrogen, soluble phosphorus and soluble potassium during the first month of the short rainy season in the years 1988 to 1991 at six sampling areas in Kitui District (n=9, except for Kanyangi 1990/1991 and for Ikanga 1990 n=18). Standard errors are indicated in brackets.

	1988		1989		1990		1991		P
■$N_{mineral}$ (mg/kg), at day 1									
Kanyangi	9.8 (0.6)	ab	7.1 (0.5)	ab	5.0 (0.5)	a	10.2 (1.5)	b	*
Ikutha-1	13.7 (2.1)	b			5.9 (0.4)	a	12.3 (1.4)	b	**
Ikutha-2			6.6 (0.4)	a	5.3 (0.2)	a	7.0 (0.8)	a	n.s.
Katulani					9.3 (1.2)	a	7.7 (1.1)	a	n.s.
Ikanga					7.1 (0.4)	a	6.9 (0.9)	a	n.s.
Maliku			14.7 (1.0)	a	17.7 (0.6)	a	33.1 (2.2)	b	***
■$N_{mineral}$ (mg/kg)									
Kanyangi	7.5 (0.3)	b	4.5 (0.1)	a	4.6 (0.2)	a	9.4 (0.5)	c	***
Ikutha-1	5.6 (0.5)	a			5.0 (0.3)	a	10.9 (0.7)	b	***
Ikutha-2			3.6 (0.2)	a	4.4 (0.2)	ab	5.3 (0.4)	b	**
Katulani					6.2 (0.7)	b	3.7 (0.4)	a	***
Ikanga					5.3 (0.3)	a	5.6 (0.6)	a	n.s.
Maliku			15.8 (1.0)	a	13.0 (0.5)	a	28.1 (1.3)	b	***
■N_{solorg} (mg/kg)									
Kanyangi	1.2 (0.2)	a	2.5 (0.1)	b	1.8 (0.1)	a	2.5 (0.2)	b	***
Ikutha-1	0.9 (0.1)	a			0.7 (0.1)	a	2.2 (0.2)	b	***
Ikutha-2			0.9 (0.1)	a	0.8 (0.1)	a	1.5 (0.1)	b	***
Katulani					0.8 (0.1)	a	0.7 (0.1)	a	***
Ikanga					1.3 (0.0)	a	1.7 (0.1)	b	**
Maliku			3.9 (0.1)	b	3.2 (0.1)	a	3.6 (0.1)	b	***

Table 2-5, *continued.*

	1988		1989		1990		1991		P
■P_{sol} (mg/kg)									
Kanyangi	0.1 (0.0)	a	0.2 (0.0)	b	0.1 (0.0)	ab	0.1 (0.0)	a	*
Ikutha-1	0.4 (0.1)	a			0.4 (0.1)	a	0.3 (0.1)	a	n.s.
Ikutha-2			1.1 (0.1)	b	1.1 (0.1)	b	0.7 (0.0)	a	***
Katulani					3.2 (1.0)	a	2.1 (0.6)	a	n.s.
Ikanga					0.1 (0.0)	a	0.1 (0.0)	a	n.s.
Maliku			0.2 (0.0)	a	0.1 (0.0)	a	0.2 (0.0)	a	n.s.
■K_{sol} (mg/kg)									
Kanyangi	158 (5)	a	190 (6)	b	172 (4)	ab	184 (6)	b	**
Ikutha-1	74 (13)	a			125 (17)	ab	155 (12)	b	*
Ikutha-2			153 (5)	a	134 (7)	a	147 (6)	a	n.s.
Katulani					181 (16)	a	158 (11)	a	n.s.
Ikanga					200 (8)	a	235 (10)	b	*
Maliku			75 (7)	b	57 (2)	a	83 (3)	b	**

Data were analysed by oneway ANOVA (n.s.: $P > 0.05$; *: $P < 0.05$; **: $P < 0.01$; ***: $P < 0.001$) followed by Tukey's multiple range test. Different letters within a horizontal row indicate significant differences ($P < 0.05$).

measured (table 2-4). As before, the two SL soils differed only with respect to phosphorus, its soluble concentration being higher in the soil with the higher total phosphorus level. In the SCL and CL soils, soluble phosphorus could hardly be detected. In the SCL soil at Ikanga the concentrations of the other soluble fractions were very similar to those in the SL soils, except for potassium which was significantly higher. Similarly, the SCL soil at Ikutha-1 hardly differed from the SL soils, except for nitrate nitrogen though the

difference was not significant. Kanyangi distinguished itself from the other SL and SCL soils mainly in having a higher ammonium and soluble organic nitrogen level. Again, the CL soil at Maliku differed most clearly; while its concentrations of mineral as well as soluble organic nitrogen were higher than in all other soils, soluble potassium was significantly lower.

Over the four years, significant differences were found in the mineral nitrogen concentration at day 1 (i.e. usually the peak concentration) at three of the six sampling areas (table 2-5). At those three sampling areas the pattern was clear: the peak in mineral nitrogen was, mostly significantly, higher in 1988 and 1991 than in 1989 and 1990. Being strongly related to these 'early' levels, the average mineral nitrogen concentrations during the entire first month of the short rainy season generally revealed a similar pattern (table 2-5). While very significant differences over the years were also observed in the soluble organic nitrogen concentration at all sampling areas, such differences were mostly absent or smaller in the soluble phosphorus and potassium concentrations. For none of the latter three soluble soil fractions a distinct pattern could be recognized over the years, though soluble organic nitrogen was relatively high in 1991 (table 2-5).

PLANTS

Sometimes after an initial increase, the levels of all plant characteristics normally decreased over time during the first 28 days of a short rainy season. This pattern was more consistent in the perennial than in the annual grass species. At Kanyangi, nitrate and organic nitrogen levels clearly differed during the four years (figure 2-5B and 2-5C); they were highest in 1988, decreased in the two subsequent years to reach the lowest level in 1990, and increased again in 1991. Total phosphorus and potassium levels differed less between years (figure 2-5D and 2-5E).

Significant differences existed between the sampling areas in the average concentrations of all plant characteristics measured (table 2-4). They can partly be attributed to the different grass species sampled at Kanyangi compared to the other sampling areas. Nitrate, for example, was virtually absent in the perennial grass at Kanyangi, while appreciable levels were found in the annual grass at all other sampling areas. Organic nitrogen and total phosphorus and potassium were also lower at Kanyangi compared to most other sampling areas. Among the areas where the annual grass was

sampled, Katulani was low in organic nitrogen and Ikanga in total phosphorus, while Ikanga and Ikutha-2 were high in total potassium.

Over the four years, the average organic nitrogen concentration was significantly higher in 1988 and 1991 than in 1989 and 1990 at Kanyangi and Ikutha-1 (table 2-6). No significant differences occurred at the other three sampling areas, except for the low organic nitrogen level found at Ikutha-2 in 1989. While total phosphorus differed little between years in the perennial grass at Kanyangi, it tended to be higher in 1989 and 1990 in the annual grass at the other sampling areas. For total potassium no distinct pattern could be recognized over the years.

ARMYWORMS

In 1988 high numbers of male African armyworm moths (more than 1500 in one week) were caught in pheromone traps in the southern part of Kitui District (Kanyangi-Ikutha-Mutha area, see figure 2-1) during the first week after the start of the short rainy season, while at least the two previous months had been free of catches anywhere in Kenya. Within two weeks gregarious caterpillars were observed in relatively low densities at many locations in the very large area where the moths had been caught. Based on the sudden disappearance of the caterpillars at most locations, synchronized pupation must have occurred around day 18 and larval duration is thus estimated to have lasted about 12 days. Subsequently, moths must have emerged from the primary outbreak area at the beginning of December. They were carried westwards by the winds, mainly into Machakos District where very high catches were then recorded.

In 1989 and 1990 very low numbers of moths (less than 25) were caught in Kitui District during the first two months of the short rainy season. No caterpillars were observed in both years during this period.

In 1991 the short rainy season started around October 20 in the lower, eastern parts of Kitui District (Mutha-Zombe-Voo area, see figure 2-1). No moth catches were reported at this time. Not until November 11 rains started in the sampling areas, and on these first rains moths were caught in pheromone traps in very low (1-4 per night at Kanyangi) to low numbers (up to 25 per night at Makueni). Catches continued for about 5 days. Subsequently, around November 20 very low catches appeared for 1 or 2 nights at most of the sampling areas. Separated by 30 days, it can be hypo-

Table 2-6. Average concentrations of organic nitrogen, total phosphorus and total potassium during the sampling periods given in table 4 in the years 1988 to 1991 at six sampling areas in Kitui District (n=9, except for Kanyangi 1990/1991 and for Ikanga 1990 n=18). Standard errors are indicated in brackets.

	1988	1989	1990	1991	P
■N_{org} (% dry wt.)					
Kanyangi	4.04 d	3.00 b	2.50 a	3.44 c	***
	(0.04)	(0.05)	(0.03)	(0.03)	
Ikutha-1	3.32 b		2.79 a	4.15 c	***
	(0.05)		(0.07)	(0.04)	
Ikutha-2		2.92 a	3.39 b	3.46 b	***
		(0.04)	(0.05)	(0.04)	
Katulani			2.22 a	2.35 a	n.s.
			(0.08)	(0.08)	
Ikanga			3.11 a	2.94 a	n.s.
			(0.06)	(0.09)	
■P (% dry wt.)					
Kanyangi	0.29 b	0.26 a	0.25 a	0.24 a	***
	(0.00)	(0.01)	(0.01)	(0.00)	
Ikutha-1	0.27 a		0.57 b	0.34 a	***
	(0.01)		(0.04)	(0.01)	
Ikutha-2		0.50 b	0.47 b	0.42 a	***
		(0.01)	(0.01)	(0.01)	
Katulani			0.52 b	0.41 a	**
			(0.02)	(0.02)	
Ikanga			0.29 a	0.28 a	n.s.
			(0.02)	(0.02)	
■K (% dry wt.)					
Kanyangi	3.98 c	3.42 b	3.20 a	3.20 a	***
	(0.06)	(0.05)	(0.03)	(0.03)	
Ikutha-1	2.70 a		3.11 ab	3.50 b	***
	(0.10)		(0.16)	(0.09)	
Ikutha-2		3.60 a	3.89 b	3.84 b	***
		(0.03)	(0.05)	(0.06)	
Katulani			3.35 a	3.17 a	n.s.
			(0.08)	(0.09)	
Ikanga			3.63 a	3.82 a	n.s.
			(0.05)	(0.09)	

Data were analysed by oneway ANOVA (n.s.: $P>0.05$; **: $P<0.01$; ***: $P<0.001$) followed by Tukey's multiple range test. Different letters within a horizontal row indicate significant differences ($P<0.05$).

thesized that these moths were descendants of moths that arrived on the October 20 rains which went unnoticed. Around December 11 high catches (up to 140 per night) were recorded at several localities in Kitui as well as Machakos District. Again, it can be hypothesized that they were descendants of the moths that arrived on the November 11 rains. This is supported by the fact that a solitarious caterpillar was found in its sixth instar on November 29 at Ikutha, an area which had been very dry previous to November 11. As pupation occurred on November 30 (i.e. day 20 at Ikutha), larval duration is estimated to have lasted 14 days. The high December 11 catches were followed by extensive outbreaks, especially in Machakos District.

Discussion and conclusions

WEATHER-SOIL INTERACTION

During the four experimental years, the drought intensity in Kitui District previous to the short rainy season was clearly most severe in 1988 and 1991, years with lower rainfall, more sunshine hours and higher soil temperatures than 1989 and 1990 (table 2-1). As rainfall was lower, vegetation was parched faster at the end of the long rainy season, thus increasing the length of the long dry season (table 2-2). The difference in drought intensity culminated in large differences in soil heating between years just prior to the start of the short rainy season; the average soil temperature over this period was lowest in 1989, intermediate in 1990, and highest in 1988 and 1991 (table 2-1). During the two warmer years extreme values of up to 50°C might well have occurred in Kitui District as a maximum of 46°C was recorded at Machakos at an altitude of 1570 m.

These differences in drought intensity and soil heating at the end of the long dry season are likely to affect the mineralization process in the soil after remoistening during the short rainy season. During the long dry season biological formation of nitrate ceases in soils due to low moisture content, while nitrate accumulation near the soil surface continues due to capillary movement upwards (Wetselaar, 1961). Subsequently when dry soil is wetted, a flush of decomposition of organic material has long been known to occur, supposedly increasing soil fertility (Lebedjantzev, 1924). Birch (1959a, 1959b, 1960b) indicated that the effect of drying was both an enhanced exposure of

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organic surface to solution, thus increasing the amount of decomposable organic material going into solution and stimulating microbial processes on the exposed surfaces upon remoistening, as well as an increased killing off of the microflora in the soil, thus providing readily decomposable organic material for a freshly and rapidly developing population of microorganisms after wetting. However, the exact underlying mechanisms causing the flush and the relative importance of the factors contributing to it are not yet clear (Jenkinson, 1966; Kieft et al., 1987, de Bruin et al., 1989; Singh et al., 1989).

The rate of mineralization and the quantity of nitrate released depend, in the first instance, on the organic carbon content, pH and total nitrogen content of a soil. In both 1990 and 1991, these constant soil characteristics were mostly well correlated with the various soluble nitrogen fractions over the six sampling areas (table 2-7), except for ammonium. Organic carbon correlated best with mineral and soluble organic nitrogen, pH with nitrate nitrogen, and total nitrogen with mineral nitrogen; interestingly, these correlations tended to be better in 1991, the year with the better flush. Ammonium

Table 2-7. Correlation matrix between some constant soil characteristics (averaged over all years) and soluble nitrogen fractions of six sampling areas in Kitui District during the first month of the short rainy season for 1990 and 1991. All correlations are Pearson correlations (*: $P<0.05$; **: $P<0.01$; ***: $P<0.001$).

	C		pH		N_{tot}	
■1990						
NO_3-N	0.647		0.805		0.725	
NH_4-N	0.818	*	0.180		0.668	
$N_{mineral}$	0.870	*	0.736		0.873	*
N_{solorg}	0.924	**	0.480		0.840	*
■1991						
NO_3-N	0.911	*	0.906	*	0.981	***
NH_4-N	0.607		-0.107		0.430	
$N_{mineral}$	0.966	**	0.806		0.992	***
N_{solorg}	0.922	**	0.622		0.911	*

accumulated at Kanyangi due to low pH (table 2-3 and 2-4). Based on the mineral nitrogen concentration, it can be concluded that the nitrogen mineralization process proceeded well even at a pH of only 5.4 (table 2-3 and 2-4).

During soil incubation under laboratory conditions, a peak in microbial activity is usually reached within a day from wetting after which a rapid decline occurs (Birch, 1958b, 1959b; Jager & Bruins, 1975; Kieft et al., 1987; de Bruin et al., 1989). Birch (1958b) showed that the mineralization of carbon and nitrogen is much higher in soils dried at 100°C when subsequently wetted and incubated than in soils dried at 25°C. Similar results were obtained by Jenkinson (1966), comparing soil drying at 20, 80, 100 and 120°C, and by Jager & Bruins (1975), comparing undried soils with drying at 30 and 85°C: the higher the temperature a soil was exposed to during drying, the more CO_2 and NO_3^- was produced after wetting. Birch (1959b, 1960b) also showed that mineralization is a function of the length of time that a soil has been dry prior to wetting.

In a study on sample preparation for soil analysis, Houba et al. (1989) showed that increased drying temperatures up to 105°C do not affect the nitrate nitrogen concentration in soil samples without additional wetting, but strongly increase the ammonium and soluble organic nitrogen concentrations compared to the levels found in fresh soil samples. To limit these changes to a minimum and simultaneously make soil samples sufficiently dry, their results indicated that drying of soil samples should preferably be carried out at 30°C. Based on these findings, higher ammonium and soluble organic nitrogen levels were expected in the soil samples taken at the end of the long dry season in 1988 and 1991, the two warmer years when soils were heated to temperatures of up to 50°C, compared to 1989 and 1990. This expectation could not be confirmed by the few dry season samples taken in the present study.

Large fluctuations of soil nitrate in response to rainfall have also been observed under field conditions, though their patterns were never studied in as much detail as in the present study (Hagenzieker, 1957; Kabaara, 1964). As nitrate is easily leached, the magnitude and duration of an enhanced nitrate level in the topsoil in the field strongly depend on the amount, intensity and distribution of the early rains. In addition, it is affected by uptake by plants and microorganisms. Only the net result of these processes in the upper 25 cm of soil was measured in the present study.

At Kanyangi, the particularly high level of nitrate nitrogen at the end of the long dry season in 1988 (figure 2-5A) can be explained by the combined effect of extremely low rainfall and high soil temperatures during the preceding year, resulting in less leaching and more upward capillary movement of nitrate than in other years. However, this pattern was not consistent over years (e.g. compare 1989 and 1991) and at other sampling areas. The rapid increase in nitrate nitrogen immediately upon the start of the short rainy season agrees well with the results obtained during incubation of soils under laboratory conditions. Moreover, the larger initial increase at day 1 and the higher level during the first two weeks in 1988 and 1991 as compared to 1989 and 1990 correlate well with the more severe drought intensity and higher soil temperatures occurring in these years. Leaching can be excluded as a factor causing this difference in nitrate level, because rainfall was equally or even more intense during the first two weeks at Kanyangi in the years with a high nitrate level. Uptake of nitrate by the sparse vegetation is still small so soon after the onset of the rains and therefore cannot be responsible either. More nitrate must have been produced in 1988 and 1991 at Kanyangi. The mineral nitrogen levels at day 1 (table 2-5) show that this was also true for Ikutha-1 and Maliku, but not for Ikutha-2, Katulani and Ikanga. Typically, the soils at the latter three locations had the lowest total nitrogen levels (table 2-3).

Though the total amount of rainfall over the first 28 days of the short rainy season hardly differed between years at most sampling areas, the rainfall pattern sometimes clearly influenced soil nitrate levels through leaching. The sudden decrease observed in 1988 at Kanyangi between day 13 and 16 (figure 2-5A) followed two nights with a total of 95 mm of rain. At Ikutha-1 peaks of approximately 13 mg NO_3-N/kg dry soil occurred on day 1 in 1988 and 1991 and of only 6 mg/kg in 1990, as at Kanyangi a pattern well associated with the drought intensity and soil heating occurring over the years. However, in 1988 excessive rainfall during two subsequent nights with a total of 92 mm caused the nitrate level to decrease rapidly to only 5 mg/kg, while it stayed close to peak level in 1990 and 1991 in the absence of excessive rainfall. Consequently, the average concentration of mineral nitrogen during the entire first month of the short rainy season was not significantly different between 1988 and 1990, in spite of a different initial flush, whilst it differed between 1988 and 1991, two years with identical initial

flushes (table 2-5). At Maliku, where the initial flush was also well associated with drought intensity, the average level was even higher than the initial flush in 1989 due to the absence of high rainfall in this year. For Ikutha-2, Katulani and Ikanga, sampling areas with similar initial flushes between years, the observed differences in the average mineral nitrogen concentrations could all be attributed to differences in rainfall pattern too.

With regard to the weather-soil interaction it can therefore be concluded that in Kitui District more severe drought, especially in terms of soil heating at the end of the long dry season, stimulated the initial flush of mineral nitrogen immediately following the first rains of the short rainy season in soils not extremely low in organic carbon (i.e. more than 0.9%) and total nitrogen (i.e. more than 700 mg/kg), their pH being less important. Furthermore, it is evident that the rainfall pattern, especially the occurrence of excessive rain (i.e. more than 40 mm in a few days), strongly influenced the mineral nitrogen level in the upper 25 cm of soil. No effect of weather on soluble phosphorus and potassium concentrations in the soil could be detected. While nitrate concentrations usually strongly decreased in the topsoil during the first four weeks of the short rainy season, mainly due to leaching, they remained at a constant level. This is to be expected as soluble phosphorus and potassium are usually well buffered in soils.

SOIL-PLANT INTERACTION

As the mineral composition of the perennial grass clearly differed from that of the annual grass, soil and plant characteristics were only correlated over the four sampling areas where the annual grass was sampled (table 2-8). In spite of the low number of sampling areas and the differences in the sampling periods among them, one of the correlations reached significance. Most prominent is the difference in sign of the correlations for nitrogen between the two years. In 1990, when differences in nitrate and mineral nitrogen levels in the soil were only small between the four sampling areas (table 2-5), correlations were negative. In 1991, the year with the better flush of mineral soil nitrogen, higher soil nitrate levels clearly resulted in higher plant nitrate and organic nitrogen levels. While soil and plant phosphorus levels were reasonably well correlated in both years, correlations for potassium were poor (table 2-8).

Table 2-8. Correlation matrix between soil (averaged over the first month of the short rainy season) and plant (averaged over the sampling periods given in table 4) characteristics of the four sampling areas where the annual grass was sampled in Kitui District for 1990 and 1991. All correlations are Pearson correlations (*: $P < 0.05$).

SOIL	NO_3-N	N_{min}	P_{sol}	K_{sol}
PLANT				
■1990				
NO_3	-0.428	-0.515		
N_{org}	-0.871	-0.907		
P			0.415	
K				0.144
■1991				
NO_3	0.969 *	0.948		
N_{org}	0.899	0.906		
P			0.713	
K				0.397

At Kanyangi, the soil nitrate level in the four years was very well correlated with the organic nitrogen level in the leaves of the perennial grass (figure 2-5A and 2-5C; $r(NO_3$-N$/N_{org})=0.990$, n=4, p<0.001). Large differences in total nitrogen level between years occurred especially during the first two weeks of the short rainy season. The initial level of 5% in 1988 indicates that the nitrogen supply to the grasses was particularly good in this year. This was also supported by a relatively high nitrate concentration in the leaves (i.e. 0.31%). Nitrate concentrations, always contributing less than 2% nitrogen to the total nitrogen level in the leaves of the perennial grass, rapidly dropped to near zero as soon as organic nitrogen concentrations decreased to values below 3.5%, a well known feature in grasses (Terman et al., 1976; Steer, 1982). The significantly lower initial levels of organic nitrogen in 1989 and 1990 clearly indicate that nitrogen was in short supply in these years.

In the leaves of the annual grass the relation between nitrate and organic nitrogen was different from that in the perennial grass; nitrate

concentrations, sometimes contributing almost 10% nitrogen to the total nitrogen content, were extremely high (i.e. up to 2.0%) at high organic nitrogen concentrations and dropped to near zero not before organic nitrogen concentrations had fallen to below 2.5% (table 2-6). Though not significant, due to the low numbers, plant organic nitrogen concentrations were well correlated with the soil nitrate levels at the two sampling areas in Ikutha over the years ($r=0.981$ and 0.913 respectively, $n=3$). For unknown reasons, the occurrence of a difference in the mineral nitrogen level in the soil between the two years at Katulani was not reflected in a difference in plant organic nitrogen level (table 2-5 and 2-6). According to expectations, significant differences in both characteristics were absent at Ikanga.

With regard to the soil-plant interaction it can thus be concluded that, in general, the organic nitrogen content in the two grass species sampled was well correlated with the soil nitrate levels during the first month of the short rainy season.

PLANT-ARMYWORM INTERACTION

Outbreaks occurred within two months after the start of the short rainy season only in 1988 and 1991, the two years in which the highest levels of nitrogen were found in the host plants of the African armyworm in Kitui District. In 1991 a generation of solitarious caterpillars seems to have been required to build up armyworm numbers to a level that had the potential of causing outbreaks (i.e. gregarious caterpillars requiring control). The solitarious generation was characterized by low moth catches, while they went virtually unnoticed as caterpillars. The question can be raised whether the gregarious generation in 1988 was also preceded by a solitarious generation. If so, it should have been triggered by off-season rain in the second half of September or in the first week of October. Monthly rainfall records indicate that in the eastern lower area of Kitui District rain was indeed unusually good in September; Voo, Zombe, Mutha, and Kanziko (figure 2-1) received an average of 38 mm during this month, likely to be enough to initiate grass growth. Thus, in 1988 a solitarious generation of the African armyworm might well have developed in the lower, remote, eastern part of Kitui District, going completely unnoticed as in 1991.

Moths often arrived on the first rains of the short rainy season in an area. Peak larval hatch can then be expected to occur on day 6. How moth

arrival could be so well timed is yet unknown, but the behaviour is certainly of adaptive value as it allows the caterpillars, especially the young ones, to take advantage of the presence of the youngest, softest and most nutritious (e.g. with highest levels of nitrogen, phosphorus and potassium) grass leaves in Kitui District. Despite the sparseness of the vegetation cover soon after the start of the short rainy season, the problem for the neonate larvae of finding a suitable host plant is likely to be easily overcome by their high dispersal potential.

As plant nitrogen, phosphorus and potassium levels differed significantly between years, they might well explain differences in outbreak development of the African armyworm between years on the condition that armyworm fitness is strongly dependent on the concentration of these minerals in its food over the ranges found in this study: 1.5 to 5.0% for nitrogen, 0.2 to 0.7% for phosphorus and 2.0 to 5.0% for potassium. The effects of these minerals on armyworm fitness will be subjected to further study. Emphasis will be placed on nitrogen, which differed greatly between years in grasses growing on soils not extremely poor in organic carbon and total nitrogen. It was high in some years and deficient in others, and it was best correlated with drought intensity preceding the short rainy season, as well as with outbreak development of the African armyworm during it. As such, this study provided basic support to the hypothesis proposed by Janssen and Rose (1990).

Acknowledgements

3   *Intraplant temporal and spatial variation in host plant quality in relation to outbreak development of the African armyworm*

Abstract

Variation in host plant quality, in terms of nitrogen, phosphorus, potassium and water content, in time and space within maize plants during the first month of the short rainy season was assessed at two locations in a primary outbreak area of the African armyworm. Highest levels of all four plant constituents were found in youngest maize plants with generally little spatial variation over leaves. They subsequently decreased over time, while the intraplant spatial variation rapidly increased especially for the three minerals. As the highest concentrations of the plant constituents found in a leaf or leaf part of 3-weeks old maize plants was generally close to or even higher than the average level of 1-week old plants, the intraplant spatial variation fully compensated the decrease over time during this period which is usually most relevant to caterpillar feeding in primary outbreak areas. The only exception occurred for nitrogen due to a rapid decrease over time which could be attributed to excessive rainfall. The consequences of these findings for caterpillar feeding are discussed.

Introduction

Host plant quality is known to vary in time and space. Studies on the effect of leaf age on herbivores have shown that young leaves, either in time or within a plant, are often preferred and of better quality than old leaves (Blais, 1953; Schweitzer, 1979; Raupp & Denno, 1983 and references therein; Walker, 1985, 1987; Hoy & Shelton, 1987). A decline in the nutritive quality of foliage over time is often thought to be due to an increase in digestibility reducing compounds, like structural carbohydrates, lignin, silica and tannins, and a concomitant decrease in water content and available nutrients, espec-

ially nitrogen (Scriber, 1984; Mattson & Scriber, 1987). All herbivores are inevitably faced with this change over time in their food, in particular when their feeding extends over a longer period and their food is produced in a single synchronous flush thus minimizing spatial variation.

If host plant quality is of critical importance to the fitness of a herbivore, phenological synchrony between the herbivore and its food of optimal quality is certainly important. This has been illustrated for the winter moth, *Operophtera brumata* (L.), which larvae feed on oak trees (Varley & Gradwell, 1960; Feeny, 1970). In this species hatching of eggs occurs very early in the season, in spite of the risk of hatching too soon to enter oak buds resulting in high mortality of the first instars. If well timed, early hatching enables the larvae to feed on the youngest, nutritionally most optimal leaves and outbreaks are more likely to develop.

Such timing might also be important for the African armyworm in its primary outbreak areas at the end of the long dry season in eastern Africa (Odiyo, 1981; Pedgley et al., 1989). Then, hardly any green grasses, host plants of the African armyworm, are remaining in these areas due to the absence of rain for about five months. However, within 2 days after the first significant rainfall of the short rainy season in October or November, the first grass leaves sprouting from rhizomes can be found everywhere (see Chapter 2). Germination of grass seeds usually takes about a week. First moth activity, as monitored by pheromone traps, tends to coincide with the first rains in primary outbreak areas (see Chapter 2). As peak larval hatch occurs 6 days after moth arrival under these conditions in primary outbreak areas (Pedgley et al., 1989), this assures that first instars will encounter young, succulent food.

When moth arrival coincides less well with the onset of the short rains or in subsequent generations, the food quality encountered by the larvae is presumably of poorer quality. Janssen (see Chapter 2) found that food quality, in terms of nitrogen, phosphorus and potassium, indeed decreased over time in wild grasses in Kitui District, an important primary outbreak area in Kenya. However, a decrease in food quality over time might be fully or partly offset by increased spatial variation within plants. If so, larvae might still perform well when able to locate and feed on food sources of better quality.

In the present study variation in food quality, in terms of nitrogen, phosphorus, potassium and water content, in time and space within plants during the first month of the short rainy season in Kitui District was assessed for maize, one of the most preferred host plants of the African armyworm (Brown, 1962; Khasimuddin & Lubega, 1979). It is extensively grown by farmers throughout eastern Africa. The question was addressed to which extent increased intraplant spatial variation in the four plant constituents can offset their decrease over time.

Materials and methods

Maize plants (*Zea mays* L. var. Katumani) were sown at two locations in Kitui District: at Katulani in 1989 and 1990, and at Maliku in 1989. These locations differ considerably in soil type (see Chapter 2): while the soil at Katulani is sandy and high in phosphorus (pH_{CaCl2} 5.9, organic carbon 0.65%, total nitrogen 0.44 g/kg, total phosphorus 0.73 g/kg), the soil at Maliku is a rich clay (pH_{CaCl2} 7.8, organic carbon 1.81%, total nitrogen 1.60 g/kg, total phosphorus 0.41 g/kg). A rain gauge was present at both locations for the duration of the experimental period. The start of the short rainy season was set according to Janssen (see Chapter 2). The day preceding the start of the short rainy season was set to day 0 (October 28 in 1989 for both locations, and October 26 in 1990 for Katulani).

At Katulani, sowing occurred two weeks before the start of the short rainy season in 1989 and on day 1 in 1990. In 1989, maize plants (n=20) were harvested 3, 8, 13, 18, and 23 days after germination. In 1990, harvesting only differed in that the final harvest occurred 22 days after germination. At harvest, maize plants were separated in stem and leaves. The leaves along the stem were numbered from stem base to top, making the lowest and thus oldest leaf of a plant leaf 1. Leaves 4 to 8 of the 18-days old maize plants and leaves 4 to 10 of the 22/23 days-old maize plants were separated in base, middle and top parts of equal lengths. Identical leaves or leaf sections were lumped, fresh weighed, dried at 70°C in a stove, and dry weighed.

At Maliku, sowing occurred 16 and 8 days before the start of the short rainy season and on day 1. As soon as seeds had been sown, they were

provided with sufficient water for germination and growth. Maize plants (n>30) of all three sowing dates were harvested at day 11 (i.e. 21, 13 and 5 days after germination respectively) and of the first sowing date only at day 19 (i.e. 29 days after germination). At harvest, the maize plants were treated as at Katulani, with the exceptions that leaves were never separated in base, middle and top parts and that fresh weights were not recorded.

Total nitrogen, phosphorus and potassium of all leaf samples were determined after Novozamsky et al. (1983). If sufficient leaf material remained, nitrate was extracted by shaking with distilled water for 30 min and analysed by Technicon AutoAnalyser after reduction to nitrite. The values of these plant constituents for a leaf which had been separated in base, middle and top parts were calculated based on the dry weights of the three leaf parts and their levels of the plant constituents. Similarly, the values for a plant were calculated based on the dry weights of its leaves and their levels.

Temporal variation in nitrogen, phosphorus, potassium and water content of the maize plants was calculated as the percentage deviation of the minimum or maximum of a plant constituent for a whole plant from its average over a certain period of time. Spatial variation over leaves was calculated as the percentage deviation of the minimum or maximum in whole leaves from the plant average at a certain day. Similarly, spatial variation over leaf parts was calculated as the percentage deviation of the minimum or maximum in whole leaves and leaf parts from the plant average at a certain day.

Results

At Katulani, the growth of the maize plants, as measured by leaf fresh weight, during the first month of the short rainy season in 1989 and 1990 was very similar, both for whole plants (figure 3-1A) as well as for their separate leaves (figure 3-1B and 3-1C). The fresh weight of whole plants increased exponentially over time in both years. Besides this similarity in growth pattern, differences were absent in the average water, nitrogen, phosphorus and potassium content between the two years (t-test, P>0.05 for all). The levels of these plant constituents usually declined over time (figure 3-1A).

Independent of the age of the maize plants, the water content tended to vary little between the lower leaves and to increase towards the youngest leaf (figure 3-1B and 3-1C). In maize plants of less than two weeks old, the nitrate content increased steadily from the oldest to the youngest leaf; subsequently, nitrate peaked in the leaf which had just become full-grown (figure 3-1B) or was completely absent (figure 3-1C). Nitrogen also showed a pattern of increasing concentrations from the oldest to the youngest leaf during the first two weeks of maize growth, after which it changed to a very constant level over the leaves (figure 3-1B) or a pattern with a peak in rather old leaves (figure 3-1C). The distribution of phosphorus over the leaves revealed a marked difference between the two years; contrary to 1990, an excessively high phosphorus level occurred in leaf 1 in maize plants older than one week in 1989, because its normal decrease over time was almost absent in this leaf (figure 3-1B). In leaf 2 and 3 the decrease over time was also too small. Apart from this difference, phosphorus peaked in the youngest leaves in both years. Potassium peaked in the youngest leaves, while having a similar spatial distribution over the leaves in both years.

Due to the different experimental design at Maliku, maize plants of similar absolute age were less far in their development at this locations than at Katulani (compare leaf numbers between figure 3-1B and 3-2). In spite of this difference in growth, only the average phosphorus concentration differed significantly from Katulani in 1989; it was lower at Maliku (t-test, P<0.05). In general, the patterns over time and space in nitrogen, phosphorus and potassium content at Maliku (figure 3-2) were similar to those at Katulani. Different was that nitrogen peaked in the youngest leaves throughout the sampling period (figure 3-2B). The pattern in phosphorus concentrations over the leaves conformed to 1990, not maintaining high levels in the oldest leaves (figure 3-2B).

The temporal variation (TIME) in the nitrogen, phosphorus, potassium and water content of the maize plants during the first month of the short rainy season was larger in 1990 than in 1989 at Katulani (table 3-1). Especially nitrogen concentrations, and correlated with this nitrate concentrations, varied considerably more in 1990 (figure 3-1A); its total deviation from the average was only 19% in 1989 compared to 71% in 1990 (table 3-1). Though calcu-
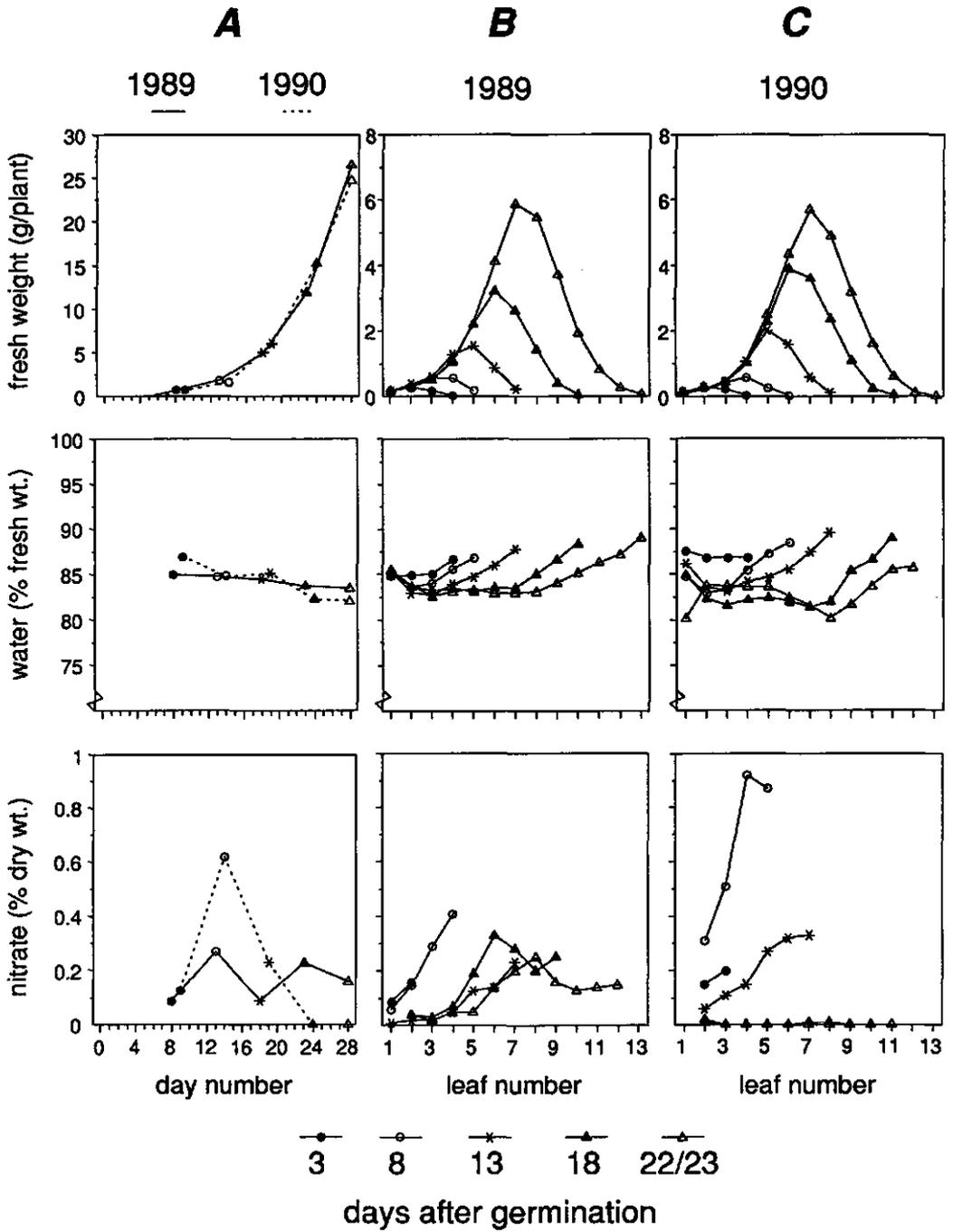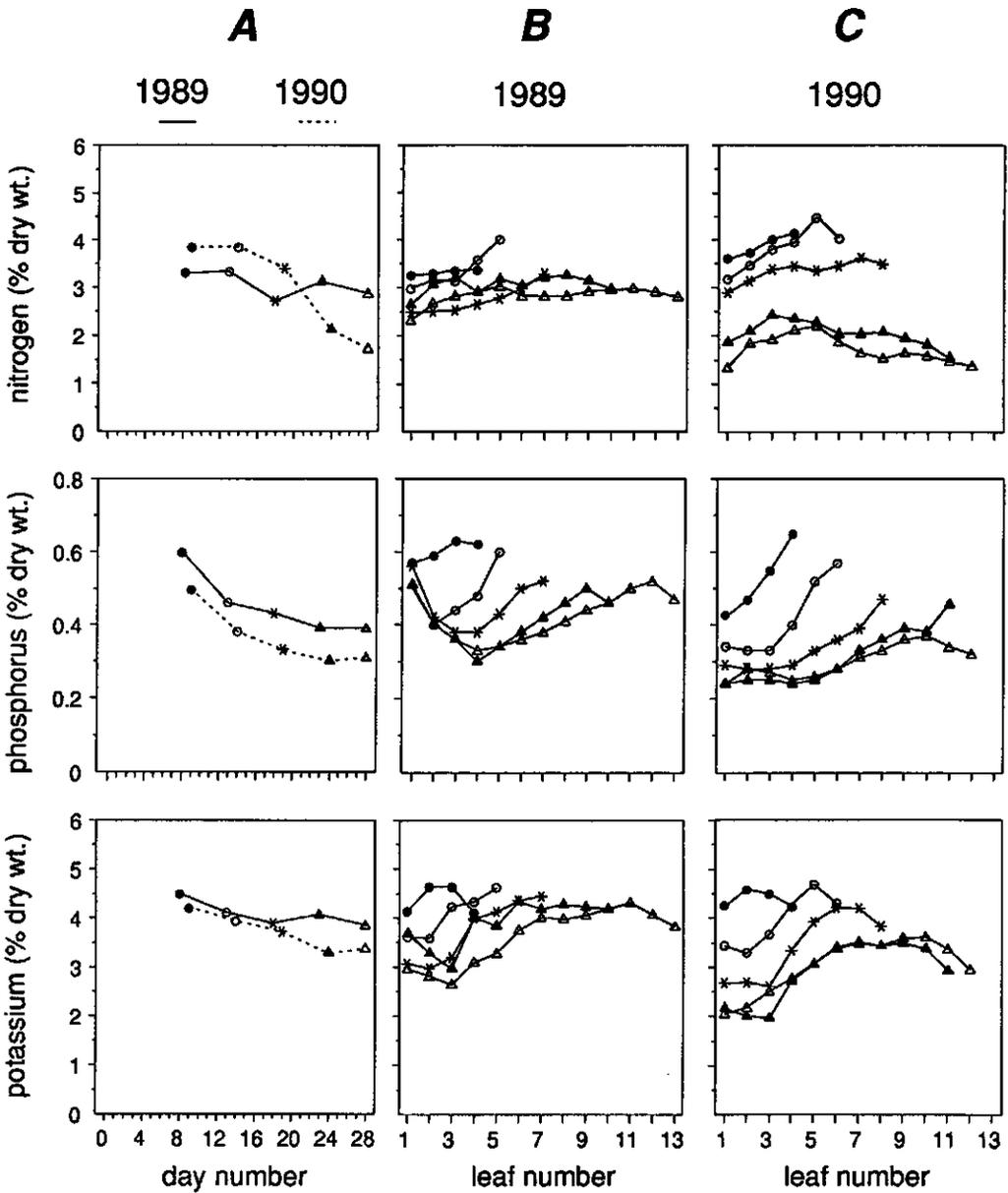
Figure 3-1. A. Fresh weight and water, nitrate, nitrogen, phosphorus and potassium content of maize plants grown at Katulani during the first month after the start of the short rainy season in 1989 and 1990, and their spatial variation over leaves in **B.** 1989 and **C.** 1990.

Table 3-1. Temporal variation over the period indicated (in days from germination, TIME) and average spatial variation over leaves (SPACE-L, n=5 for Katulani, n=4 for Maliku) during this period in nitrogen (N), phosphorus (P), potassium (K) and water (H_2O) content of maize plants grown at Katulani in 1989 and 1990 and at Maliku in 1989. For the definition of the temporal and spatial variation see materials and methods.

		N		P		K		H_2O	
		min	max	min	max	min	max	min	max
■KATULANI-1989									
3-23 days	TIME	11	8	15	32	6	10	1	1
	SPACE-L	11	11	14	26	21	10	1	4
■KATULANI-1990									
3-22 days	TIME	42	29	17	37	12	14	3	3
	SPACE-L	18	15	17	39	26	10	2	5
■MALIKU-1989									
3-29 days	TIME	10	10	13	19	10	10		
	SPACE-L	14	10	19	23	23	13		

lated over a longer period of time, the temporal variation at Maliku was similar or even smaller (for phosphorus) than at Katulani in 1989 (table 3-1).

The average spatial variation over leaves (SPACE-L) in the four plant constituents during the first month of the short rainy season was also always larger in 1990 compared to 1989 at Katulani, and was similar for all minerals at both locations in 1989 (table 3-1). For nitrogen this spatial variation was equal to the temporal variation in 1989, but only half the temporal variation in 1990. For phosphorus and water both types of variation were always very similar, and for potassium spatial variation over leaves was considerably larger than temporal variation.

The average spatial variation over leaf parts (SPACE-LP) was assessed during the last two harvests at Katulani. As these harvests were only separated by 5 and 4 days in 1989 and 1990 respectively, temporal variation was small (table 3-2). Comparison between the two types of spatial variation

Table 3-2. Temporal variation over the period indicated (in days from germination, TIME) and average spatial variation over leaves (SPACE-L, n=2) and leaf parts (SPACE-LP, n=2) during this period in nitrogen (N), phosphorus (P), potassium (K) and water (H_2O) content of maize plants grown at Katulani in 1989 and 1990. For the definition of the temporal and spatial variation see materials and methods.

	N		P		K		H_2O	
	min	max	min	max	min	max	min	max
■KATULANI-1989								
18-23 days TIME	4	4	1	1	3	3	0	0
SPACE-L	17	5	20	32	29	9	1	6
SPACE-LP	28	20	25	32	49	42	8	6
■KATULANI-1990								
18-22 days TIME	10	10	2	2	1	1	0	0
SPACE-L	24	21	21	35	40	7	2	6
SPACE-LP	34	39	23	40	48	35	8	7

reveals that, when considering leaf parts instead of whole leaves, in both years very substantial additional variation is found in all plant constituents except for phosphorus. Phosphorus was also the only plant constituent with no fixed gradient in concentration from top to base in leaf 4 to 10, though in leaf 7 to 10 it always increased from top to base. Independent of the leaf number, the nitrogen level decreased and the potassium, water as well as nitrate level increased from top to base in a leaf. While nitrate was virtually absent in the top part of leaves, always more than 70% was present in the base part. Due to their high spatial variation over leaf parts, highest concentrations of nitrogen and potassium in the maize plants were sometimes located in a part of leaves which did not contain the highest overall concentration. Typically, when considering leaf parts, both minerals always peaked in the leaf which was nearing its full-grown size (leaf 6 in 18-days old maize plants and leaf 7 in 22/23-days old maize plants), nitrogen in its top and potassium in its base part.
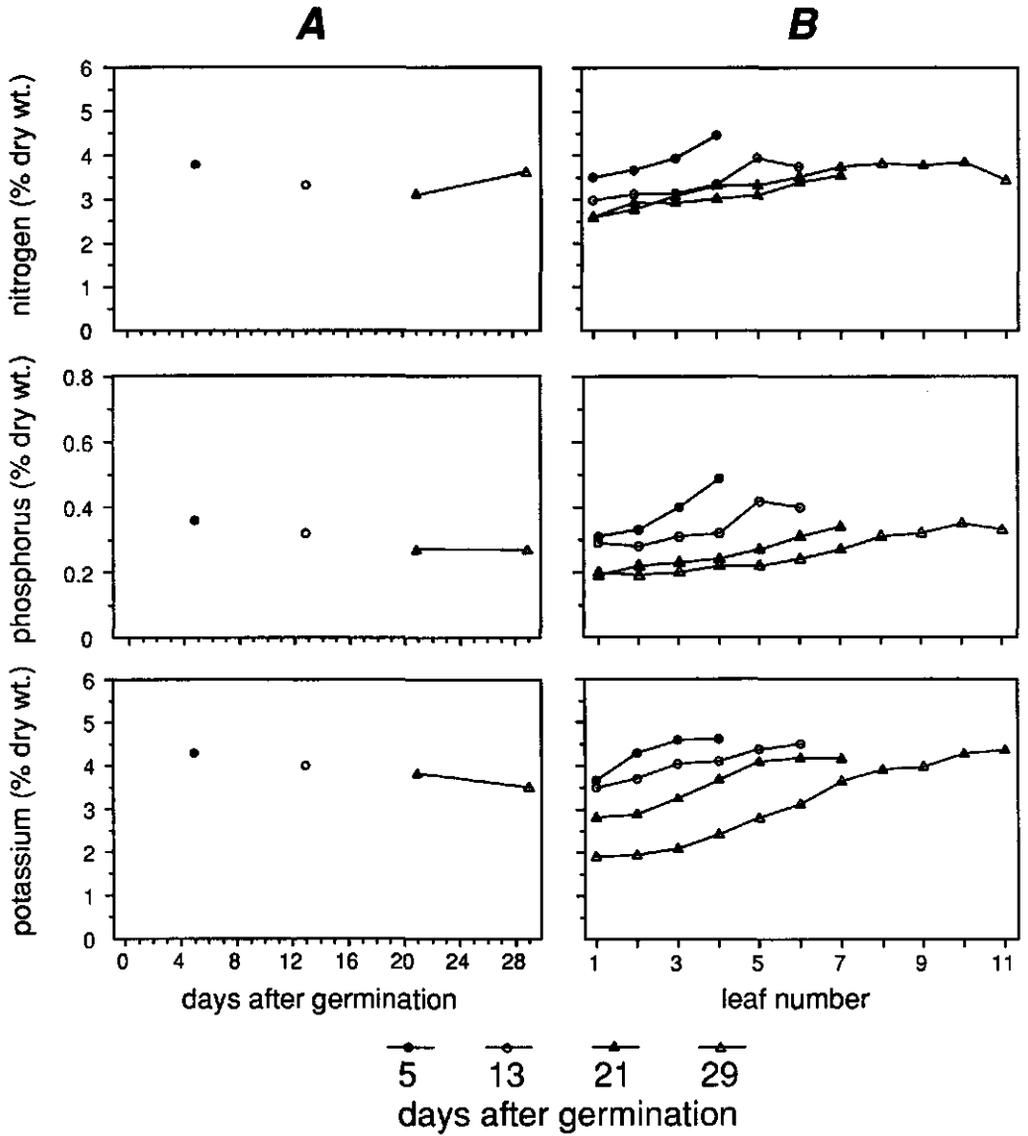
Figure 3-2. A. Nitrogen, phosphorus and potassium content of maize plants grown at Maliku in 1989, and **B.** their spatial variation over leaves. Symbols in **A.** were only connected by a line when they refer to plants sown at similar dates.

The water content of the maize plants always varied less in time and space than the nitrogen, phosphorus and potassium content; of the three minerals, potassium varied least in time (table 3-1). Variation over leaves was always largest for phosphorus, followed by potassium and smallest for nitrogen (table 3-1). When leaf parts were considered, spatial variation was clearly largest for potassium (table 3-2).

Discussion and conclusions

Though the maize plants were growing at very different soils at Katulani and Maliku, their levels of nitrogen and potassium hardly differed; only phosphorus was significantly higher at Katulani, likely a result of the much higher phosphorus availability in the sandy soil at this location compared to Maliku (see Chapter 2). This high availability might also be the reason for the excessively high levels of phosphorus in the oldest leaves of the maize plants in 1989 (figure 3-1B). This was confirmed by similar findings for maize plants grown at another location in Kitui District with high soil phosphorus levels (Ikutha-2 in Chapter 2). However, it remains unclear why the high levels in the oldest leaves were absent in 1990 (figure 3-1C).

The difference in growth of the maize plants at the two locations showed that the watering prior to the start of the short rainy season was clearly not sufficient for optimal growth at Maliku. This is underlined by the rapid growth between day 11 and 19 (i.e. 21 and 29 days after germination respectively, figure 3-2B), when the rains had wetted the clay soil thoroughly, thus enabling the roots to extend throughout the soil. In spite of this rapid growth, the nitrogen level increased during this period (figure 3-2). Rainfall, especially on day 12 and 14 (figure 3-3B), which increased soil nitrate to a very high level of about 20 mg/kg dry soil, should be held responsible for this. Phosphorus and especially potassium could not be supplied sufficiently to prevent a decrease in these minerals between day 11 and 19 (figure 3-2).

Also at Katulani, rainfall influenced plant nitrogen concentrations in both years. In 1989 the dip in nitrogen on day 18 (i.e. 13 days after germination, figure 3-1A) followed heavy rainfall between day 12 to 14 (figure 3-3A). As the nitrogen level subsequently recovered in spite of more rain, on one occasion even almost 25 mm, it seems that downpours of 40 mm or more
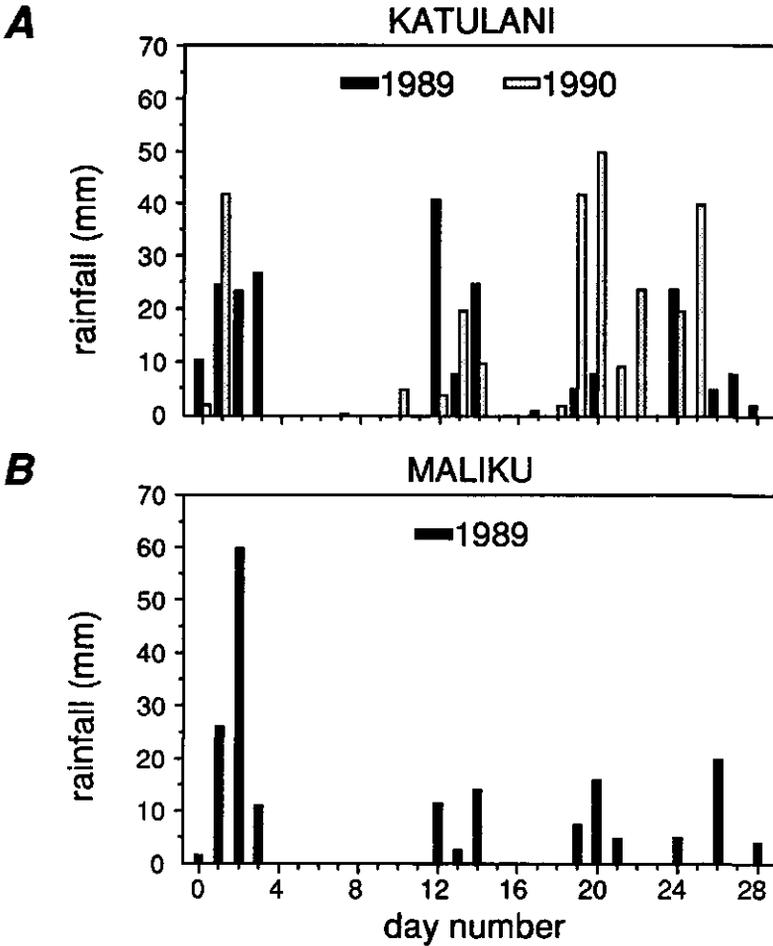
Figure 3-3. Rainfall pattern of daily totals during the first month after the start of the short rainy season for **A.** Katulani in 1989 and 1990, and **B.** Makindu in 1989.

are required to influence plant nitrogen levels. This is confirmed by the pattern observed in 1990, when heavy rainfall between day 19 to 25 (figure 3-3A) caused the plant nitrogen concentration to drop rapidly to a very low level on day 24 and 28 (figure 3-1A). More pronounced, these changes in plant nitrogen due to rainfall were reflected in plant nitrate, and even potassium seemed to be slightly affected. Phosphorus was not influenced.

Because growth of the maize plants was identical in both years at Katulani (figure 3-1A), excessive rain must have influenced plant nitrogen levels via its effect on soil nitrate availability. Soil nitrate is easily leached to deeper layers, and when soils become saturated with water some nitrate might be lost through denitrification. Janssen (see Chapter 2) also found substantial evidence for a strong influence of excessive rainfall on soil nitrate levels.

In plant nutritional studies of maize, mineral concentrations are virtually always determined in samples of all leaves combined (e.g. Mederski & Wilson, 1960; Chevalier & Schrader, 1977; Uriyo & Singh, 1978). Rarely, variation in concentrations over leaves within a maize plant has been measured. Hanway (1962) found a distinct gradient over leaves in maize plants less than one month old, with highest concentrations for nitrogen, phosphorus and potassium in the youngest leaves. The gradient was least distinct for nitrogen. These findings agree well with the results obtained in the present study.

Janssen (see Chapter 4) used this intraplant variation in mineral concentrations in a laboratory study on host plant quality, also separating leaves in three sections. The distribution of potassium over leaves and the gradients in nitrogen, potassium and water content within leaves he found are identical to those observed in the present study; for unknown reasons, the gradient in phosphorus within leaves generally differed between both studies. His finding that nitrogen or phosphorus peaks in the leaf which became full-grown most recently when its supply is abundant compared to the other mineral, is not confirmed by the patterns observed under field conditions at Katulani and Maliku (figure 3-1 and 3-2). Especially the nitrogen peak in older leaves at Katulani in 1990, when nitrate availability to the plants was low, disagrees with this finding. Phosphorus concentrations might have been too low for it not to peak in the youngest leaves; the excessively high values of up to 1.3% found by Janssen (see Chapter 4) never occurred in field samples, even not at Katulani.

In host plant quality studies in which whole maize plants are used it is important to recognize that the maximum nitrogen, phosphorus and potassium concentration in a leaf part can deviate by up to 40% from the average for all leaves combined (table 3-2). Especially when not all food material

offered is consumed by herbivores, they might perform better than expected due to selective feeding.

As in wild grasses (see Chapter 2), nitrogen, phosphorus and potassium decreased over time in maize in Kitui District. Highest levels of these minerals as well as of water were found in youngest maize plants, with generally little spatial variation in all four plant constituents over the leaves (figure 3-1 and 3-2). For older maize plants, spatial variation over leaves was usually much higher. When considering the largest intraplant spatial variation measured at Katulani (i.e. over leaf parts) and Maliku (i.e. over leaves), the decrease over time for potassium and water was fully offset by their intraplant spatial variation: the highest concentration of these plant constituents found in a leaf or leaf part at the final sampling date was always close to and sometimes even higher than the plant average at the first sampling date. For phosphorus, only the high initial plant average in both years at Katulani was not covered by the intraplant spatial variation at the last sampling date. Nitrogen in 1990 at Katulani yielded the clearest example of lack of compensation by intraplant spatial variation for a decrease over time in a plant constituent: its spatial variation at the last two sampling dates did not cover the plant averages of the first three sampling dates. Clearly, rather large decreases in the plant constituents over time are required to prevent full compensation by intraplant spatial variation. These seem to be rare during the first month after the start of the short rainy season.

The usual concurrence of first moth activity of the African armyworm with the first rains of the short rainy season (see Chapter 2) assures that caterpillars will encounter wild grasses and maize plants containing high concentrations of nitrogen, phosphorus and potassium to feed on. Peak larval hatch on day 6 confronts the first instars with the youngest, softest and most nutritious (e.g. with highest levels of nitrogen, phosphorus and potassium) stages of their host plants. However, even caterpillars hatching later than day 6 during the first month of the short rainy season can generally still feed on plant material containing almost similar levels of these minerals due to their large intraplant spatial variation; only in 1990, caterpillars hatching three weeks after the start of the short rainy season would not have been able to feed on nitrogen levels encountered by larvae on day 6.

The main problem for caterpillars hatching later is to locate their optimal food quality. Maximization of all three minerals simultaneously is impossible in older maize plants as their maximum levels are found in different leaves or leaf parts. Old leaves are certainly of low quality; highest concentrations of phosphorus occur in the youngest leaves, and of nitrogen and potassium in the top respectively base of the leaf which is almost full-grown. Under laboratory conditions first instars preferred the rapidly growing leaves below the whirl in 5-weeks old maize plants, clearly avoiding the youngest leaf (unpublished results). B. Persson (unpublished report) found a preference of fifth instars for these leaves under field conditions. These observations indicate that larvae do choose those leaves containing highest levels of nitrogen and potassium, and reasonably high levels of phosphorus.

As larval duration lasts 12 to 14 days in Kitui District (see Chapter 2), food up to about day 20 is of interest to the caterpillars hatching on day 6. Each caterpillar needs about 4 gram of fresh leaf material to complete its development, of which about 3 gram is consumed during the final 3 to 4 days (see Chapter 4). Taking into account a slower growth of a maize plant subject to caterpillar feeding, the leaf fresh weight of 7 gram per plant at day 20 (figure 3-1A) seems barely enough food for one caterpillar. Thus, most probably armyworms must feed on several host plants during the final days of their development. Avoiding the large intraplant spatial variation in food quality in their environment has then become impossible as well.

Acknowledgements

4

Effects of the mineral composition and water content of excised leaf sections on the fitness of the African armyworm [1]

Abstract

The effects of intraplant variation of nitrogen, phosphorus, potassium and water content within maize plants on fitness of the African armyworm, *Spodoptera exempta* (Walker), was studied in three experiments by using an excised leaf system. Maize plants were phosphorus deficient in one of the experiments. Various leaf categories were distinguished differing in age and position on the plants. Leaf sections on which caterpillars fed were daily refreshed. Changes in the four plant variables measured, due to the excision and subsequent placement of the leaf sections in the excised leaf system for one day, were small and mostly insignificant. Very significant differences were found between the composition of the various leaf categories in all three experiments. Over all experiments, nitrogen concentrations ranged from 2.4 to 4.1%, phosphorus from 0.1 to 1.3%, and potassium from 1.4 to 4.8% dry weight, while water content varied from 83 to 90% fresh weight. Of all insect fitness parameters observed, only larval growth rate was consistently and significantly affected by leaf category. Fecundity was strongly correlated with pharate adult weight. Only for phosphorus were significant positive correlations found with larval fresh weight, especially in the experiment with phosphorus deficient plants. Multiple regression models revealed that in all experiments a significant part of the variation in larval fresh weight between the leaf categories could be explained by the four plant variables, of which only phosphorus

was included in all models. Lumping of all leaf categories used in the three experiments again stressed the importance of phosphorus for larval growth rate in these experiments, further showing that variation in nitrogen, potassium and water was of little or no significance. The consequences of these findings for outbreak development of the African armyworm are discussed.

Introduction

Larvae of the African armyworm feed almost exclusively on plants of the families Gramineae and Cyperaceae (Brown, 1962; Brown & Dewhurst, 1975). They periodically reach very high densities causing extensive and severe damage to crops, including maize, sorghum, millet and rice, as well as to pasture and rangeland grasses (Odiyo, 1979). Though occasional outbreaks have been reported from elsewhere, it is especially the east side of the African continent where the species is a major agricultural problem (Haggis, 1986).

Spectacular differences between years in outbreak development of the African armyworm have been observed in eastern Africa (Brown, 1962; Odiyo, 1979; Haggis, 1986) and it was hypothesized that these differences are due to differences in host plant quality between years (Janssen & Rose, 1990). Especially plant nitrogen, which is often thought to be of key importance in the nutritional ecology of herbivores (McNeill & Southwood, 1978; Scriber & Slansky, 1981; Mattson & Scriber, 1987), was predicted to have a strong impact on armyworm fitness. Validation of this prediction was the main objective of this study.

Though the importance of host plant quality for outbreak development of the African armyworm has often been recognized (van der Goot, 1931; Hattingh, 1941; Khasimuddin & Lubega, 1979), hardly any experimental evidence is available to support this relationship. Yarro (1984a, 1984b, 1985) compared insect performance on different host plant species, also measuring plant nitrogen in one study (Yarro, 1984b). His results suggested that larvae developed better on hosts containing more nitrogen. Larval development and survival on various maize cultivars were determined in a study on host plant resistance, in which the causes of the found differences were not thoroughly

addressed (Okello-Ekochu & Wilkins, 1988). In all instances excised leaves were used without supplementation of water, inevitably leading to dehydration and accelerated senescence of the leaf tissues. This is undesirable as water content of the leaves might be an important factor influencing insect performance (Scriber, 1977, 1979).

In the present study the effects of intraplant variation of nitrogen, phosphorus, potassium and water content within maize plants of the same cultivar on fitness of the African armyworm was studied in three experiments by using an excised leaf system. Naturally occurring variation in the composition of leaf categories differing in age and position within a maize plant was used to confront larvae with different levels of the four plant variables.

Materials and methods

EXPERIMENT 1

Plants. Maize plants (Zea mays L. cv. Katumani) were sown in Mitscherlich pots in an experimental glasshouse at 25°C(L):20°C(D), RH 60±10% and under natural day-length conditions (May-June in the Netherlands). Additional artificial light was provided by SONT lamps yielding a light intensity of 40±10 W/m^2 (12 h(L):12 h(D)).

The day before sowing, Mitscherlich pots were filled with a mixture of 6 kg dried phosphorus-poor loamy soil and 720 ml demineralized water. On the day of sowing, another 720 ml of demineralized water were added in three equal portions in order to reach the proper water capacity level. Subsequently pots were weighed and during the crop growing period their weights were checked regularly and kept constant by adding demineralized water after correction for crop weight. The loamy soil was collected near Eysden (the Netherlands) in 1983 and relevant soil properties are: pH$_{H_2O}$ 6.0, organic carbon (according to Kurmies; see Mebius, 1960) 1.69%, total nitrogen 1.04 g/kg, total phosphorus 0.42 g/kg.

One maize plant was grown per pot and pots were sown for 16 days. The leaves along the stem were numbered from stem base to top, making the lowest and thus oldest leaf of a plant leaf 1. The growth of the maize plants planted on the first day (n=12) was accurately followed by measuring their leaf lengths until a leaf became full-grown. Maize plants of similar age

(31 days from germination) were harvested just after the length of all their leaves had been measured in order to assess the physiological age of the plants. At harvest six categories of leaf material were carefully excised: the top 25 cm (0-25 cm) of leaf 5, 6, 7 and 8, and the middle (25-50 cm) and base (50-75 cm) 25 cm of leaf 6.

Immediately upon excision the leaf sections of each category (n≥3) were transferred to tubes containing demineralized water, fresh weighed, and placed in three units of the excised leaf system (figure 4-1). During one day caterpillars could feed on them (treatment '+caterpillars'), whereupon they were replaced by newly excised leaves, fresh weighed, dried at 70°C in a stove, and dry weighed. A blank without caterpillars (treatment '-caterpillars') and of leaves not placed in the excised leaf system (treatment 'blank') were included approximately every two days to obtain information about changes in the leaf sections (n=3 for both treatments) over time and during the day they were standing in the excised leaf system.

The leaf sections of the same category and treatment were lumped for fresh and dry weight measurements and for subsequent chemical analysis. Total nitrogen, phosphorus and potassium contents of all leaf samples were determined after Novozamsky et al. (1983).

Insects. A culture of the African armyworm was maintained on standing 2-weeks old wheat seedlings (*Triticum aestivum* L. var. Okapi) at 25°C, RH 90%, 12 h(L):12 h(D) and a light intensity of 10 W/m^2. The seedlings, which were grown on paper towel in a glasshouse under a light intensity of 25 W/m^2, were refreshed every 2-4 days. Pupation took place in sterilized river sand from which pupae were subsequently sieved. Moths could feed on a 10% sugar solution while kept in large plastic containers of which the walls were covered with paper as a substrate for oviposition.

On day 0, ten neonate larvae were released per unit of the excised leaf system. They were offered leaf sections of one of the six food categories on which they could feed *ad lib* and which were refreshed daily. Leaf fresh weight eaten per caterpillar per day was estimated by dividing the decrease in fresh weight of the leaf sections by the average number of live caterpillars feeding on them during that day. Total larval fresh weight and survival were assessed daily for each unit up to day 16. On day 11, all caterpillars were weighed individually. When caterpillars in a unit were nearing pupation, the
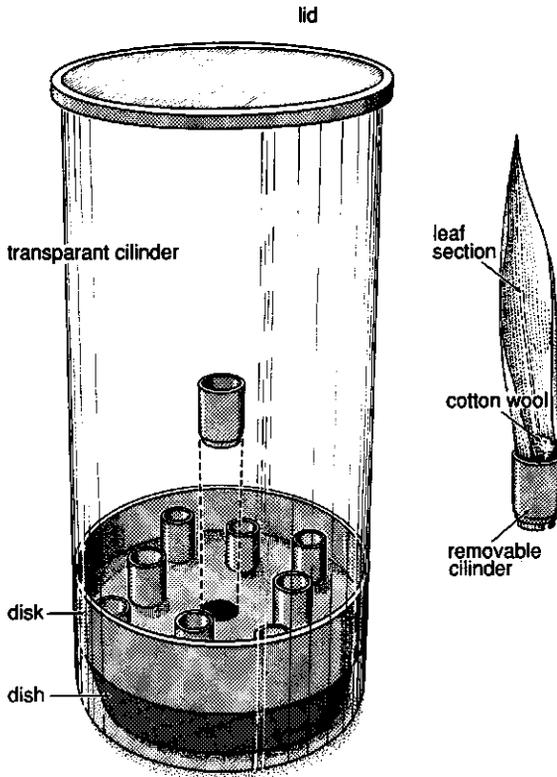
Figure 4-1. A unit of the excised leaf system. Leaf sections were placed in small removable cylinders (diam. 2.0 cm, 2.5 cm high) located in holes in a plastic disk (diam. 22 cm, standing edge 4 cm). The remaining openings in the small cylinders were filled with cotton wool. The plastic disk was placed on top of a plastic dish containing demineralized water, thus immersing the base of the excised leaf sections. A transparent plastic cylinder (diam. 22 cm, 50 cm high) tightly fitting around the plastic disk, with a lid of nylon netting (mesh-width 0.3 mm) on top providing air ventilation, prevented the caterpillars from escaping.

plastic disk (figure 4-1) was filled with sterilized river sand as a substrate for pupation. The plastic disks holding river sand were replaced daily and three days after pupation pupae were sieved out. Due to the experimental design all caterpillars developed into the gregarious phase. The experiment was run

in triplicate in a climate room at 25°C, RH 60%, 16 h(L):8 h(D) and a light intensity of 25 W/m^2.

EXPERIMENT 2

As experiment 1, with the following differences.

Plants. The most important difference was the addition of 40 g P$_2$O$_5$/pot during the crop growing period in order to supply the maize plants with sufficient phosphate. The light intensity in the experimental glasshouse was 65±10 W/m^2 (July-August) and three maize plants were grown per pot. The treatments '-caterpillars' and 'blank' were included daily. Maize plants of similar physiological age (leaf 10 visible in whirl, about 33 days from germination) were harvested while ten categories of leaf material were distinguished: the top 25 cm of leaf 5, 6, 7, 8 and 9, the middle 25 cm of leaf 6, 7 and 8, and the base 25 cm of leaf 6 and 7.

Insects. Caterpillars were not weighed individually on day 11. Pupae were placed singly in transparent plastic cups (250 ml) at 25°C, RH 90%, 12 h(L): 12 h(D) and a light intensity of less than 3 W/m^2. Pharate adult weights were measured within 6 h before eclosion, which can be anticipated by the darkening of the pupal cuticle (Gunn & Gatehouse, 1985). Eclosion generally occurred at night. Moths were placed in pairs on the following morning, and were provided with filter paper as a substrate for oviposition and with demineralized water presented on cotton wool plugs in small 4 ml plastic pots which were renewed daily. In order to provide each female with a male from eclosion, individuals from different treatments sometimes had to be paired. All eggs were removed and counted, and females were dissected at death to see whether they had mated properly. Any moth which failed to eclose properly, failed to free itself after mating or in which a spermatophore was not or only partially inserted, was excluded. For each moth the longevity and for each female the preoviposition period and fecundity were recorded.

EXPERIMENT 3

Experiment 3 was run simultaneously with experiment 2, to which it was identical except for the following differences.

Plants. At harvest sixteen categories of leaf material were carefully excised: the top and middle 25 cm of leaf 4, 5, 6, 7, 8 and 9, and the base 25 cm of leaf 5, 6, 7, and 8.

Insects. On day 0 (day 10 in experiment 2) thirty neonate caterpillars were released per unit of the excised leaf system while no replicates were run. Total fresh weight, survival and larval stage were daily assessed up to day 6, on which all caterpillars were also weighed individually.

Results

Plants. Because identical plants were used in experiment 2 and 3, the data of the leaf variables obtained in these experiments could be lumped for comparison with experiment 1. Preharvest leaf growth, as measured by length, of the maize plants showed a linear increase over time for all leaves until a few days before reaching their maximum length (figure 4-2). At harvest the physiological age of the different leaves clearly differed: while leaf 6 had just reached its full-grown size, leaf 4 had been senescing for about 2 weeks and leaf 8 was still growing rapidly in all experiments. However, the plants used in experiment 2 and 3 were significantly more advanced in their development at harvest than those used in experiment 1 (table 4-1). Though the latter were two days younger, comparison of the length of leaf 8, 9 and 10 on day 30 in both graphs of figure 4-2 shows that this difference in absolute age could not fully account for the observed difference in physiological age at harvest. Moreover, the full-grown sizes of leaf 5 and 6 used in experiment 1 were significantly smaller than in experiment 2 and 3 (table 4-1).

The maize plants in experiment 1 were deficient in phosphorus which first became visible as a brownish discoloration and subsequent premature senescence of leaf 1 about two weeks from germination, generally affecting leaves 2 and 3 as well before harvesting. Due to the addition of phosphorus fertilizer, these deficiency symptoms were not observed in experiment 2 and 3.

Comparison of the nitrogen, phosphorus and potassium concentrations in the leaf samples at harvest reflects this difference in phosphorus nutrition of the maize plants between experiment 1 and experiment 2 and 3 (figure 4-3 and table 4-2). Phosphorus concentrations were extremely low in all leaf categories used in experiment 1 and were high in experiment 2 and 3, the
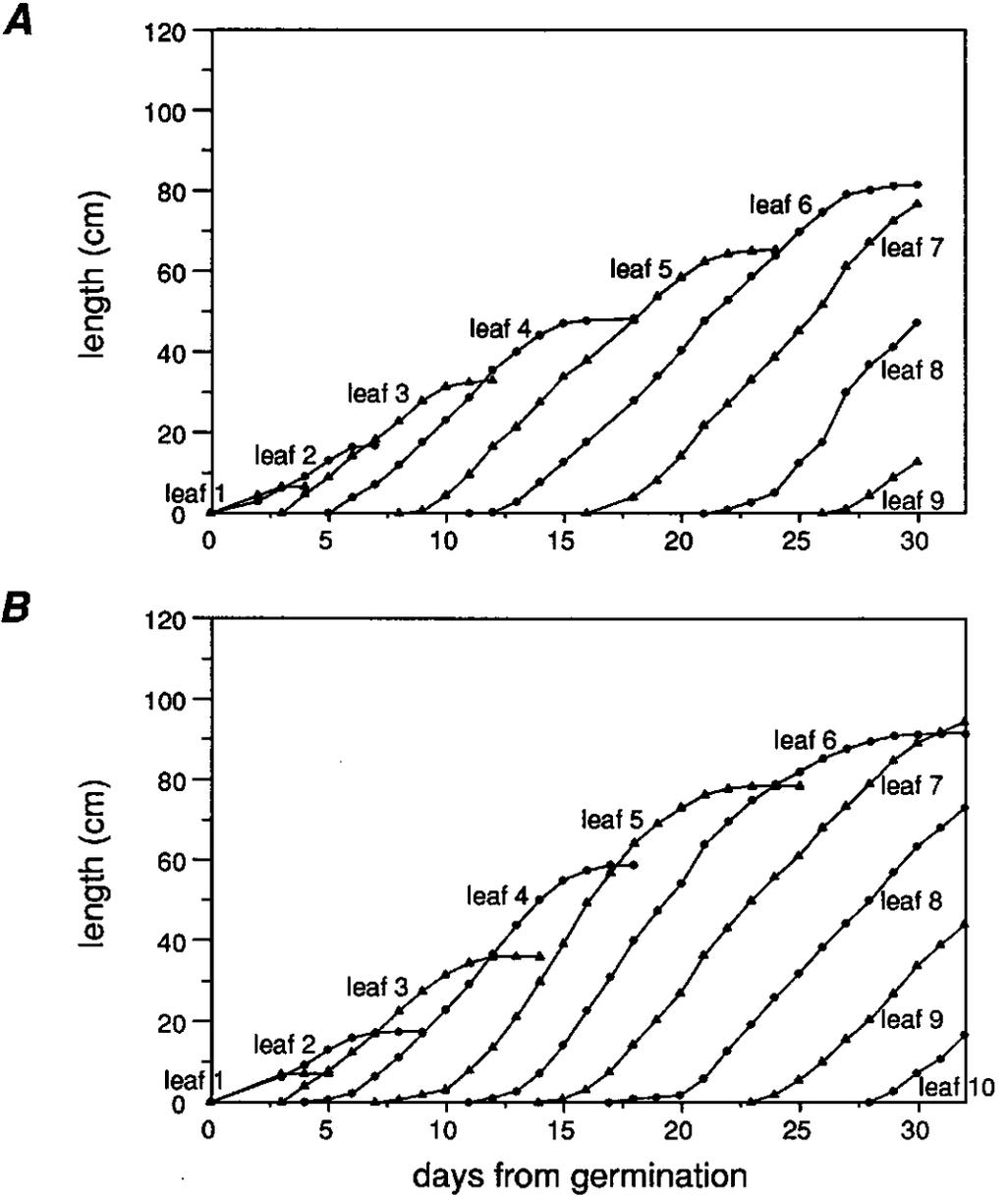
Figure 4-2. Leaf length from germination until harvest of the maize plants (n=12) planted on the first day for **A**. Experiment 1, and **B**. Experiment 2 and 3. Triangles for uneven leaf numbers, circles for even leaf numbers.

Table 4-1. Comparison of the leaf lengths at harvest between the plants used in experiment 1 and in experiment 2 and 3. Standard errors are given in brackets.

	experiment 1	experiment 2 and 3	P
∎No. of days	16	16	
Leaf 5	73.3	81.2	***
	(0.6)	(0.6)	
Leaf 6	82.7	97.2	***
	(1.0)	(0.8)	
Leaf 7	65.7	103.2	***
	(3.0)	(0.9)	
Leaf 8	31.4	82.8	***
	(3.5)	(1.0)	
Leaf 9	3.8	50.5	***
	(1.7)	(1.0)	

Values for the same leaf were compared by t-test (***: $P<0.001$).

Table 4-2. Comparison of leaf variables in the blank treatment between experiment 1 and experiment 2 and 3. Leaf categories only used in experiment 2 and 3 are excluded. Standard errors are given in brackets.

	experiment 1	experiment 2 and 3	P
∎No. samples	53	96	
Water (% fresh wt.)	86.3	84.8	***
	(0.3)	(0.2)	
Nitrogen (% dry wt.)	4.34	3.64	***
	(0.06)	(0.06)	
Phosphorus (% dry wt.)	0.14	1.12	***
	(0.01)	(0.02)	
Potassium (% dry wt.)	3.42	1.85	***
	(0.13)	(0.05)	

Values for the same leaf variable were compared by t-test (***: $P<0.001$).

difference being highly significant. The nitrogen, potassium and water content were significantly lower in experiment 2 and 3 (table 4-2).

When the supply of phosphorus to the maize plant was adequate, its concentration peaked in leaf 6, the leaf which became full-grown most recently (figure 4-2B), and decreased towards the oldest as well as the youngest leaf (figure 4-3). With deficient supply, the peak shifted to younger leaves. This is in contrast to the concentration of nitrogen which peaked in leaf 6 in experiment 1 and which peak shifted to younger leaves in experiment 2 and 3. Potassium always peaked in the youngest leaves. Independent of the nutritional status of the plants, the nitrogen and phosphorus level decreased and the potassium and water level increased from top to base in a leaf (figure 4-3).

Comparison of the leaf samples between the two treatments without caterpillars shows that nitrogen, phosphorus, potassium and water concentrations always decreased during the day the leaf sections were standing in the excised leaf system (table 4-3). None of these changes was significant in all three experiments. While the decreases in mineral concentrations of the leaf sections can only be attributed to an increase in dry weight of the leaf sections as a consequence of their ongoing metabolism during the day in the excised leaf system, changes in water content will be influenced by changes in fresh weight as well. Based on an average dilution of the minerals, it can be estimated that the dry weight of the leaf sections increased by 9%, 4% and 4% in experiment 1, 2 and 3 respectively. Simultaneously, on average over all leaf categories the fresh weight decreased by 1%, 3% and 3% in the respective experiments. These changes in dry and fresh weights reinforce each other in the water content.

Comparison of the two treatments only differing in the presence of the caterpillars for experiment 3 reveals that caterpillar feeding during the first six days was too small to affect the leaf composition significantly (table 4-3). Generally less than 25% of the leaf material offered at day 6 was consumed by the caterpillars. Even for experiment 1 and 2, in which feeding damage towards the end of the 16-day period increased to 50-70% of the offered leaf material at anyone day, leaf variables were not always significantly changed by caterpillar feeding. This lack of differences indicates that the variation in composition within the leaf samples offered to the caterpillars was small.
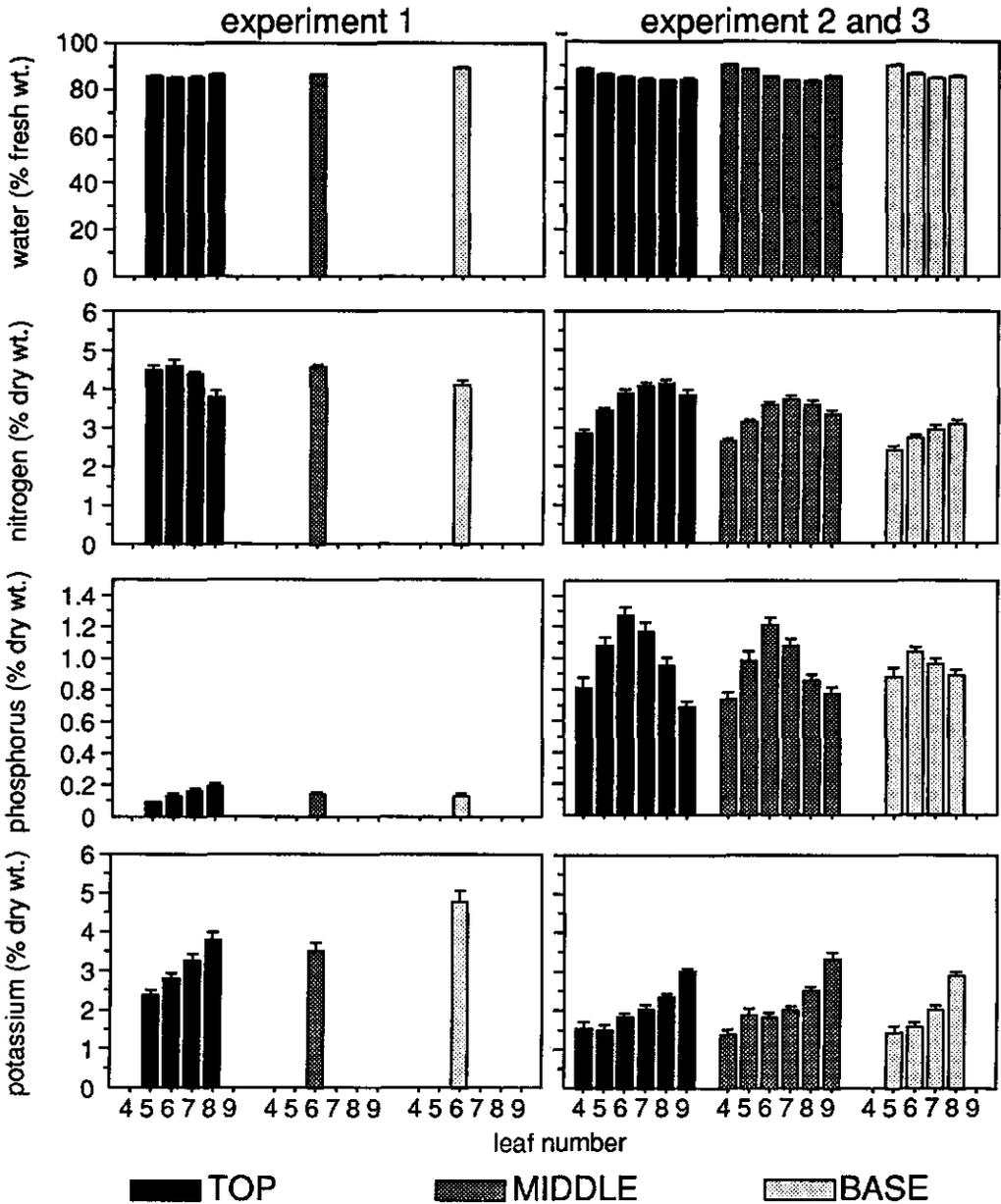
Figure 4-3. Levels of nitrogen, phosphorus, potassium and water for all leaf categories in the blank treatment of experiment 1 (n=9) and experiment 2 (n=16) and 3 (n=6). Standard errors are indicated.

Table 4-3. Comparison of leaf variables between the treatments during the full duration of experiment 1, 2 (both 16 days) and 3 (6 days only). All leaf categories are included. Standard errors are given in brackets.

	+caterpillars		-caterpillars		blank		P
EXPERIMENT 1							
■No. of samples	95		51		53		
Fresh weight (g/leaf)	0.828	a	0.861	a	0.848	a	n.s.
	(0.042)		(0.059)		(0.056)		
Water (% fresh wt.)	85.3	b	85.4	ab	86.3	a	*
	(0.2)		(0.3)		(0.3)		
Nitrogen (% dry wt.)	3.96	a	4.13	ab	4.34	b	***
	(0.04)		(0.07)		(0.06)		
Phosphorus (% dry wt.)	0.13	a	0.12	a	0.14	a	n.s.
	(0.00)		(0.00)		(0.01)		
Potassium (% dry wt.)	3.34	a	3.11	a	3.42	a	n.s.
	(0.09)		(0.09)		(0.13)		
EXPERIMENT 2							
■No. of samples	160		160		160		
Fresh weight (g/leaf)	1.126	a	1.153	a	1.137	a	n.s.
	(0.034)		(0.036)		(0.036)		
Water (% fresh wt.)	81.8	c	83.5	b	84.3	a	***
	(0.1)		(0.1)		(0.1)		
Nitrogen (% dry wt.)	3.30	a	3.56	b	3.59	b	***
	(0.04)		(0.04)		(0.04)		
Phosphorus (% dry wt.)	1.00	b	0.95	a	1.03	b	**
	(0.02)		(0.01)		(0.02)		
Potassium (% dry wt.)	1.96	a	2.04	a	2.07	a	n.s.
	(0.04)		(0.04)		(0.04)		
EXPERIMENT 3							
■No. of samples	96		96		96		
Fresh weight (g/leaf)	1.092	a	1.076	a	1.076	a	n.s.
	(0.040)		(0.039)		(0.039)		
Water (% fresh wt.)	83.9	b	84.3	b	86.0	a	***
	(0.2)		(0.2)		(0.2)		
Nitrogen (% dry wt.)	3.50	a	3.38	a	3.41	a	n.s.
	(0.05)		(0.05)		(0.06)		
Phosphorus (% dry wt.)	0.90	a	0.93	ab	0.98	b	*
	(0.02)		(0.02)		(0.02)		
Potassium (% dry wt.)	1.94	a	2.02	a	2.15	a	n.s.
	(0.06)		(0.06)		(0.06)		

Data were analysed by oneway ANOVA (n.s.: $P>0.05$; *: $P<0.05$; **: $P<0.01$; ***: $P<0.001$) followed by Tukey's multiple range test. Different letters within a horizontal row indicate significant differences ($P<0.05$).

Insects. During the first day of larval development the amount of leaf fresh weight eaten by the caterpillars was very small (figure 4-4A) and could therefore easily be overestimated as a result of a decrease in fresh weight of the leaf sections while standing in the excised leaf system due to slight dehydration. As caterpillars grew older and ate more, the relative importance of this error in the estimated leaf fresh weight eaten per caterpillar was bound to decrease and to become insignificant during the last days of larval development.

In experiment 1, however, the trend between the leaf categories in the cumulative amount of leaf fresh weight eaten per caterpillar that emerged during the first 6 days hardly changed thereafter; at the end of the experiment the amount of leaf material eaten decreased from leaf 8 to 5 for the top sections and from base to top within leaf 6. More clearly, a similar trend was visible in the fresh weight of the caterpillars (figure 4-4). Larval fresh weight at day 11 was measured for the individual caterpillars and revealed a highly significant difference in larval growth rate between the leaf categories (table 4-4); as on average caterpillar fresh weight tended to double every day, it can be derived that the caterpillars on the top section of leaf 5 lagged behind in their development to those developing on the top section of leaf 8 by about 5 days. Faster larval growth in a leaf category resulted in earlier occurrence of the first pupation; while none of the caterpillars feeding on the top section of leaf 5 and 6, the two leaf categories of poorest quality, had pupated at the end of the experiment, all caterpillars feeding on the top section of leaf 8 had (figure 4-4B and table 4-4). Because of this complete pupation on the top section of leaf 8, the amount of leaf fresh weight eaten by one caterpillar during its whole larval period can be estimated to have been about 4000 mg (figure 4-4B). Just prior to pupation individual caterpillars weighed between 500 and 800 mg.

Differences in caterpillar performance between the various leaf categories of this size were not found in experiment 2 and 3, in which caterpillars developed faster (table 4-4). While caterpillar weight at day 6 differed significantly between the leaf categories in all experiments, survival at day 6 only did in experiment 1 due to high larval mortality (63%) on the top section of leaf 5. As a result of the differences in growth rate of the larvae, highly significant differences were found in the percentage pupation at the end of experiment 1 and 2 and in the average instar at the end of experiment 3.

Table 4-4. Insect variables for all leaf categories used in experiment 1, 2 and 3. Standard errors are given in brackets.

Leaf part	TOP						MIDDLE						BASE				P[1]
Leaf number	4	5	6	7	8	9	4	5	6	7	8	9	5	6	7	8	
EXPERIMENT 1																	
■No. of replicates	0	3	3	3	3	0	0	0	3	0	0	0	0	3	0	0	
Weight at day 6 (mg)[2]		1.4 (0.3)	2.7 (0.2)	6.4 (1.3)	9.9 (2.4)				3.8 (0.7)					4.9 (0.8)			*
Survival at day 6 (%)[3]		37 (9)	87 (9)	87 (3)	97 (3)				80 (6)					83 (12)			***
Pupation at day 16 (%)		0 (0)	0 (0)	73 (18)	100 (0)				53 (13)					87 (7)			***
■No. of individuals		11	24	18	15				23					23			
Weight at day 11 (mg)		13.2 (4.2)	36.2 (5.6)	94.4 (11.7)	272.0 (28.2)				58.1 (7.0)					81.4 (6.4)			***
■No. of individuals		0	0	11	15				8					13			
Pupal weight (mg)				171.9 (13.9)	151.4 (6.0)				157.6 (5.5)					155.0 (6.6)			n.s.
EXPERIMENT 2																	
■No. of replicates	0	3	3	3	3	3	0	0	3	3	3	0	0	3	3	0	
Weight at day 6 (mg)		12.3 (1.0)	17.6 (3.9)	11.2 (2.2)	10.7 (4.4)	4.6 (0.3)			8.5 (0.7)	6.1 (0.5)	6.5 (1.4)			9.0 (2.6)	6.7 (0.9)		*
Survival at day 6 (%)		80 (6)	87 (9)	90 (0)	86 (4)	70 (6)			90 (6)	67 (7)	61 (3)			79 (7)	73 (3)		n.s.
Pupation at day 16 (%)		100 (0)	100 (0)	68 (11)	93 (7)	73 (20)			44 (12)	37 (19)	89 (11)			29 (23)	81 (12)		***
■No. of individuals		22	17	12	15	8			6	6	13			3	6		
Pupal weight (mg)		143.0 (4.2)	147.7 (3.3)	137.6 (8.8)	142.4 (6.5)	165.6 (6.5)			121.2 (9.4)	143.4 (6.1)	146.8 (9.5)			76.7 (10.6)	123.3 (11.5)		**

Table 4-4, *continued.*

| Leaf part | TOP | | | | | | MIDDLE | | | | | | BASE | | | | P |
Leaf number	4	5	6	7	8	9	4	5	6	7	8	9	5	6	7	8	
Larval duration (days)		13.7 (0.2)	11.9 (0.2)	12.5 (0.3)	13.5 (0.3)	14.4 (0.2)			13.2 (0.7)	13.8 (0.3)	13.8 (0.3)			14.0 (1.0)	13.7 (0.6)		**
Pupal duration (days)[4]		9.5 (0.1)	9.9 (0.1)	10.1 (0.1)	9.6 (0.1)	10.3 (0.2)			10.3 (0.3)	9.7 (0.3)	9.8 (0.2)			10.0 (0.6)	9.7 (0.2)		*
Larval-pupal duration (days)		23.2 (0.3)	21.8 (0.2)	22.6 (0.3)	23.1 (0.3)	24.6 (0.2)			23.5 (0.8)	23.5 (0.5)	23.6 (0.3)			24.0 (0.6)	23.3 (0.8)		***
Adult longevity (days)		7.1 (0.4)	7.0 (0.6)	6.2 (0.7)	6.5 (0.4)	8.1 (0.3)			6.3 (0.9)	7.3 (0.7)	7.1 (0.6)			3.7 (0.7)	6.3 (0.6)		n.s.
■No. of females		14	3	4	8	3			2	4	7			1	0		
Preoviposition period (days)		2.9 (0.3)	2.3 (0.3)	2.5 (0.5)	2.9 (0.4)	3.0 (0.6)			2.5 (0.5)	2.5 (0.3)	2.1 (0.1)			3.0			n.s.
Fecundity (eggs/female)		745 (77)	670 (223)	752 (184)	703 (175)	589 (27)			455 (272)	898 (145)	740 (156)			26			n.s.
Weight-related fecundity (eggs/mg)		4.99 (0.48)	4.33 (1.45)	4.92 (0.85)	4.48 (1.01)	3.60 (0.46)			3.12 (1.79)	6.06 (0.85)	4.67 (0.75)			0.28			n.s.
EXPERIMENT 3																	
■No. of individuals	26	28	28	24	22	26	26	28	25	27	19	25	23	27	26	26	
Weight at day 6 (mg)	5.6 (0.5)	9.5 (0.9)	12.6 (0.9)	11.8 (0.8)	12.8 (1.2)	8.8 (0.8)	8.6 (0.5)	9.7 (0.7)	11.3 (0.9)	12.1 (0.9)	12.4 (1.1)	10.5 (0.9)	13.5 (1.1)	11.7 (0.8)	14.8 (0.9)	13.6 (1.0)	***
Survival at day 6 (%)	87	93	93	80	81	87	87	93	86	93	83	83	77	93	90	87	n.s.
Instar at day 6	3.04 (0.04)	3.04 (0.04)	3.39 (0.09)	3.54 (0.10)	3.45 (0.11)	3.50 (0.10)	3.08 (0.05)	3.36 (0.09)	3.56 (0.10)	3.63 (0.09)	3.63 (0.11)	3.48 (0.10)	3.65 (0.10)	3.70 (0.09)	3.85 (0.07)	3.77 (0.08)	***

1 n.s.: P>0.05; *: P<0.05; **: P<0.01; ***: P<0.001.

2 All variables, except those expressed as a percentage, were analysed by the Kruskal-Wallis test.

3 Variables expressed as a percentage were analysed by the RxC test of independence using G-test (Sokal & Rohlf, 1981).

4 Includes the prepupal stage.
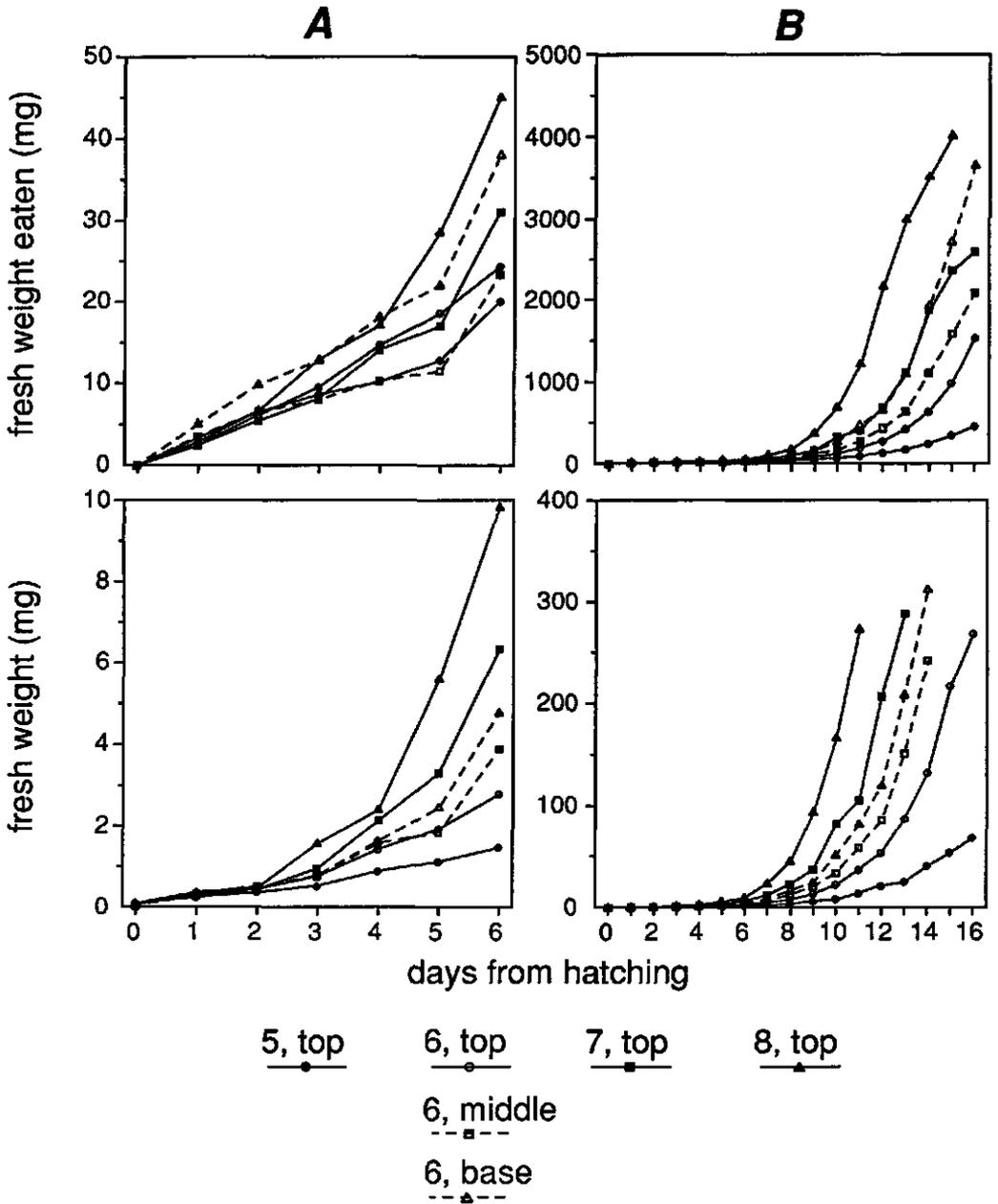
Figure 4-4. The cumulative amount of leaf fresh weight eaten per caterpillar and caterpillar fresh weight for the different leaf categories during **A.** the first 6 days only, and **B.** the total duration of experiment 1. Caterpillar fresh weight is only shown until the day of first pupation for each leaf category.

Table 4-5. Comparison of insect variables between females and males in experiment 2. Standard errors are given in brackets.

	females	males	P
■No. individuals	47	61	
Pharate adult weight (mg)	147.1	136.4	*
	(3.9)	(3.4)	
Larval duration (days)	13.6	13.0	*
	(0.2)	(0.2)	
Pupal duration (days)	9.4	10.1	***
	(0.1)	(0.1)	
Larval-pupal duration (days)	23.0	23.2	n.s.
	(0.2)	(0.2)	
Adult longevity (days)	6.5	7.0	n.s.
	(0.2)	(0.3)	

Values for the same insect variable were compared by Mann-Whitney U test (n.s.: $P>0.05$; *: $P<0.05$; ***: $P<0.001$).

As not all individuals had an opportunity to pupate in experiment 1 and 2, larval duration is biased. In addition, pupal and adult variables should be considered with some care. Contrary to the large difference in larval growth rate, adult weight was not significantly different between the leaf categories in experiment 1. The significant effect on adult weight found in experiment 2 was caused by premature pupation of some caterpillars feeding on certain leaf categories (middle section of leaf 6 and base section of leaf 6 and 7), due to virus infection which became apparent just prior to pupation. Larval development up to day 10 seemed not to be affected. In spite of the virus, other purely pupal and adult variables showed no significant difference between the leaf categories in experiment 2, except for pupal duration which varied between 9.5 and 10.3 days. However, as pupal duration differed very significantly between males and females (table 4-5), unequal numbers of the sexes in the various leaf categories was responsible for some of this variation. Males and females also differed significantly in adult weight (table 4-5). To reach their higher adult weight, females needed slightly but significantly

more time for larval development. As their pupal duration was equally shorter, larval-pupal duration was similar for both sexes. Adult longevity was also similar for both sexes. Moths usually lived for about 7 days and females started oviposition 2 to 3 days after eclosion (table 4-4).

Over all leaf categories, fecundity was significantly correlated with the pharate adult weight (figure 4-5). A logarithmic curve setting the potential fecundity at a certain pharate adult weight could be detected. Points below this curve represent females that did not realize their potential reproduction under the artificial experimental conditions. In the graph of the weight-related fecundity a maximum conversion efficiency of body mass to eggs of about 7 eggs/mg seemed to be reached at a pharate adult weight of 130 mg; females weighing less were decreasingly efficient in converting body mass into eggs (figure 4-5).

The plant-insect interaction. As very significant differences occurred in the levels of nitrogen, phosphorus, potassium and water between the leaf categories in all experiments (figure 4-3), the conditions were suitable for studying the dependence of armyworm fitness on food quality set by these plant variables. Although changes in the variables were usually insignificant during the day the leaf sections were standing in the excised leaf system (table 4-3), the average over the two treatments without caterpillars was used as their daily best estimate.

Of all insect variables measured, only larval weight differed significantly between the leaf categories in all experiments (table 4-4). Therefore, this variable was selected for correlation and regression analysis. Caterpillar weight at day 6 was selected because it was measured in all three experiments while showing the largest differences between leaf categories. In addition, caterpillar weight at day 9 was selected for experiment 1 and 2 because it was not influenced by pupation while showing the largest differences between leaf categories.

The correlation coefficients of caterpillar weight with the four plant variables representing food quality were calculated for each experiment separately and for all experiments combined (table 4-6). Only phosphorus had significant positive correlation coefficients, being significant at day 6 in experiment 1 and 2 and at day 9 in experiment 1. The only other significant correlations found in the separate experiments were for nitrogen in experi-
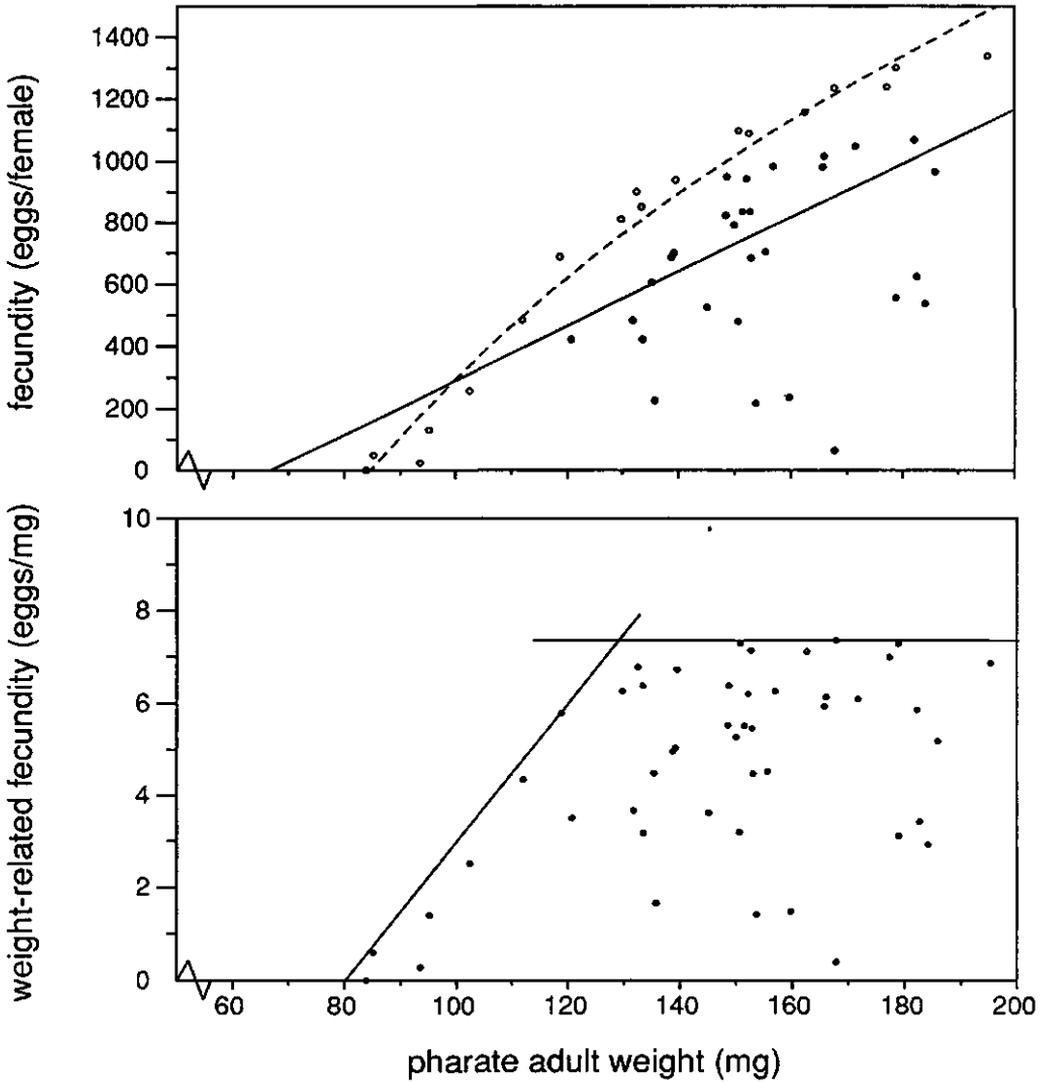
Figure 4-5. Fecundity and weight-related fecundity in relation to pharate adult weight for all leaf categories in experiment 2. In the upper graph, the solid line is the linear regression line of fecundity on pharate adult weight ($Y=-583.6+8.7X$, $r=0.646$, $n=47$, $p<0.001$). The dotted line is the logarithmic regression through a selection of points (open circles) setting the potential fecundity at a certain pharate adult weight ($Y=-7890.1+1776.8\ln X$, $r=0.987$, $n=18$, $p<0.001$). In the lower graph the lines are drawn by hand.

Table 4-6. Correlation matrix of caterpillar fresh weight at day 6 and 9 with plant nitrogen (N), phosphorus (P), potassium (K) and water (H_2O) content for experiment 1, 2, 3 and all three experiments combined. Plant variables were averaged over the first 6 and 9 days respectively. All correlations are Pearson correlations (*: $P<0.05$; **: $P<0.01$; ***: $P<0.001$).

	n	N		P		K	H_2O
EXPERIMENT 1							
Weight at day 6	6	-0.885	*	0.924	**	0.514	-0.318
Weight at day 9	6	-0.876	*	0.905	*	0.446	-0.199
EXPERIMENT 2							
Weight at day 6	10	0.328		0.733	*	-0.544	0.174
Weight at day 9	10	0.434		0.454		-0.206	-0.133
EXPERIMENT 3		.					
Weight at day 6	16	0.224		0.482		0.285	-0.466
EXPERIMENT 1, 2 and 3							
Weight at day 6	32	-0.332		0.720	***	-0.346	-0.193
Weight at day 9	16	0.347		0.580	*	-0.351	-0.414

ment 1, the sign of the correlations being negative. Lumping of all leaf categories used in the three experiments once again revealed the importance of phosphorus, the only plant variable correlating significantly with larval growth.

Because the plant variables studied were often mutually correlated, the results of the correlation analysis may not represent direct effects of the plant variables on caterpillar weight. To assess their separate effects, stepwise multiple regression analysis was performed (table 4-7). While in all experiments separately, as well as their combination, significant regression models were obtained, indicating that the observed differences in larval weights between the leaf categories could well be explained by the four plant variables, phosphorus was again the only variable included in all models. Water content was never included. Nitrogen was only included in the regression model for experiment 1, as a factor negatively influencing larval growth.

Table 4-7. Stepwise multiple regression (forward) for caterpillar fresh weight at day 6 on plant nitrogen (N), phosphorus (P), potassium (K) and water (H_2O) content in experiment 1, 2, 3 and all three experiments combined. Plant variables were averaged over the first 6 days. F-to-enter>4.00, F-to-remove<4.00.

VARIABLES IN THE MODEL	F-REMOVE	VARIABLES NOT IN THE MODEL	F-ENTER	P[1]
EXPERIMENT 1	$Y=18.88+6.24P-0.51N$	$R^2_{adj.}=0.99$		***
1. Phosphorus	65.00	3. Potassium	1.52	
2. Nitrogen	97.89	4. Water	0.75	
EXPERIMENT 2	$Y=-3.58+1.27P$	$R^2_{adj.}=0.48$		*
1. Phosphorus	9.28	2. Nitrogen	1.57	
		3. Potassium	0.61	
		4. Water	0.06	
EXPERIMENT 3	$Y=-2.04+1.00P+0.19K$	$R^2_{adj.}=0.35$		*
1. Phosphorus	8.21	3. Water	0.03	
2. Potassium	4.73	4. Nitrogen	3.32	
EXPERIMENT 1, 2 and 3	$Y=-3.77+1.02P+0.22K$	$R^2_{adj.}=0.57$		***
1. Phosphorus	33.81	3. Nitrogen	0.04	
2. Potassium	5.37	4. Water	1.23	

[1] Significance level for the full regression based on analysis of variance (*: P<0.05; ***: P<0.001).

Discussion and conclusions

Adequate concentrations of phosphorus in leaves of maize plants of the age used in the present study range from 0.3 to 0.5% (Hanway, 1962; Bingham, 1974). The level of 0.1% found in experiment 1 clearly indicates a suboptimal supply of this mineral to the maize plants. In contrast, phosphorus was available in excessive amounts in experiments 2 and 3 due to fertilization (table 4-3 and figure 4-3). These extreme differences in phosphorus availability most likely explain the differences in growth of the maize plants between experiment 1 and experiment 2 and 3 (figure 4-2), the difference in light intensity being of secondary importance.

As the maize plants used in experiment 2 and 3 grew better due to the fertilization, they were unable to obtain the nitrogen and potassium levels of experiment 1 (table 4-3 and figure 4-3). The distribution of nitrogen and phosphorus over the leaves indicates that the concentration of either of these minerals peaks in the leaf which became full-grown most recently when its supply is abundant compared to the other mineral; the peak shifts to younger leaves for the mineral which is relatively less available. In the extreme situation of a deficiency, nitrogen and phosphorus seem to peak in the youngest leaf. Whether this pattern is generally valid is unclear. At least for nitrogen it seems to be confirmed by Hanway (1962).

Advantages of the excised leaf system used in this study as compared to experimentation with excised leaves without supplementation of water, as has often been used in host plant quality studies (e.g. Slansky & Feeny, 1977; Yarro, 1984a, 1984b, 1985; Chang et al., 1987; Okello-Ekochu & Wilkins, 1988; Cohen et al., 1988), are obvious. In the first place and probably most important, larval performance can be studied on food which water content is not sharply decreasing during herbivore feeding. Secondly, relative humidity can be maintained at more normal levels for most herbivores. Excessively high humidity levels in closed containers, used in studies with excised leaves without supplementation of water to prevent severe dehydration of the plant material, might negatively affect herbivores either directly or indirectly by increasing disease incidence. Thirdly, caterpillars are less likely to come in contact with their faecal pellets as these drop down while they are feeding on the standing leaf sections, thus increasing hygiene. These advantages, likely to increase the relevance of the results obtained, outweigh the disadvantage of the excised leaf system of being more time consuming, especially in experiments with leaves that are very susceptible to dehydration.

Water content of the food has been shown to be an important factor influencing larval growth of many herbivores (Scriber, 1977, 1979). In the culture in which larvae of the African armyworm could feed *ad lib* on standing wheat seedlings, the first larvae burrowing for pupation were usually observed 10-12 days after hatching. This timespan is presumed to be a minimum for larval development at 25°C, only realized on food of optimal quality. When excised maize leaves without supplementation of water were

provided to larvae about once every 3 days, their development was extended by more than 10 days, survival hardly being affected (unpubl. data). This detrimental effect of dehydration of food on larval growth of the African armyworm could well explain the longer larval duration found when larvae were fed excised leaves not supplemented with water (ICIPE, 1974; Yarro, 1984b).

In the present study changes in the plant variables measured, occurring during the day the leaf sections were standing in the excised leaf system, were small and mostly insignificant (table 4-3). Leaf sections were daily refreshed as most changes in their composition are known to accelerate after the first 24 hours upon excision (van Loon, 1980). First pupations occurred on day 12 in experiment 1 (figure 4-4B) and on day 11 in experiment 2, indicating that larval development was optimal on some leaf categories in both experiments.

All plant variables measured differed significantly between the various leaf categories, between as well as within experiments (table 4-2 and figure 4-3). Within an experiment differences were due to variation in age between leaves and location within leaves of maize plants of similar physiological age. This intraplant variation has rarely been measured (Hanway, 1962) and has, to my knowledge, never been used to assess host plant quality.

Studies on the effect of leaf age on herbivores have shown that young leaves, either within a plant or in time, are often preferred and of better quality than old leaves (e.g. Schweitzer, 1979; Walker, 1987; Hoy & Shelton, 1987), and this can strongly influence the spatial distribution of herbivores on their host plants (Raupp & Denno, 1983; Denno & McClure, 1983). Van der Goot (1931) observed that larval development of the African armyworm was shorter on young maize plants compared to old ones. A decline in the nutritive quality of foliage with aging is often thought to be due to an increase in digestibility reducing compounds, like structural carbohydrates, lignin, silica and tannins, and a concomitant decrease in water content and available nutrients, especially nitrogen (Scriber, 1984; Mattson & Scriber, 1987). Qualitative allelochemicals (sensu Feeny, 1975) might be involved as well, though their influence on adapted herbivores is generally thought to be insignificant at naturally occurring concentrations (Rosenthal & Janzen, 1979). A gradient in foliage quality can also be expected within a leaf, as

Table 4-8. Ranges of plant nitrogen (N), phosphorus (P), potassium (K) and water (H_2O) content found in experiment 1, 2, 3 and all three experiments combined. For reference, the values of these plant variables in leaf samples of whole maize plants of similar physiological age (i.e. 9-10 leaves) collected at a field site in Kitui District, Kenya, are presented.

	N (% dry wt.)	P (% dry wt.)	K (% dry wt.)	H_2O (% fresh wt.)
EXPERIMENT 1	3.81-4.59	0.09-0.19	2.38-4.78	84.9-89.5
EXPERIMENT 2	2.73-4.13	0.69-1.27	1.51-3.01	83.1-86.2
EXPERIMENT 3	2.41-4.13	0.69-1.27	1.43-3.32	83.1-90.0
EXPERIMENT 1, 2 and 3	2.41-4.13	0.09-1.27	1.43-4.78	83.1-90.0
FIELD	3.15	0.45	4.04	85.0

base sections have more structural compounds than middle and top sections of the same leaf. In grasses nitrogen concentrations usually fall rapidly with aging, while the amount of sclerenchyma as well as silica levels increase; allelochemicals are known to protect the very young, soft tissues in some cases (Bernays & Barbehenn, 1987). Though leaf categories clearly differed in more characteristics than the four plant variables measured, it was tested how well their nutritional quality was represented by the nitrogen, phosphorus, potassium and water contents.

The ranges of the plant variables encountered in all three experiments combined encompassed their values found in leaf samples of whole maize plants of similar physiological age collected in the field in Kenya (table 4-8). Comparison of the ranges in the separate experiments with the field values reveals that nitrogen was high in experiment 1, phosphorus was low in experiment 1 and high in experiment 2 and 3, and potassium was low in experiment 2 and 3. These comparisons are important as the location of the range of a plant variable might determine the outcome of its correlation and regression analysis with an insect fitness parameter. When an optimum curve describes their relationship, correlations may be positive, negative or absent.

For nitrogen, an optimum relationship has been shown to exist in some nutritional studies, all including a wide range of nitrogen concentrations (Brewer et al., 1985, 1987; Broadway & Duffey, 1986; Karowe & Martin, 1989). The often cited inconsistency in the effect of plant nitrogen on herbivore fitness encountered in the literature (Scriber, 1984) might partly be explained by the existence of an optimum relationship. Jansson & Smilowitz (1985), for example, found a negative correlation between the nitrogen content in leaves of potato plants and the developmental rate of Colorado potato beetles, possibly due to the narrow range of high nitrogen concentrations (3.9-4.6%) encountered in this study. Schroeder (1986) showed that larval development of an arbivorous leaf chewing insect was similar on food containing 2.9 and 4.1% nitrogen, which does not exclude that it might be impaired below and above these concentrations. For another arbivorous leaf chewing insect different correlations were obtained in two separate studies, indicating the existence of an optimum curve; while larval growth was positively affected by higher nitrogen concentrations between 0.5 and 2.0% (Fox & Macauley, 1977), no effect was found in the range 1.8 to 2.7% nitrogen (Miles et al., 1982). Thus, a valid generalization might be that herbivore fitness is optimized within a range of nitrogen levels, the width of which depends on the compensatory capacity of the species; below the optimum fitness is reduced because the nitrogen deficit can not be compensated for anymore by the herbivore, above the optimum excess nitrogen is detrimental either as a consequence of processing costs or increased levels of nitrogen-based secondary plant compounds.

In spite of the very significant differences in the composition of the various leaf categories, fitness of the African armyworm generally differed little; only larval growth rate was significantly affected by leaf category in all three experiments, while significant differences in survival and fecundity were absent except for low survival on the leaf category poorest in quality of phosphorus deficient plants (table 4-4). Caterpillars must have compensated for the large differences in food quality by changing their rate of consumption or by changing the utilization efficiency of the various nutrients (Simpson & Simpson, 1990); selection of certain leaf tissues better suiting the need of the caterpillars can likely be excluded as a possible mechanism for compensation due to the large differences in mineral levels between the various leaf

categories and the observation that the leaf variables were hardly changed by caterpillar feeding (table 4-3).

The preoviposition periods of 2-3 days (table 4-4) indicate that females were not arresting oocyte development (Page, 1988). The strong correlation of fecundity and adult weight has often been found for lepidopterous insects (i.e. Smith, 1986) and confirms the conclusion of Gunn & Gatehouse (1985) that for moths of the African armyworm provided with water the main factor limiting fecundity is moth weight. However, the curve setting the potential reproduction obtained in the present study does not fit to their data, that referred to smaller females with comparatively high fecundities. Though their weight-related fecundity was high even for small females, its maximum was found to be about 7 eggs/mg like in the present study (figure 4-5).

Larval growth rate was significantly correlated with phosphorus concentrations; correlations were strongest at very low levels of this mineral, but were also found at high levels and over the wide range of phosphorus encountered in all experiments (table 4-6); moreover, larval fresh weight could well be predicted by its concentrations in all cases (table 4-7). This relationship between phosphorus content and larval growth might have resulted from larval growth responses to other, not measured, leaf characteristics that covaried with phosphorus content over the leaf categories. However, as the distribution of phosphorus over the leaf categories clearly differed between experiment 1 versus experiment 2 and 3 (figure 4-3), such covariation seems unlikely.

Herbivores certainly need appreciable amounts of phosphorus in their food, a mineral vitally important for normal metabolism of numerous compounds. Concentrations in 9-days old caterpillars of the African armyworm have been measured to be about 1.0% dry weight, much higher than the levels found in the phosphorus deficient plants (table 4-3). The very strong correlation found in experiment 1 was therefore likely due to a direct effect of phosphorus on larval growth rate. The deficient levels for phosphorus found in experiment 1 were never encountered in host plants of the African armyworm in primary outbreak areas; moreover, phosphorus levels either differed little between years or were found to be higher in years with poor armyworm performance (see Chapter 2). Therefore, this mineral can not be

held responsible for the observed differences between years in outbreak development of this insect.

An analysis of the effect of nitrogen level on armyworm fitness was the main objective of this study. More leaf categories were included in the subsequent experiments in order to extend the range of nitrogen concentrations offered to the caterpillars. This was successfully done as the size of the range increased from 0.78% nitrogen in experiment 1 to 1.40% in experiment 2 and 1.72% in experiment 3 (table 4-8). Over all experiments nitrogen ranged from 2.41 to 4.13% dry weight, but nevertheless it did not appear to affect larval growth rate (table 4-6 and 4-7). Apparently, levels lower than 2.4% are required to affect fitness of the African armyworm negatively. As these are unlikely to occur in the field during the first month after the start of the short rainy season (i.e. also the start of the armyworm season) in eastern Africa (see Chapter 2), it also seems unlikely that the nitrogen content in host plants of the African armyworm can explain the spectacular differences between years in outbreak development of this pest.

Acknowledgements

5

Effects of the mineral composition and water content of intact plants on the fitness of the African armyworm [1]

Abstract

The effects of organic nitrogen, nitrate, phosphorus, potassium and water content in leaves of intact maize plants, grown in a gravel culture system, on fitness of the African armyworm were studied. Organic nitrogen concentrations ranged from 1.3% to 3.7% over four treatments differing only in nitrate supply to the plants. Water content and other mineral levels were all positively correlated with the organic nitrogen level. Feeding damage by the caterpillars was most severe on the lowest nitrate treatments, where it could be least well compensated for by new leaf growth. Larval and pupal fitness variables were not affected by treatment, except for larval development on the lowest nitrate treatment which was delayed by just one day. The large compensatory capacity of the larvae was underlined by a similar mineral composition of the pupae in all treatments. Adult fitness variables hardly differed between the upper three nitrate treatments, but revealed a trend over all treatments: the higher the organic nitrogen content of the leaves, the shorter the preoviposition period and the higher the fecundity. This trend, however, might have been due to differences in available food quantity rather than in food quality. It is concluded that fitness of the African armyworm is only slightly affected over a wide range of nitrogen concentrations in its food. Though effects might be larger under field conditions, the large differences in outbreak development between years seem not to be attributable to observed differences in nitrogen levels in

host plants between years in primary outbreak areas. Other environmental factors appear to be of greater importance.

Introduction

Outbreak development of the African armyworm differs enormously between years in eastern Africa (Brown, 1962; Odiyo, 1979; Haggis, 1986). Drought has often been mentioned as a factor related to and possibly responsible for the observed large fluctuations in population densities of this pest species, but its exact working mechanism has remained unclear (Hattingh, 1941; Tucker, 1984b; Graham, 1971; Dewhurst, 1985).

Drought-outbreak relationships have been observed for many herbivorous insect species. While direct effects of drought on herbivore fitness were initially thought to be mainly responsible for these relationships, indirect effects through the first trophic level by increasing host plant quality (White, 1969, 1974, 1976; Haukioja & Hakala, 1975; Rhoades, 1983, 1985), or through the third trophic level by decoupling natural enemy-herbivore interactions (Price, 1980; Risch, 1987) have received most attention during the last decades. Drought could conceivably improve host plant quality by increasing the levels of important nutrients and by decreasing the levels of secondary plant chemicals. In these indirect effects through the first trophic level, drought was always thought to operate instantaneously.

In the case of the African armyworm, however, drought frequently preceeds the actual outbreaks which usually seem to develop on unstressed plants. A direct or indirect **instantaneous** effect of drought can not then be effective in causing the outbreaks but a **delayed** indirect effect is required. Consequently, Janssen & Rose (1990) hypothesized that host plant quality might be influenced by drought via its effect on the nitrogen mineralization process in the soil. More severe drought conditions during dry seasons in eastern Africa were thought to stimulate the mineralization process in soils upon remoistening during subsequent rainy seasons. The resulting higher soil nitrate levels and higher nitrogen levels in host plants of the African armyworm were hypothesized to increase the insects' developmental rate, survival (especially of the very young larvae (White, 1984)) and fecundity. Thus, outbreak development would be more likely.

In a study on the weather-soil-plant interactions in a primary outbreak area during four years, Janssen (see Chapter 2) provided evidence for the existence of large differences in nitrogen levels in leaves of host plants of the African armyworm between years varying in drought intensity, whereas phosphorus and potassium varied less markedly. Higher leaf nitrogen levels during the first month after the start of the short rainy season, due to higher soil nitrate levels, were associated with a more intense drought during the preceding year. Moreover, armyworm outbreaks during the first two months after the start of the short rainy season only developed in years with high nitrogen levels (i.e. more than 4% in very young grasses).

The observed large differences in the leaf nitrogen level might be responsible for the differences in outbreak development on the condition that armyworm fitness is strongly dependent on the nitrogen content of its food. This condition was tested in the present study using a gravel culture system. It enabled the use of intact plants in which a wide range of nitrogen concentrations could be established, thus simulating the field situation in different years.

Materials and methods

Plants. Maize plants (*Zea mays* L. cv. Katumani) were grown in a gravel culture system (figure 5-1) in an experimental glasshouse at fluctuating temperatures (32°C(L, maximum):20°C(D, minimum)), RH 60 ± 10% and under natural day-length conditions (May-June in the Netherlands). Additional artificial light was provided by SONT lamps yielding a light intensity of 75±10 W/m^2 (12 h(L):12 h(D)) near the top leaves of the plants.

Seeds were planted in four units of the gravel culture system, each of which was provided with 80 dm^3 of Hoagland's solution at 1/4-strength. The nutrient solutions of the four units only differed in nitrate and chloride concentrations, the total of both anions always being 3.75 mM. The nitrate concentrations imposed were 0.50, 1.25, 2.50 and 3.75 mM. Nutrient solutions were renewed weekly and their pH was adjusted to 5.5 by adding HNO_3. Initially, 60 maize plants were allowed to grow in each small tank. Subsequent thinning occurred when plants were harvested for analysis.
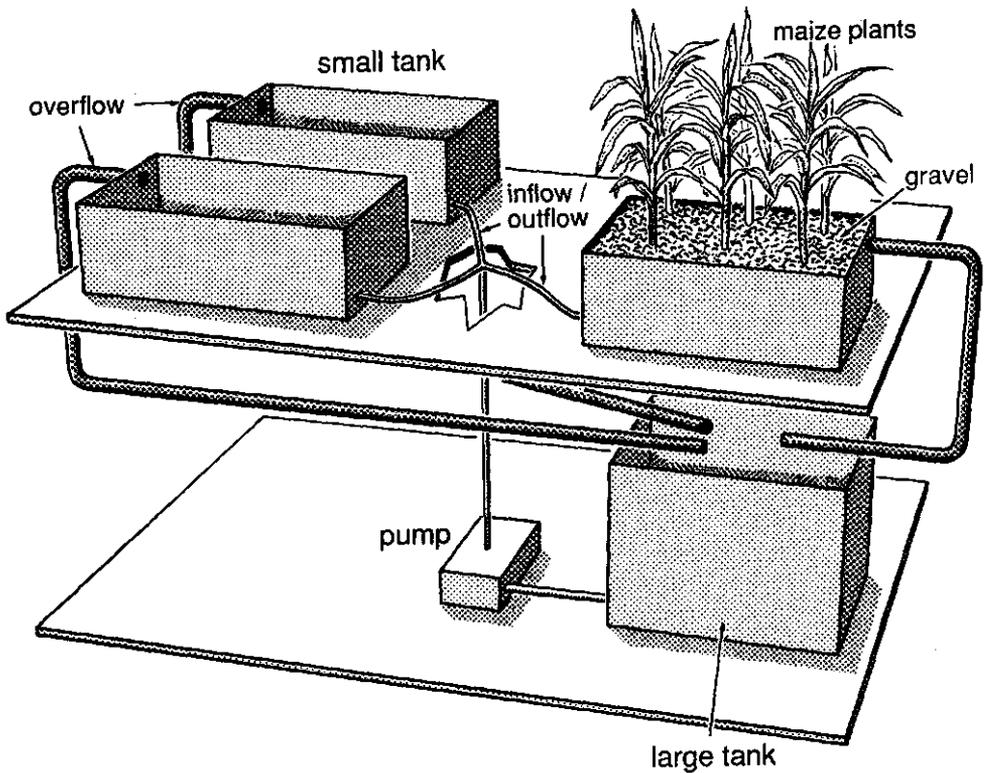
Figure 5-1. A unit of the gravel culture system. Maize plants are grown in gravel (diam. 2-4 mm) in small tanks (vol. 50 dm^3). Four times a day, nutrient solution is pumped (Iwaki pump, model MD-10, cap. 10 dm^3/min) from a large tank (vol. 100 dm^3) into three small tanks for 15 minutes. The level of the nutrient solution in the small tanks rises just to the upper gravel layer. Then excess nutrient solution is carried back to the large tank through the overflow. When the pump stops operating, the nutrient solution in the small tanks flows back through the outflow in about 10 minutes.

To provide the caterpillars with plants of similar physiological age, planting date differed for the four treatments; with increasing nitrate supply, the respective treatments were planted 25, 20, 15 and 13 days prior to the

day the caterpillars were released (day 0). Germination took 5 days in all treatments.

The day before the caterpillars were released (day -1), cages (0.6x0.4x0.8 m) of netting (mesh-width 0.2 mm) with a transparent plastic top were placed over the maize plants of each small tank to prevent caterpillars from escaping. While relative humidity was not affected by the caging, light intensity dropped to 60 ± 10 W/m^2 near the top leaves of the maize plants. In previous experiments, this had been shown to increase the nitrate concentration in the leaves of the plants to unnaturally high levels as well as to decrease the differences in organic nitrogen content between the treatments. To avoid these undesired changes, the nitrate concentrations in the nutrient solutions were reduced to 0.05, 0.25, 1.00 and 3.00 mM in the respective treatments as soon as the maize plants were caged. These concentrations were arrived at empirically based on the previous experiments.

Maize plants were harvested at day -1 (before the caging), 7 and 15. During the first two harvests a random selection of plants was taken from each small tank. Each plant was separated into leaves and stem and individually weighed. After drying at 70°C in a stove, dry weight was recorded. Leaf material from several plants was pooled for chemical analysis. During the last harvest at the end of the experiment all remaining plants were treated similarly, except that all plants from one small tank were pooled prior to weighing.

Nitrate (NO_3^-) was extracted by shaking with distilled water for 30 min, and analysed by Technicon AutoAnalyser. Total nitrogen, phosphorus and potassium contents were determined after Novozamsky et al. (1983). Organic nitrogen (N_{org}) was calculated by subtracting nitrate nitrogen from total nitrogen.

Insects. A culture of the African armyworm was maintained as described by Janssen (see Chapter 4). The moths which offspring was used in the experiment had been in culture for only one generation.

On day 0, a number of 85 neonate larvae were released per treatment. Larval fresh weight of about half the larvae was recorded on day 8 and 9. When all caterpillars had started to pupate, prepupae and pupae were carefully removed from the gravel. They were placed singly in transparent plastic cups (250 ml) at 25°C, RH 90%, 12 h(L): 12 h(D) and a light intensity

of less than 3 W/m^2. Survival up to pupation was assessed per small tank. Pupae that died before eclosion were analysed for total nitrogen, phosphorus and potassium after Novozamsky et al. (1983). Pharate adult weights were measured within 6 h before eclosion, which can be anticipated by the darkening of the pupal cuticle (Gunn & Gatehouse, 1985). Eclosion generally occurred at night. Moths were placed in pairs on the following morning, and were provided with filter paper as a substrate for oviposition and with demineralized water presented on cotton wool plugs in small 4 ml plastic pots which were renewed daily. In order to provide females with a male from eclosion, individuals from different treatments sometimes had to be paired. All eggs were removed and counted, and females were dissected at death to see whether they had mated properly. Any moth which failed to eclose properly, failed to free itself after mating or in which a spermatophore was not or only partially inserted, was excluded. For each each female the preoviposition period and fecundity were recorded, together with longevity for both sexes.

Results

Plants. Due to the different planting dates, leaf fresh weight differed little between the treatments at day 7, except for the lowest nitrate treatment (figure 5-2A). Because damage to the leaves by the caterpillars was still minor during the first week of caterpillar feeding, maize plants were obviously growing very slowly in this treatment. The harvest on day 15, at the end of the experiment when all caterpillars had pupated, reveals the severe damage done by the caterpillars; for all treatments leaf fresh weight was lower than at day 7. Damage was most severe on the two lowest nitrate treatments, where leaf fresh weight was significantly reduced. It was compensated for by new leaf growth on the two highest nitrate levels. The leaf/stem ratio based on fresh weights decreased over time and with a lower nitrate supply to the maize plants (figure 5-2A).

In comparison with the other treatments, the water content was always slightly but significantly lower in the leaves of the maize plants growing on the lowest nitrate level (figure 5-2A). Leaf nitrate content was almost zero for the two lowest nitrate treatments at all three harvests (figure 5-2B). In spite

of the reduction of the nitrate supply to the maize plants, it was still significantly affected by the caging in the highest nitrate treatment, which is demonstrated by the much higher leaf nitrate level on day 7 compared to day -1. However, caging did not remove significant differences in leaf organic nitrogen levels between treatments (figure 5-2B). A wide range from 1 to 4% was obtained for this variable, with consistent significant differences between the treatments nearly throughout the experiment. In all treatments it decreased over time. Leaf phosphorus and potassium levels differed less, though also significantly between treatments (figure 5-2B). While they tended to be higher for the higher nitrate treatments during the first two harvests, an opposite trend occurred during the last harvest. Thus, patterns in time varied among treatments for both minerals.

Insects. The fresh weights of the caterpillars at day 8 and 9 show that larval development was equally fast for all treatments except the lowest nitrate level, on which it was delayed by less than a day (table 5-1). It can be seen that caterpillars roughly doubled their weight in a day. First pupation occurred on day 9 and all caterpillars had started to pupate on day 14. Survival up to pupation was more than 90% for all treatments.

While adult weight was significantly lower for the lowest nitrate treatment (table 5-1), pupal concentrations of nitrogen, phosphorus and potassium in this treatment were mostly significantly higher than in the two highest nitrate treatments (figure 5-3). Larval-pupal duration only differed by a maximum of one day between the treatments and differences in adult longevity were not significant (table 5-1).

Only the reproductive fitness variables showed a trend related to the treatment: the higher the nitrate supply to the plants, the shorter the preoviposition period and the higher the absolute fecundity as well as the weight-related fecundity (table 5-1). Over all treatments, fecundity was significantly correlated with pharate adult weight (figure 5-4). The graph of the weight-related fecundity reveals a maximum of about 7 eggs/mg for the conversion efficiency of body mass to eggs.

Female pupae weighed significantly more than male pupae and female moths lived for a shorter period than male moths (table 5-2). Larval-pupal duration was identical for both sexes.

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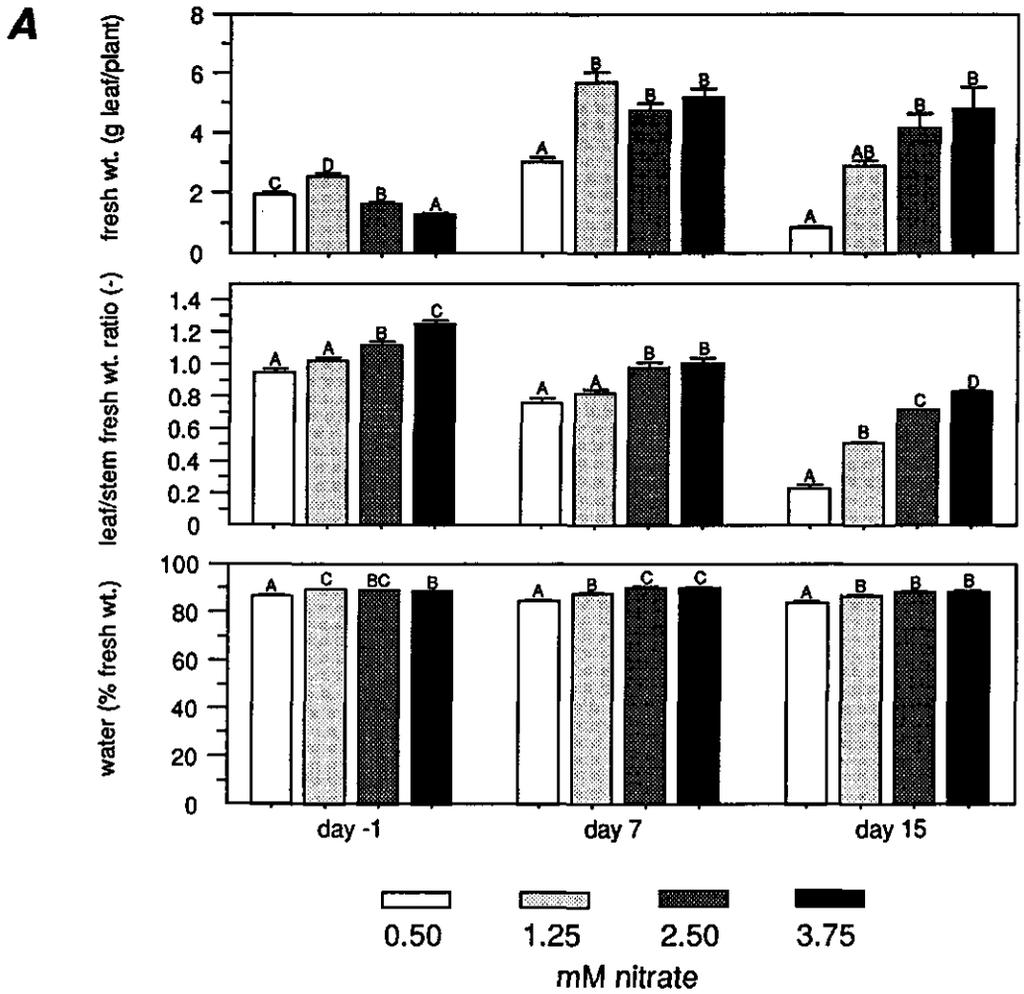
Figure 5-2. A. Leaf fresh weight per plant, leaf/stem ratio based on fresh weights and leaf water level in maize plants grown on four nutrient solutions differing in nitrate concentration and harvested at three dates: day -1 (n=45), day 7 (n=24) and day 15 (n=3). **B.** Levels of nitrate, organic nitrogen, phosphorus and potassium in the leaves of maize plants grown on four nutrient solutions differing in nitrate concentration and harvested at three dates: day -1 (n=9), day 7 (n=12) and day 15 (n=3). Standard errors are indicated. Data were analysed by oneway ANOVA (all P<0.001, except for fresh weight (p<0.01) and potassium (p>0.05) at day 15) followed by Tukey's multiple range test. Different letters within one harvest indicate significant differences (p<0.05).
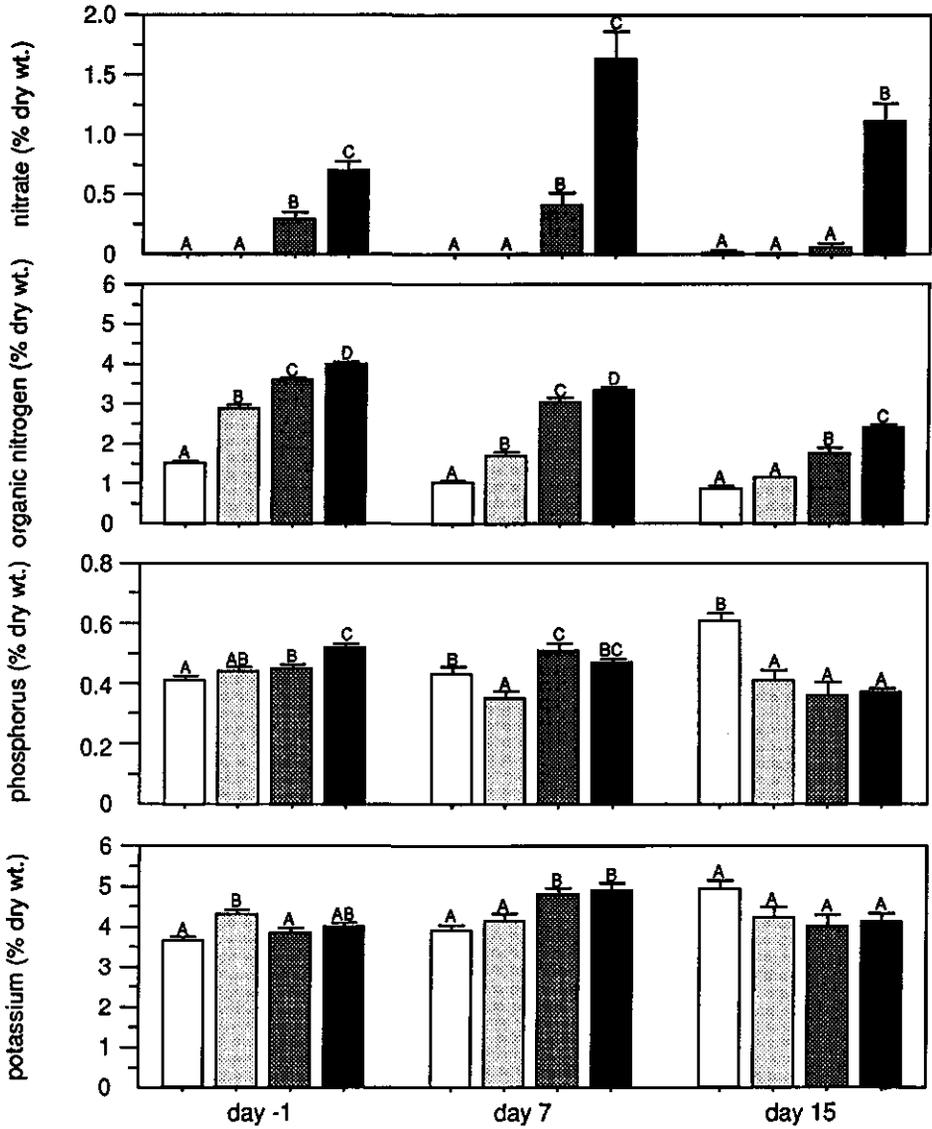
Table 5-1. Insect variables for the four nutrient solutions differing in nitrate concentration. Standard errors are given in brackets.

Nitrate concentration	0.50		1.50		2.50		3.75		P[1]
■No. of individuals	44		44		44		42		
Weight at day 8 (mg)[1]	130.8	a	208.5	b	230.2	b	222.6	b	***
	(9.3)		(10.5)		(15.0)		(13.6)		
■No. of individuals	44		44		40		39		
Weight at day 9 (mg)	291.4	a	439.4	b	412.1	b	428.4	b	***
	(21.3)		(15.6)		(15.8)		(16.2)		
■No. of replicates	3		3		3		3		
Survival (%)[2]	91	a	95	a	91	a	92	a	n.s.
	(3)		(1)		(3)		(3)		
■No. of individuals	46		55		56		43		
Pharate adult weight (mg)	136.6	a	158.8	b	163.0	b	162.2	b	***
	(3.6)		(3.1)		(4.6)		(2.8)		
Larval-pupal duration (days)	21.5	c	20.8	ab	21.3	bc	20.5	a	***
	(0.2)		(0.2)		(0.2)		(0.1)		
Adult longevity (days)	8.0	a	8.5	a	7.9	a	8.3	a	n.s.
	(0.2)		(0.3)		(0.3)		(0.2)		
■No. of females	25		26		19		29		
Preoviposition period (days)	3.5	b	3.0	ab	2.8	ab	2.6	a	*
	(0.2)		(0.2)		(0.3)		(0.2)		
Fecundity (eggs/female)	596	a	841	b	954	b	1003	b	***
	(47)		(51)		(64)		(43)		
Fecundity (eggs/mg)[3]	4.1	a	5.1	ab	5.2	bc	6.0	c	***
	(0.3)		(0.2)		(0.3)		(0.2)		

[1] Except for survival, data were analysed by oneway ANOVA (n.s.: $P>0.05$; *: $P<0.05$; ***: $P<0.001$) followed by Tukey's multiple range test. Different letters within a horizontal row indicate significant differences ($P<0.05$).

[2] Survival up to pupation was analysed by the RxC test of independence using G-test (Sokal & Rohlf, 1981).

[3] Weight-related fecundity.
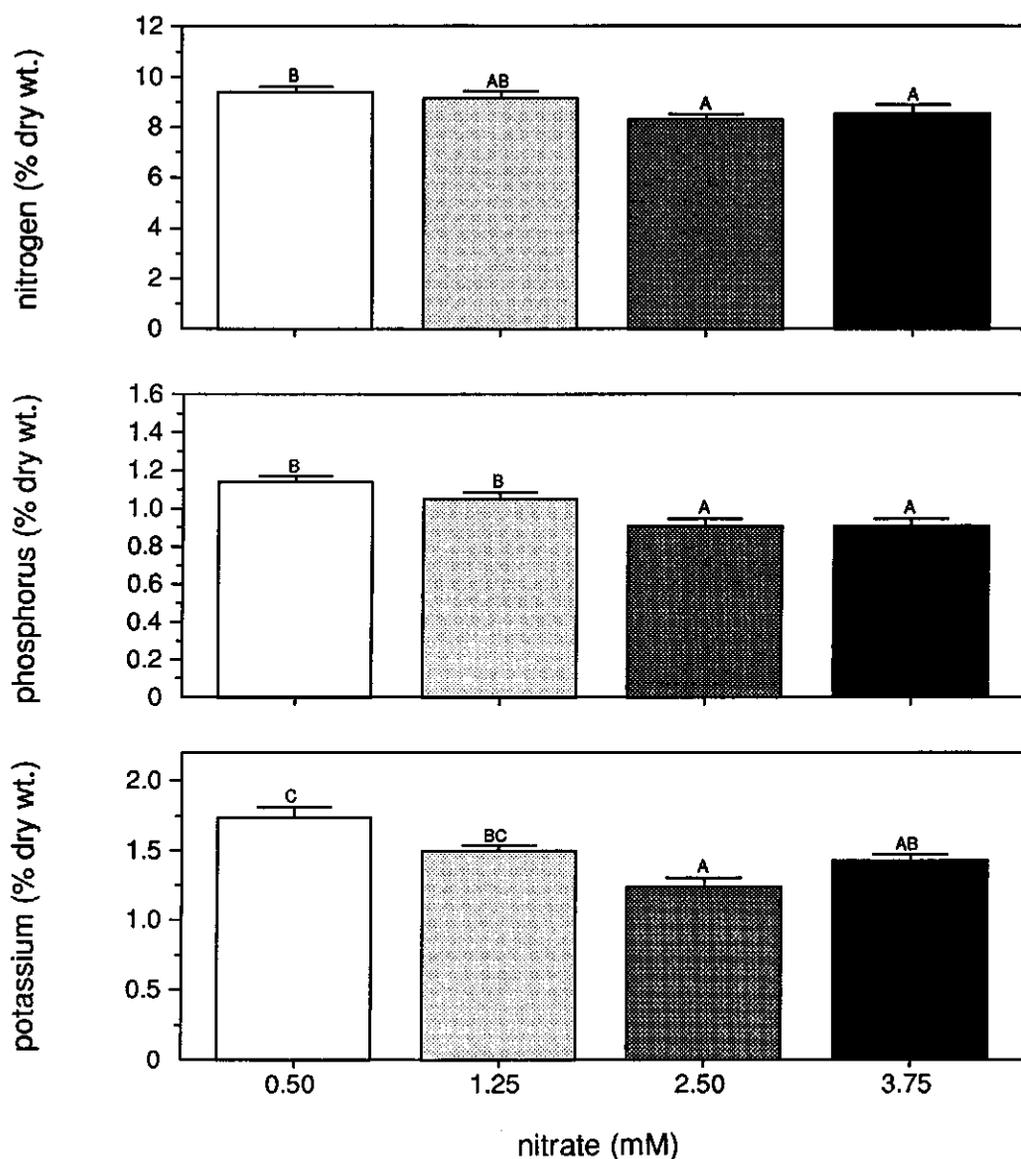
Figure 5-3. Levels of nitrogen, phosphorus and potassium in pupae from caterpillars which had fed on maize plants grown on four nutrient solutions differing in nitrate concentration: 0.50 mM (n=12), 1.50 mM (n=8), 2.50 mM (n=8) and 3.75 mM (n=11). Standard errors are indicated. Data were analysed by oneway ANOVA (all P<0.001) followed by Tukey's multiple range test. Different letters indicate significant differences (p<0.05).
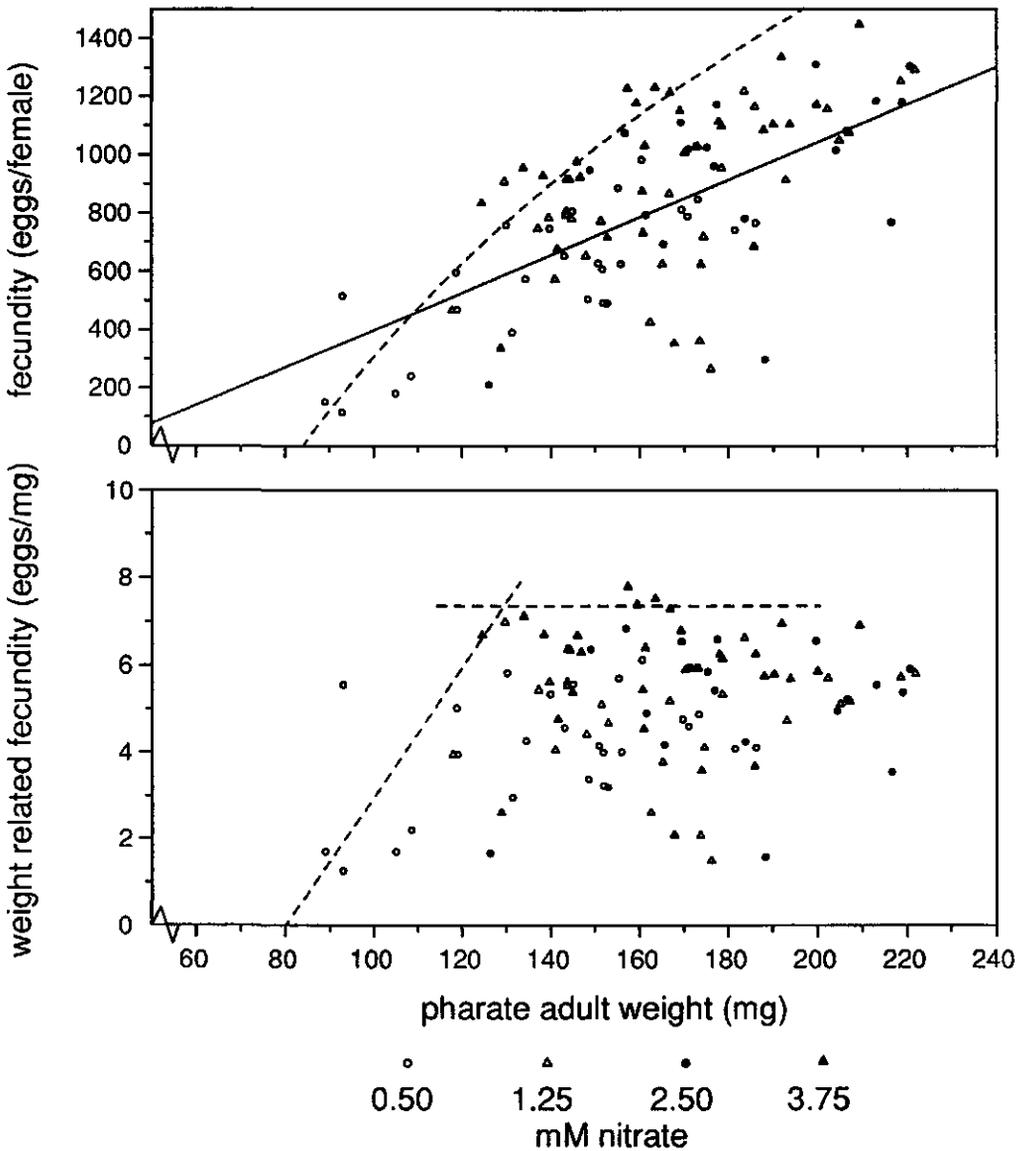
Figure 5-4. Fecundity and weight related fecundity in relation to pharate adult weight for moths from caterpillars which had fed on maize plants grown on four nutrient solutions differing in nitrate concentration. In the upper graph, the solid line is the linear regression line of fecundity on pharate adult weight (Y=-271.8+6.8X, r=0.657, n=102, p<0.001). All dotted lines are taken from Janssen (see Chapter 4).

Table 5-2. Comparison of insect variables between females and males over all treatments. Standard errors are given in brackets.

	females	males	P
■No. individuals	99	101	
Pharate adult weight (mg)	163.0	148.3	***
	(3.0)	(2.1)	
Larval-pupal duration (days)	20.9	21.0	n.s.
	(0.1)	(0.1)	
Adult longevity (days)	7.8	8.6	***
	(0.1)	(0.2)	

Values for the same insect variable were compared by Mann-Whitney U test (n.s.: $P>0.05$; ***: $P<0.001$).

Table 5-3. Correlation matrix of plant-plant and plant-insect interactions for the four treatments. Plant variables were averaged over the harvests at day -1 and day 7. Their ranges over the four treatments are given. All correlations are Pearson correlations (*: $P<0.05$; **: $P<0.01$).

Plant variable	N_{org}	NO_3^-	P	K	H_2O
Range	1.29-3.68	0.01-1.18	0.40-0.50	3.78-4.44	85.5-89.3
■PLANT-PLANT					
N_{org}		0.810	0.828	0.961 *	0.945
NO_3^-			0.855	0.726	0.594
P				0.646	0.622
K					0.973 *
■PLANT-INSECT					
Weight at day 8	0.911	0.531	0.544	0.963 *	0.995 **
Pharate adult weight	0.901	0.532	0.515	0.967 *	0.990 **
Preoviposition period	-0.961 *	-0.794	-0.676	-0.993 **	-0.941
Fecundity	0.981 *	0.727	0.705	0.994 **	0.984 *

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The plant-insect interaction. The water content and mineral levels in the leaves of the maize plants averaged over the first two harvests were chosen as the best estimate of these plant quality variables encountered by the caterpillars during their development. They were all positively correlated over the four treatments (table 5-3). Significant plant-plant correlations occurred between organic nitrogen and potassium and between potassium and water.

Of the insect variables measured, those which showed relatively large differences between the treatments were chosen for correlation analysis. The three plant variables which covaried most in the maize leaves, were best correlated with the insect fitness variables, often yielding significant correlations (table 5-3). Higher levels of organic nitrogen, potassium and water in the maize leaves resulted in faster larval development, higher adult weights, shorter preoviposition periods and higher fecundity of the subsequent female moths. For phosphorus, potassium and water the ranges over which correlations were obtained were small.

Discussion and conclusions

The gravel culture system as used in the present study was developed to closely simulate the soil-plant interaction as occurring in the field. By not permanently immersing the roots of the maize plants in the nutrient solution, rapid depletion of minerals in the nutrient solution was avoided. Consequently, a fairly constant supply of nitrogen to the maize plants, the level of which was set by the nitrate concentration in the nutrient solution, could be realized in a simple way.

Reduction of the nitrate concentrations in the nutrient solutions as soon as the maize plants were caged had the desired effects: the leaf nitrate concentration did not increase to unnaturally high levels due to the caging and the differences in organic nitrogen between all treatments remained significant throughout most of the experiment.

The maximum leaf nitrate concentration of 1.6% found on day 7 for the highest nitrate treatment is almost identical to the maximum found by Janssen (see Chapter 2) in a wild grass species in a primary outbreak area of the African armyworm. However, nitrate concentrations of over 1% in maize leaves are rare (Hanway, 1962; Terman et al., 1976; Steer, 1982) and

indicate that nitrogen supply to the plants is excessive under the prevailing light conditions, which usually limit the conversion of nitrate into organic compounds (Huffaker & Rains, 1978). Consequently, the corresponding organic nitrogen content of 3.7% might well have been the maximum obtainable in the leaves of the maize plants at day 7.

Because plant nitrate nitrogen can not be used by herbivores in their nitrogen metabolism, the calculation of organic nitrogen from total nitrogen and nitrate nitrogen is preferable in studies on host plant quality. This is especially important when the fraction of nitrate nitrogen in total nitrogen differs strongly between treatments, as in the present study (figure 5-2B). Then, differences in total nitrogen between treatments might be due solely to differences in nitrate nitrogen, there being no differences in organic nitrogen which are more relevant for herbivores. This situation was encountered in two previous experiments in which four treatments were included, as in the present study, with the aim of obtaining different organic nitrogen levels in leaves of maize plants. In both these experiments, these differences were not significant at day 7 between the upper three treatments, for which a value of 3.2% then seemed to be the maximum set by the light conditions.

This underlines the importance of measuring total as well as nitrate nitrogen in host plant quality studies, especially when nitrate concentrations of over 1% can be expected. Moreover, nitrate nitrogen does not always constitute a constant fraction of total nitrogen (figure 5-2B). It is only above a certain threshold concentration of total nitrogen, below which nitrate is always close to zero, that a linear relationship is usually found (Hanway, 1962; Terman et al., 1976; Steer, 1982). Consequently, correlations between organic nitrogen, instead of total nitrogen, in host plants and insect fitness variables are likely to give better results if nitrogen is important.

Comparison of the insect fitness variables with those obtained in a study with an excised leaf system (see Chapter 4) in general reveals a good match. As pupal duration is about 10 days at 25°C, larval duration was between 10 and 12 days in all treatments (table 5-1). This is slightly shorter than in the study with the excised leaf system, probably due to the higher day-time temperature, and it indicates that larvae developed at their maximal rate (see Chapter 4). The curve describing the relationship between the potential fecundity and pharate adult weight obtained in the study with the excised leaf system,

fits the data obtained in the present study well (figure 5-4); only 9 females, 6 of which came from the highest nitrate treatment, realized a fecundity higher than the one set by the curve. Similarly, the lines setting the maximum weight-related fecundity at a certain pharate adult weight also fit well (figure 5-4). While pupae weighed more and moths lived longer in the present study, the differences found between the sexes were identical in both studies.

The correlation analysis shows that none of the treatment effects on armyworm fitness can be attributed to the differences in organic nitrogen only. Especially water and potassium were important, covarying variables (table 5-3). However, when also considering the size of the ranges of the various variables, greatest significance should definitely be attached to the correlations for organic nitrogen.

In spite of the large differences in leaf organic nitrogen between the three highest nitrate treatments in the present study (averaged over the first two harvests, they ranged from 2.30 to 3.68%), larval and pupal fitness variables were identical (table 5-1). Similarly, the extreme differences in plant nitrate concentration did not affect fitness. Only the extremely low organic nitrogen level of the lowest nitrate treatment (1.29% averaged over the first two harvests) slightly affected larval developmental rate during the first 8 days (table 5-1). Subsequent effects on developmental rate were absent. The significantly lower adult weight for this treatment should be considered with caution as larvae virtually ran out of food as they approached pupation (figure 5-2A). This forced the caterpillars to spend more time searching for food and might have resulted in premature pupation of some individuals. It can not, however, be held responsible for the significantly lower fresh weight at day 8 and 9 as food was then still abundant.

Clearly, larvae could compensate very well for the low organic nitrogen concentrations in their food. Based on the mineral composition of the pupae (figure 5-3), they actually seemed to achieve higher nitrogen concentrations in their tissues on the lower nitrate treatments, simultaneously accumulating more phosphorus and potassium as well. In a previous experiment, higher levels of phosphorus and potassium were also found in caterpillars feeding on leaves low in nitrogen (table 5-4). A nitrogen level of about 9% occurred in the larvae as well as the pupae and is commonly found for folivorous insects (Mattson & Scriber, 1987). It implies that the caterpillars feeding on

Table 5-4. Water content and mineral composition of caterpillars at day 9 during a previous experiment, including four treatments with increasing plant nitrogen level.

Plant nitrogen level	LOW		---->		---->		HIGH		P
■No. of replicates	3		3		3		3		
Water (% fresh wt.)	90.6	b	90.4	b	90.5	b	89.7	a	**
Nitrogen (% dry wt.)	8.48	a	8.58	a	8.45	a	9.01	a	n.s.
Phosphorus (% fresh wt.)	1.32	b	1.16	ab	1.05	a	1.16	ab	*
Potassium (% dry wt.)	5.52	b	5.36	b	5.27	b	4.84	a	**

Data were analysed by oneway ANOVA (n.s.: $P>0.05$; *: $P<0.05$; **: $P<0.01$) followed by Tukey's multiple range test. Different letters within a horizontal row indicate significant differences ($P<0.05$).

the two lowest nitrate treatments accumulated nitrogen by a factor of 4 to 7 from their food in their present study. For phosphorus, with a level of about 1% in both larvae and pupae, this factor was only slightly higher than 2. Potassium levels differed very significantly between the two insect stages, a phenomenon also reported for other noctuids (Levy & Cromroy, 1973). Even the levels in the larvae, although high, indicate that no accumulation of this mineral was required, as they were similar to the potassium concentrations found in the maize leaves. Water content of larvae and their food was also identical.

How did caterpillars feeding on the low nitrate treatments compensate for the large discrepancy in nitrogen between their tissues and food? Simpson & Simpson (1990) distinguished three types of compensatory responses: a new diet can be selected, the utilization efficiency of nutrients can be altered, and the rate of consumption can be altered by changing meal size and by changing intermeal intervals.

Selection of certain leaves of the maize plants by the caterpillars was not observed. While it was impossible for the larvae on the lowest nitrate treatment, as they ate virtually all leaf material, it can also be excluded as a possible mechanism for compensation due to the large differences in organic nitrogen between all treatments. Though intraplant variation was not assessed in the present study, highest organic nitrogen concentrations in a

maize plant deviate less than 40% from the average for the whole plant (see Chapter 3). This is not enough to cover the differences between the treatments.

Nitrogen utilization efficiencies for lepidopterous larvae are known to vary between 30 and 80% with extremes of 20 and 90% (e.g. Slansky & Feeny, 1977; Scriber, 1978b; Scriber & Feeny, 1979). Manuwoto & Scriber (1985) found values of about 35% for the last two instars of *Spodoptera eridania* feeding on maize plants containing high total nitrogen levels. When assuming this value for the highest nitrate treatment in the present study, calculations based on the total amount of nitrogen accumulated in the pupae and the organic nitrogen and water content of the maize plants on day 7 indicate that the larvae in this treatment ate 3.6 gram of fresh leaf material during their whole larval development. This amount agrees well with an earlier estimate obtained by Janssen (see Chapter 4). It can also be calculated that the larvae on the lowest nitrate treatment should have consumed twice as much leaf material to accumulate their total amount of pupal nitrogen without changing the nitrogen utilization efficiency of 35%. At the other extreme, they might have doubled their nitrogen utilization efficiency without needing to consume more.

An estimate based on the leaf/stem ratio at day 7 (certainly an overestimate of its value during the final days of the experiment, see figure 5-2A), and the stem fresh weight at day 15, reveals that, for the 76 larvae feeding on the lowest nitrate treatment, a maximum of 430 gram leaf fresh weight were available, requiring a nitrogen utilization efficiency of at least 50% to acquire the total amount of nitrogen accumulated in the pupae. As such an efficiency would imply an improbably low consumption of only 2.5 gram for the larvae on the highest nitrate treatment, it is likely that the larvae on the lowest nitrate treatment used the nitrogen they consumed more efficiently than the larvae on the highest nitrate treatment. Whether they also consumed more can not be determined from these data, though it has often been observed in studies with other insects using diets varying in nitrogen content (e.g. Slansky & Feeny, 1977; Simpson & Abisgold, 1985; Karowe & Martin, 1989).

Adult fitness variables, though showing a trend, differed only slightly between the three highest nitrate treatments (table 5-1). Again, a more pronounced effect was found at the lowest nitrate treatment. The decrease in

weight-related fecundity over the nitrate treatments shows that the decrease in fecundity was not due only to lower adult weights. As in most migratory insects (Johnson, 1969), the available evidence suggests that migration occurs prereproductively in the African armyworm (Brown & Swaine, 1966; Rose & Dewhurst, 1979). Though not the most satisfactory measure for the prereproductive period of females, the preoviposition period gives a good indication of the time over which an insect can express its migratory potential. The increase in the preoviposition period with decreasing nitrogen level might therefore indicate that moths from the lower nitrate treatments would migrate over a longer period of time than those from the higher nitrate treatments.

Food influenced reproduction in the present study, albeit to a limited extent. The question remains whether the observed effects were really the result of the variation in organic nitrogen in the food (i.e. food quality) or of differences in density experienced by the caterpillars (i.e. food quantity). While caterpillar numbers were identical among treatments, the quantity of food remaining at day 15 increased from the lowest to the highest nitrate treatment (figure 5-2A). Crowding has a pronounced effect on the morphology, physiology and behaviour of many insects and has been shown to prolong the preoviposition period (e.g. McDonald & Cole, 1991). In common with some other Noctuidae, the African armyworm shows a density-dependent phase polyphenism (Faure, 1943; Matthee, 1946). Whereas uncrowded larvae remain pale and green until pupation, crowded larvae become very conspicuous during development, changing from green to black with yellow stripes. These two forms, termed by Faure (1943) *solitaria* and *gregaria* in analogy with locusts, represent the extremes of a continuum; intermediate *transient* forms, brownish in colour, are known as well. Crowding has often been suspected to be a factor in the causation of migration (Johnson, 1969). Woodrow et al. (1987) showed that female moths from *gregaria* type caterpillars fly longer, likely to be an adaptation to escape the detrimental consequences of high larval densities. Gunn et al. (1988) found a trade-off between flight and reproduction, evident in moths denied access to a source of carbohydrate after flight. They also concluded that lipid, and not protein, is the resource limiting fecundity. This is supported by the negative association between pupal nitrogen level and weight-related fecundity in the present study (figure 5-3 and table 5-1). Though, according to their coloration, most

caterpillars were of the *solitaria* and *transient* type just prior to pupation in all treatments, presumably as a result of the large quantity of food available to them during the first week of larval development, variation in crowding during the final days of larval development might still have affected the physiology and behaviour of the subsequent adults. Thus, the longer preoviposition period and lower fecundity on the lowest nitrate treatment might have resulted from a greater tendency of these moths to migrate in response to crowding which was independent of an apparent indicator (i.e. coloration) of phase differences.

Thus, the results of the present study confirm those obtained in the study with the excised leaf system (see Chapter 4): fitness of the African armyworm is only slightly affected over a wide range of nitrogen concentrations in its food. The range can now be extended to values as low as 1.3%, which only delay larval development slightly. Possibly they also affect reproduction, though this can not be concluded with certainty. The water content and mineral composition of the maize plants agreed well with those encountered under field conditions in a primary outbreak area (see Chapter 2). As organic nitrogen levels hardly ever decrease below 2.0% during the first month after the start of the short rainy season in a primary outbreak area, it seems unlikely that the observed variation between years in plant organic nitrogen is responsible for the spectacular differences in outbreak development of the African armyworm.

Though armyworm fitness might be more affected by differences in food quality under field conditions (e.g. when caterpillars have to consume more foliage to obtain sufficient organic nitrogen, they may be more vulnerable to other mortality factors (e.g. Loader & Damman, 1991)), it is felt that other environmental factors must be of greater importance in explaining outbreak development of this pest. Based on own field observations, rainfall during larval development is suspected to be such a factor. In addition, environmental factors prevalent during the long dry season might be of major importance as the moth numbers appearing in a primary outbreak area on the first rains of the short rainy season can already differ largely between years (see Chapter 2). The question of how the African armyworm survives the long dry season will be addressed in a further paper (see Chapter 6). Although the hypothesis put forward by Janssen & Rose (1990) seems

inappropriate for the African armyworm, it might still explain variation in performance of other herbivores which fitness is strongly dependent on the organic nitrogen content in their food.

Acknowledgements

6

How does the African armyworm survive the long dry season? Continuous development versus aestivation [1]

Abstract

Though it is generally believed that the African armyworm survives the long dry season at low densities in the coastal regions of eastern Africa, moving inland around the start of the short rainy season to form primary outbreaks, some field observations are still difficult to reconcile with this scenario. Aestivation of the moths, induced by a deteriorating habitat under the dry conditions prevailing during the long dry season in the semi-arid lowlands of eastern Africa, has been proposed to provide a better explanation. In a laboratory experiment and a field trial, the effects of differing adult diets and of relative humidity on longevity and reproduction of moths were studied. None of the moths entered aestivation, though extended preoviposition periods indicated that in a few cases reproductive development was delayed in the field. Additional observations under laboratory conditions yielded some extremely long-lived moths (i.e. up to 5 weeks). However, as moths seem not to be able to aestivate for the duration of the long dry season, continuous development appears to be required. It needs to be established whether the semi-arid lowlands are truly unsuitable for sustaining armyworm larvae during this period. Fermentation traps revealed that many other moth species remain active.

Introduction

In eastern Africa a marked seasonal occurrence of outbreaks of the African armyworm, coinciding with the seasonal rains that are associated with the inter-tropical convergence zone (ITCZ) in the tropics (Riehl, 1979), has long been recognized (Brown et al., 1969; Haggis, 1986). The importance of rainstorms to outbreak development is twofold: the airflow associated with a rainstorm concentrates flying moths and rain starts new grass growth which serves as food for the subsequent caterpillars. Radar observations have shown that moths rapidly disperse when they move downwind, likely to result in widespread but low-density populations (Riley et al., 1983; Rose et al., 1985). Consequently, concentration of moths seems to be a prerequisite for outbreak development. Additional effects of rain are to induce flying moths to descend (Riley et al., 1983) and to provide moths with a readily available source of free water which is required by the females for completion of their reproductive maturation (Gunn & Gatehouse, 1985). The frequently reported association between wind convergence, rainstorms and subsequent out-breaks (Brown et al., 1969; Blair, 1972; Rose & Law, 1976; Haggis, 1979; Rose, 1979; Blair et al., 1980; Tucker, 1983; Tucker & Pedgley, 1983; Pedgley et al., 1989) is therefore not surprising.

During the long dry season (June-October in equatorial eastern Africa), population densities are very low and, especially towards the end, hardly any armyworms are observed and no outbreaks are reported (Rose, 1979; Odiyo, 1984; Haggis, 1986). This period is called the 'off-season' (Odiyo, 1981). At the beginning of the short rains (October-November), a rapid buildup of the population may occur in the so-called primary outbreak areas due to favour-able conditions. These areas are located in the foothill area in Tanzania and Kenya, which is the zone separating the lower desert area to the east from the highlands to the west, and are generally characterized by low and erratic rainfall. Adults from these primary outbreaks migrate downwind on the prevailing easterly winds, sometimes over large distances, to give rise to subsequent generations further west in secondary outbreak areas (Pedgley et al., 1989). When the ITCZ moves northwards from February onwards, a progression of outbreaks can occur from Tanzania, Kenya and Uganda through Ethiopia and Somalia, reaching the Yemen in June (Brown et al., 1969; Betts, 1976; Odiyo, 1987). As yet, however, there is no good evidence

for a subsequent return movement from Ethiopia southwards into Kenya, mainly due to the dominant winds being in the wrong direction (Tucker, 1984a; Pedgley et al., 1989). A southwards movement from Tanzania through Malawi and Zimbabwe to South Africa has also been suggested (Blair & Catling, 1974). The occurrence of such extensive migration is supported by the very low genetic diversity among populations in eastern Africa (den Boer, 1978).

It is still not known exactly where the moths which appear in the primary outbreak areas come from. How does the African armyworm survive the long dry season? As it has been shown quite clearly that the moths causing these first outbreaks of the season originate from an easterly direction (Tucker, 1984a; Pedgley et al., 1989), and because the vegetation in the area between the coast and the primary outbreak areas is believed to be unsuitable to sustain armyworm larvae during the long dry season, the best answer to this question seems to be that larvae survive at low densities in the coastal regions of eastern Africa (Rose et al., 1987; Pedgley et al., 1989), where sporadic showers fall even during the long dry season. Moths developing from these caterpillars might be blown inland on the easterly winds which dominate at the start of the short rainy season (Tucker et al., 1982; Pedgley et al., 1989), being concentrated on the first rainstorms to form primary outbreaks.

However, some observations are difficult to reconcile with this scenario (W.W. Page, unpublished report). At the coast, moth activity is known to be at its minimum around the onset of the short rains and usually builds up to peak two months later. In primary outbreak areas, moths are virtually absent during the last months of the long dry season; first catches in pheromone traps usually coincide with the very first rains, and catches subsequently decrease to very low numbers during the next two weeks. As a result, larval development is highly synchronized in primary outbreak areas (e.g. see Chapter 2). Winds would have to carry moths inland just before or during, and not following the start of the short rainy season, for which there is no evidence.

Page proposed an alternative theory based on moths going into aestivation under dry conditions. Such behaviour would be especially adaptive in a habitat such as the eastern African lowlands where rainfall is unpredictable and where migration into dry areas, which may subsequently receive

rain, is probably a regular phenomenon. The moths that are blown inland from the coast, as well as those coming from breeding areas in the lowlands, are thought to enter aestivation due to low humidity conditions in these lowlands. Aestivating moths might accumulate over weeks or months due to the continuous movement of moths into the dry areas from the coast. Extension of the long dry season is then likely to result in greater accumulation, which might even help to explain why more severe outbreaks often follow more severe droughts (Graham, 1971; Pedgley et al., 1989). The first rains of the short rainy season will end aestivation, resulting in very synchronized oviposition and subsequent larval development, very much the pattern which is observed.

Migration and aestivation are well known adaptations by which insects cope with seasonality in their habitat (Dingle, 1978; Tauber et al., 1984). They are part of the life history strategies of many noctuid moths (Oku, 1983). Both adaptations might enable the African armyworm to survive the adverse environmental conditions during the long dry season. While migration of the African armyworm was initially disputed (Hattingh, 1941), it is now evident that moths are capable of migratory flights covering hundreds of kilometres (e.g. Brown & Swaine, 1966; Brown et al., 1969; Haggis, 1984; Rose et al., 1985). The occurrence of dormancy in the African armyworm, although it seems unlikely, can still not be excluded with certainty. Hattingh (1941), Faure (1943) and Brown (1962) found no evidence for its existence. Reports on larval and pupal diapause were subsequently published by Fonseca Ferrao & Santos (1965) and Khasimuddin (1977) respectively. Contrary to this, Gatehouse (1986) reported that extensive work in his laboratory provided no indication of arrested development in the pre-imaginal stages. Page (1988) showed that female moths vary significantly in post-emergence reproductive development and concluded that this variation is mainly due to the presence or absence of water (i.e. humidity) and to a genetic component. He found a maximum duration for arrest of oocyte development of six days, oviposition of viable eggs taking place on night 7 after emergence. As the available evidence suggests that migration occurs prereproductively in the African armyworm (Brown & Swaine, 1966; Rose & Dewhurst, 1979), such extended preoviposition periods as a result of arrested oocyte development, must considerably enhance the potential for dispersal by the moths. They can not be considered a true dormancy unless

they can be extended to durations which are likely to enable the moths to encounter suitable environmental conditions for mating and breeding. Six days seem too short compared to the temporal and spatial separation of these suitable habitats during the final months of the long dry season in the eastern African lowlands.

The occurrence of dormancy in this species has never been subjected to rigorous experimental investigation. Clearly, the most compelling questions are whether moths can live for more than the normally-observed maximum of two weeks and whether preoviposition periods can be extended over periods longer than a week under the low humidity conditions prevailing during the long dry season in the lowlands in eastern Africa. These questions were addressed during the present study.

Materials and methods

A culture of the African armyworm was maintained as described by Janssen (see Chapter 4). The pupae used in the experiments were taken randomly from different strains which had been in culture for one up to 15 generations.

Laboratory experiment. Pupae from the culture were placed singly in transparent plastic cups. Pharate adult weights were measured within 6 h before eclosion, which can be anticipated by the darkening of the pupal cuticle (Gunn & Gatehouse, 1985). Eclosion generally occurred at night. Moths were placed in pairs on the following morning in open plastic containers (volume 1,300 ml or 19,000 ml) with a lid of netting (mesh-width 2 mm) to provide sufficient ventilation. Dry river sand covered the bottom of the containers. Each was provided with filter paper as a substrate for oviposition and with a dark hiding-place for the moths during the day.

The experiment was performed in a climate chamber at $25°C(L):21°C(D)$, $12h(L):12h(D)$ and a light intensity of $25 \ W/m^2$. RH was either 35% constant or 35%(L):90%(D). Under both relative humidity regimes moths were provided with (i) **no water**, (ii) a wet **filter paper** placed in the hiding-place, (iii) **demi**(neralized)**-water** or (iv) 10% **sugar water**. The latter two feeding substrates were both presented on a cotton wool plug in a small

4 ml plastic pot. All feeding substrates were renewed daily, early in the morning.

The eggs laid by each female were removed and counted (with a maximum set to 200 per female to safe time). Females were dissected at death to see whether they had mated and whether eggs were developed. Any moth which failed to free itself after mating was excluded. For each moth, the longevity and, for each female, the preoviposition period and fecundity were recorded.

Field trial. In 1991 during the last month of the long dry season, 80 moths were released in large cages (1x1x1 m or 2.5x2.5x1 m) made of netting (mesh-width 2 mm) at Katulani and Maliku in Kitui District, one of the most important primary outbreak areas of the African armyworm in Kenya (see Chapter 2). Moths were released between September 20 and 27. The cages were placed underneath trees having varying amounts of foliage, resulting in a wide range of shading patterns between them. In the cages, hiding-places were abundant as the natural dry vegetation cover was not removed.

In addition, 18 moths were placed, individually or in pairs, inside the cages in open plastic containers (volume 1,300 ml) with a netting lid (mesh-width 2 mm). They were provided with filter paper as a substrate for oviposition and with a dark hiding-place for the day. In contrast to the cages, accurate observations on oviposition and mortality of the moths in these plastic containers could be made, while predators were excluded.

Plain water and/or 10% sugar water was provided for the moths in some cages and most plastic containers. All moths were taken from the laboratory culture. Pharate adult weights were not measured. Survival and oviposition of the moths were assessed daily at sunrise and/or sunset. When none of the moths released in a cage had been observed for several days, the cage was thoroughly searched.

A rain gauge as well as a pheromone and fermentation trap were present at both locations from the start of the experimental work up to one month after the start of the short rainy season (i.e. about December 8). Both traps were of the funnel type (Cork et al., 1989). The pheromone trap gave detailed information on activity of male African armyworm moths. The fermentation trap contained 10% port wine, 15% sugar and water (McDonald & Cole, 1991). Moths are especially strongly attracted to this fermenting

solution. They drown in the lure once they have entered the trap. Temperature and relative humidity were recorded by a thermohygrograph at Katulani.

Results

Laboratory experiment. The pharate adult weight showed no significant differences between the eight treatments (table 6-1). A very significant treatment effect was evident in the longevity of the moths. Under both relative humidity regimes they lived longest in the filter paper and demi-water treatments. Significantly shorter longevities were found in the absence of water, and on sugar water under the variable relative humidity regime. Also, under the constantly low relative humidity regime, moths lived for a shorter time on sugar water compared to demi-water but the difference was not significant.

Mating of the females was most irregular in the absence of water, under the constantly low relative humidity regime (table 6-1). In this treatment, females were unable to develop any eggs and thus to oviposit. Females in the absence of water but under the variable relative humidity regime mated more frequently and were sometimes capable of developing and laying some eggs. In the presence of water, all females mated and developed eggs under the variable relative humidity regime, which contrasts with the constantly low relative humidity regime, where mating and development of eggs were incomplete in one treatment. When females had mated and developed eggs, they still failed to oviposit in a few cases under both relative humidity regimes.

Females that oviposited usually exceeded the number of 200 eggs per female, except in the absence of water when never more than 100 eggs were laid by a single female. Consequently, the fecundity of females with no access to water was significantly lower than that of females which had access to water (table 6-1). Preoviposition periods tended to be longer under the constantly low, compared to the variable relative humidity regime but none of the treatments differed significantly.

Comparison of both sexes reveals that female pupae weighed significantly more than male pupae and that male and female moths lived for similar lengths of time (table 6-2).

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Table 6-1. Variables for moths offered different feeding substrates under two relative humidity regimes. Standard errors are given in brackets.

Relative humidity regime	35% (L): 35% (D)				35% (L): 90% (D)				P[1]
Food supply[2]	no water	filter paper	demi-water	sugar water	no water	filter paper	demi-water	sugar water	
∎No. of individuals	18	25	25	31	10	7	12	13	
Pupal weight (mg)	138.1 a	128.9 a	126.2 a	124.3 a	144.9 a	146.1 a	141.9 a	140.9 a	n.s.
	(5.0)	(4.2)	(3.5)	(3.4)	(4.8)	(7.2)	(5.7)	(5.4)	
Adult longevity (days)	2.6 a	7.3 b	7.4 b	6.3 b	3.6 a	7.4 b	7.7 b	4.1 a	***
	(0.2)	(0.4)	(0.5)	(0.5)	(0.4)	(0.5)	(0.4)	(0.3)	
∎No. of females	8	11	13	15	5	4	7	8	
Mated (%)	25	100	69	100	60	100	100	100	
Eggs developed (%)	0	100	85	93	40	100	100	100	
Oviposition (%)	0	100	77	87	40	75	100	88	
∎No. of ovipositing females	0	11	10	13	2	3	7	7	
Preoviposition period (days)		2.8 a	2.7 a	2.5 a	2.1 a	2.0 a	2.0 a	2.3 a	n.s.
		(0.3)	(0.4)	(0.2)	(0.1)	(0.0)	(0.0)	(0.2)	
Fecundity (eggs/female)[3]		185 b	186 b	200 b	46 a	200 b	200 b	200 b	***
		(15)	(14)	(0)	(34)	(0)	(0)	(0)	

1 Data were analysed by oneway ANOVA (n.s.: P>0.05; ***: P<0.001) followed by Tukey's multiple range test. Different letters within a horizontal row indicate significant differences (P<0.05).

2 For a precise description of the food supply, see materials and methods.

3 A maximum was set to 200 eggs/female.

Table 6-2. Comparison of insect variables between females and males over all treatments. Standard errors are given in brackets.

	females	males	P
■No. individuals	71	70	
Pharate adult weight (mg)	139.7	125.8	***
	(3.9)	(3.4)	
Adult longevity (days)	6.0	5.9	n.s.
	(0.3)	(0.3)	

Values for the same insect variable were compared by Mann-Whitney U test (n.s.: P>0.05; ***: P<0.001).

Field trial. At Katulani, 5 mm of rain fell in the first night after the first moths had been released. Furthermore, a slight drizzle occurred very early in the morning of the fourth day at this location. This was the only precipitation to which the released moths were exposed at either location. Temperature and relative humidity cycled very regularly during the last month of the long dry season at Katulani. They varied from 15-20°C and 90-100% at sunrise to 32-35°C and 30-40% at 3 p.m.

Most of the 80 moths in the cages could no longer be seen within two days after they had been released. A maximum longevity of 6 days was recorded in a cage where water as well as sugar water were provided. In the absence of water, the maximum was only 3 days. Though loose wings were found in a few cages as evidence of predation, most moths disappeared without leaving any signs. Eggs were only observed once on the netting of a cage in which no water was provided, 3 days after the moths had been released. They were only few in number.

The maximum longevity of the 18 moths in the plastic containers was 4 days in the absence of water and 8 days when water was supplied. Females lived longer than males (5.3 versus 3.1 days). Of the 10 females, only 4 oviposited, in all cases less than one day before they died; their average preoviposition period was 5.0 days. One of these females produced many eggs without being supplied with water.

From the start of the experimental period to one month after the start of the short rainy season, a total of only eight African armyworm moths was trapped at both locations. All were caught by the pheromone traps, and only after the rainy season had started. Though the fermentation traps never caught African armyworm moths, they caught large numbers of other moths throughout the entire experimental period. The numbers tended to decrease during the final weeks of the long dry season and rose sharply as soon as the rainy season started.

Discussion and conclusions

In studies in which the effect of food quality on fitness of the African armyworm was investigated (see Chapter 4 and 5), the maximum longevity recorded for a moth was 14 days at 25°C, a relative humidity of 90% and with access to water. Usually they died within 10 days after emergence and the average adult longevity generally ranged between 7 and 8 days. Most female moths started oviposition between 2 and 4 days after emergence; the maximum preoviposition period, followed by deposition of viable eggs, was 8 days. These data agree well with those observed in other studies (e.g. Gunn & Gatehouse, 1985, 1987; Gunn et al., 1988) and they indicate that none of the moths entered aestivation in the present study.

Pupae weighed less and lived for a shorter period than in the two host-plant quality studies (see Chapter 4 and 5). Though the experimental design in which the moths were placed was clearly different in the present study, a positive correlation between adult weight and longevity is evident over the three studies.

The laboratory experiment showed that post-emergence reproductive development is strongly influenced by the presence of water. In addition, the differences between the two relative humidity regimes, particularly in the absence of water, suggest that high air humidities can stimulate reproductive development in moths. As found by Gunn & Gatehouse (1985, 1986), female moths clearly require water for hydration and maturation of their oocytes to achieve their potential fecundity. Based on the adult weights, this can be estimated to have been over 600 eggs/female (see Chapter 4 and 5).

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Although the conditions to which the moths were exposed in the laboratory experiment, especially under the variable relative humidity regime, resembled the conditions encountered in primary outbreak areas of the African armyworm at the end of the long dry season, there were some differences. The very sudden changes in temperature and relative humidity in the climate chamber contrast strongly with the very gradual changes in the field, where temperatures tended to fluctuate more strongly. Of even greater significance might be the exposure of the moths in the laboratory experiment to only artificial light. Moreover, these moths could not contact dry vegetation and were always living in close proximity with a male. Clearly, many environmental factors might have prevented the moths from entering aestivation in the laboratory experiment. The conditions to which the moths were exposed during their larval or pupal stages might also be important in triggering aestivation.

Consequently, many more moths from gregarious as well as solitarious caterpillars were exposed to various other environmental conditions. Unusual observations were made on only two occasions. Firstly, three female moths from gregarious caterpillars, which had access to water under constantly low relative humidity conditions (i.e. 30-50%), had extended preoviposition periods of 7, 7 and 11 days, while living for 9, 13 and 12 days respectively. Secondly, two female and two male moths from gregarious caterpillars, under similar conditions but in the presence of soil and dry grasses and in the absence of mates, lived for 36, 22, 27 and 28 days respectively. Such extreme longevities have never been reported before; only Gunn & Gatehouse (1985) have mentioned exceptional longevity in a single female which lived for 20 days. When these long-lived moths died they had no fat reserves or eggs left in their abdomen. Lack of opportunity to mate and/or the presence of dry grasses seemed to have induced the moths to live longer and refrain from oviposition.

Although at one stage it appeared that moths survived better in the absence of artificial light, this seemed to be refuted by the two extremely long-lived males which were exposed to artificial light only. Further observations also showed that caterpillars can survive well on desiccating food but that their rate of development is greatly reduced. When excised maize leaves, that were not kept hydrated by supplementation of water, were provided to larvae about once every 3 days, their development was extended

by more than 10 days compared to a situation in which fresh food was provided to larvae. However, subsequent moths did not survive for more than 14 days in the presence of soil and dry grasses and in the absence of mates.

The field trial revealed that even under the quite natural conditions in the field cages, moths did not enter aestivation. Interestingly, however, post-emergence reproductive development of the female moths differed distinctly from that in the laboratory experiment under the variable relative humidity regime, which resembled the field situation most closely: in the field the proportion of females in the plastic containers which laid eggs was low and their preoviposition periods were greatly extended.

Even in the field, the artificial confinement of the moths might have prevented them from entering aestivation. They might not have been able to find an appropriate hiding-place with the necessary environmental conditions or a suitable feeding substrate, within the cages. The importance of a proper hiding-place was underlined by the signs of predation observed in some cages. As in the laboratory experiment, the conditions to which the moths were exposed during their larval or pupal stages might have also been important.

The catches in the fermentation traps showed that many insect species, in particular moths, are still active towards the end of the long dry season in the semi-arid foothill area in eastern Africa. The absence of African armyworm moths in these traps might have been due to their overall very low numbers in the area during the experimental period as revealed by the pheromone traps. More intensive trapping, using various trapping techniques, throughout Kitui District during the last months of the long dry season over several years is required to establish whether moths of the African armyworm are present or absent and, if present, whether they are active or aestivating.

The findings of the present study, in combination with results obtained in other studies on post-emergence reproductive development of moths of the African armyworm (Gunn & Gatehouse, 1986, 1987; Page, 1988; Chapter 5) and other Noctuid species with very similar life history strategies (Han & Gatehouse, 1991a, 1991b; McDonald & Cole, 1991), indicate that these moths may at least delay their reproductive development under the influence

of various environmental factors related to habitat deterioration and that a genetic component is involved. Although moths of the African armyworm seem unable to survive for periods of over one month, this can still not be excluded with certainty.

For the African armyworm, an environmental factor shown to induce delayed reproductive development is decreased food quantity and/or quality experienced by the larvae (see Chapter 5). Lack of food is likely to operate through the density-dependent phase polyphenism: *solitaria* and *gregaria* phases, extremes of a continuum, are known to differ not only in colour but also in biochemical composition, behaviour and physiology (Faure, 1943; Matthee, 1945, 1946; Gunn & Gatehouse, 1987; Woodrow, 1987). Typically, the above mentioned extended preoviposition periods were all observed for moths from gregarious caterpillars only. Gunn & Gatehouse (1987) also found longer preoviposition periods for *gregaria* compared to *solitaria* in all their treatments. Of course, food quantity and quality might be appraised by the moths as well.

During the long dry season, food quantity and quality are strongly limited by lack of rainfall. Other environmental factors that might induce delayed reproductive development of the African armyworm at this time of the year are low humidity and lack of mating opportunity. Though affecting reproduction, the laboratory experiment indicates that low humidity is unlikely to be responsible for a significant delay. This is in contrast to lack of mating opportunity, the exact influence of which certainly deserves further attention. Likewise, as sugar is known to be required to replenish a moth's fat reserves in this species (Gunn et al., 1988), sugar water, as opposed to plain water, might be required to sustain the life of moths over more than the observed maximum of five weeks with subsequent deposition of viable eggs.

As moths appear to be unable to aestivate for the duration of the long dry season, continuous development seems imperative. With regard to this, it is important to establish whether the area between the coast and the primary outbreak areas is truly unsuitable to sustain armyworm larvae during the long dry season. My observations revealed the presence of small patches of green grass in Kitui District throughout this period in 1991, a warm and dry year (see Chapter 2). In addition, two permanent rivers (i.e. the Tana and Athi) cross the area. Trapping, as proposed above, should focus especially

on these locations and might provide a conclusive answer to the question posed in the title of this paper.

The ability of moths of the African armyworm to delay their reproductive development slightly helps to explain, to some extent, the coincidence of the first catches in pheromone traps with the very first rains of the short rainy season in primary outbreak areas. However, more work is definitely needed to explain the large differences in moth numbers appearing in the primary outbreak areas between years.

Acknowledgements

7

General discussion:
consequences for strategic control

The answers to the questions dealing with aspects of the nutritional ecology of the African armyworm addressed during the present study (see Chapter 1) can be recapitulated as follows. More intense drought, resulting in soil heating to extreme temperatures towards the end of the long dry season in primary outbreak areas of the African armyworm, stimulates the nitrogen mineralization process, especially in soils that are not extremely poor in organic carbon and total nitrogen (Chapter 2). The mineralization process, which comes to a standstill during the long dry season, starts immediately after the first rains of the short rainy season have wetted the soil. A peak in the mineral nitrogen level in the soil is usually reached during the first day of rain. This peak is strongly determining the average mineral nitrogen concentration during the entire first month of the short rainy season. Furthermore, this average mineral nitrogen concentration is mainly influenced by the rainfall pattern, especially the occurrence of excessive rain (i.e. more than 40 mm in a few days) which can seriously decrease the nitrate level in the upper 25 cm of soil through leaching. No consistent effect of drought intensity on soil phosphorus and potassium levels seems to exist.

Large differences in soil nitrate level between years, due to different drought intensities and rainfall patterns, result in large differences in the average organic nitrogen content in host plants of the African armyworm during the first month of the short rainy season (Chapter 2). After warm, dry years young perennial as well as annual grasses can contain organic nitrogen concentrations of maximally 5.0%, compared to only 3.5 to 4.0% after cool, wet years. Differences in phosphorus and potassium levels between years are relatively small. Outbreaks of the African armyworm in the primary outbreak area developed only in years in which organic nitrogen concentrations of 5% were found.

In the formulation of the hypothesis to explain the drought-outbreak relationship (see Chapter 1), the emphasis was initially laid on nitrogen and not on phosphorus and potassium. This choice was thus confirmed by these results. However, all three minerals as well as the water content were included as parameters of food quality throughout the present study.

Both in wild grasses (Chapter 2) and in maize plants (Chapter 3), these plant constituents decrease over time during the first month of the short rainy season. In maize plants, the decrease is normally smallest in the water content and largest in the nitrogen and phosphorus content. However, the maximum levels of all four constituents in a maize plant do usually not or only slightly decrease during the same period, due to increased intraplant spatial variation (Chapter 3). For nitrogen in maize, maximum and minimum levels can deviate by up to 40% from the whole plant average. When assuming a similar intraplant spatial variation for wild grasses, it can be concluded that the ranges of nitrogen concentrations in the field in the years 1988 to 1991 always overlapped in spite of the, sometimes very large, differences in the average nitrogen content between the years. If caterpillar fitness is dependent on food quality, it is important for them to locate their optimal food. This becomes more and more difficult in time as spatial variation increases. Thus, the advantage for caterpillars of hatching soon after the start of the rainy season is that they will encounter the assumedly best quality of food (e.g. with highest levels of nitrogen, phosphorus, potassium and water), on a certain soil type in a certain year, with only little intraplant spatial variation.

The two systems used in the laboratory to relate the fitness of the African armyworm to the mineral composition and water content of maize leaves (Chapter 4 and 5) yielded a consistent picture: development, survival and fecundity are generally only little affected by differences in the naturally occurring levels of the four plant constituents. Moreover, at least during the first six days of larval development growth and survival are not influenced by leaf toughness (Chapter 4). Fecundity is strongly dependent on adult weight (Chapter 4 and 5). Extremely low phosphorus levels (below 0.15% dry wt.) decrease larval growth and survival very significantly (Chapter 4). Extremely low nitrogen levels (below 1.5% dry wt.) decrease larval growth slightly and probably affect fecundity, but do not influence larval survival (Chapter 5). However, these concentrations rarely occur in primary outbreak areas of the African armyworm during the first month after the start of the short rainy season (Chapter 2 and 3). Phosphorus and nitrogen concentrations in the caterpillars are about 1 and 10% dry weight. respectively (Chapter 5) and hence accumulation of both minerals by a factor of more than 6 seems outside the compensatory capacity of the species.

Table 7-1. Recovery of armyworm caterpillars released as neonate larvae on maize plants differing in nitrogen fertilization level at Katulani and Maliku in 1991, and their mean instar at recovery.

treatment (kg N/ha)[1]	number released	number recovered	% recovered	mean instar
0.0	200	11	6	1.9
12.5	200	14	7	2.0
25.0	200	11	6	1.9

[1]   Supplied as calcium ammonium nitrate (CAN).

As such, the findings of the present study support the hypothesis proposed to explain the drought-outbreak relationship for the African armyworm only partly. The observed weather-soil-plant interactions agree with the hypothesis, but are more differentiated than originally thought: soil type and rainfall pattern turned out to be important factors. However, the assumed plant-armyworm interaction, as studied under laboratory conditions, seems to be incorrect. The observed large differences between years in plant nitrogen level are therefore probably not of key importance in explaining the differences between years in outbreak development of this insect.

This is supported by field data from a fertilization experiment with maize plants laid out at Katulani and Maliku in 1991 (table 7-1). The nitrogen level in the leaves of the maize plants was not determined, but had previously been shown to increase significantly at both locations due to fertilization with 12.5 kg N/ha. Fertilization with 50 kg N/ha did not result in any further increase. Six hundred neonate larvae were released on three consecutive days in equal numbers over the three treatments. At recovery, their average absolute age was 6 days for all treatments. No effect of the fertilization treatment on survival as well as development, rated by the mean instar, were detected.

Survival was much lower than under laboratory conditions. Though the caterpillars might have left the patch of maize plants on which they were

Table 7-2. Recovery of armyworm caterpillars released as neonate larvae at Katulani and Maliku in 1991, and their mean instar at recovery. The total amount of rain experienced by the caterpillars between release and recovery is shown as well.

releasing date	recovering date	age (days)	number released	number recovered	% recovered	mean instar	rainfall (mm)
091291	161291	7	339	7	2	1.0	17.3
101291	161291	6	90	2	2	2.0	16.3
111291	161291	5	171	27	16	2.2	0.8

released, mortality factors like natural enemies and unfavourable weather are likely to have taken their toll. Rainfall seems to be such a detrimental factor to armyworm survival (table 7-2). While only few (2%) of the caterpillars released on the first two days in 1991 could be recovered, a reasonable number (16%) survived of those released on the last day. Moreover, the mean instar at the recovering date shows that the later larvae were released, the better they developed; while the larvae released on the first day were all still first instars on the recovering date when their absolute age was 7 days, the larvae released on the last day were in their second and some even third larval stage at the time of recovery when their absolute age was only 5 days. These differences in survival and development of the larvae released on the three subsequent days are thought to be due to the meteorological conditions prevailing during these days. December 9 and 10 were very wet and damp in the area around the two locations where the caterpillars were released. Though no heavy rainfall was recorded (table 7-2), slight showers occurred on and off during these two days even at day-time, thus keeping the sun away for long periods something which is quite unusual for Kitui District during the short rains. On the morning of December 11, while the last caterpillars were released, fog was covering the area and final showers fell. Then, the weather turned sunny and no rain was recorded anymore up to December 16, the recovering date.

   In a similar experiment, only 7 (1%) of 675 released caterpillars were recovered in 1989. The high mortality could then be attributed to a very heavy downpour of rain (57 mm in a few hours time) in the night preceding the day on which the caterpillars were recovered; many more caterpillars were observed on the preceding day, though no exact counts were made.

   Like the laboratory experiments, these field observations indicate that the nitrogen status of host plants, within the range encountered in the field during the first month of the short rainy season, is of no importance to the larvae (table 1). Moreover, they show that natural enemies are not the only factor causing mortality among the larvae; rain and very high relative humidities are also detrimental to young caterpillars.

   Though food quality clearly seems to be of minor importance to armyworm fitness, it is felt that a more extensive study of its interactions with other mortality factors is still required. As interactions might not show up during the first week of larval development (table 2), such a study should cover the whole period from larval hatch up to pupation. For example, caterpillars that are feeding on food low in organic nitrogen might have to consume more foliage to obtain a sufficient amount of this nutrient, which might render them more vulnerable to other mortality factors especially during the last instars when most food is consumed. Ideally, the effects of natural enemies and rainfall on caterpillars that are feeding on maize plants differing in nitrogen level, and possibly also in age as this might be another important determinant of armyworm fitness, should be assessed under field conditions. The factors 'nitrogen level' and 'age' of the maize plants could be laid out in a randomized block design with a number of repetitions. Exclusion of natural enemies and rainfall in some blocks, and not in others, could then reveal the relative importance of these four factors in shaping armyworm fitness.

For two reasons the question of how the African armyworm survives the long dry season (Chapter 6) became more important towards the end of the present study. First, the original hypothesis seemed more and more to be partly incorrect in the course of the study, and thus unable to explain the drought-outbreak relationship. Second, large differences between years were found to exist in the moth numbers caught at and near sampling areas in Kitui District at the start of the armyworm season (Chapter 2), presumably

before any feeding by caterpillars on host plants had occurred in the area. This would exclude host plant quality as a factor possibly influencing these moth numbers. The question of survival during the long dry season then seemed to be of critical importance.

The occurrence of aestivation in the adult stage should doubtlessly be a major issue in further study on the epidemiology of the African armyworm (Chapter 6). If it exists, it seems most likely that moths can survive for the duration of the whole long dry season. If it is nonexistent, the ability of moths to delay their reproductive development under dry season conditions seems, at best, to offer them an improved chance of locating suitable oviposition sites in the eastern African lowlands during this period. The extent to which reproduction can be successfully delayed should then be determined. Furthermore, it needs to be established whether the eastern African lowlands are truly unsuitable for sustaining armyworm larvae during the long dry season.

The observed occurrence of armyworms in 1988 and 1991 suggests that a generation of caterpillars, developing in the lower, eastern part of Kitui District, might have preceded the moths that were caught at and near the sampling areas when the short rainy season started at these locations. Though in that case host plant quality would at least theoretically have the potential to influence the number of these moths, poor rainfall is thought to be of greater significance. Especially when a first generation would be initiated by, usually very localized, 'off-season' rain in the second half of September or the first half of October, like presumably happened in 1988 (Chapter 2), caterpillars are likely to develop in the absence of any further rain under very sunny and warm weather conditions, thus probably allowing very high survival. When the short rainy season subsequently starts towards the end of October or in the first half of November and wets whole Kitui District, a rather large population of moths (which were possibly holding their reproductive development until further rain) can cause the first outbreaks.

Clearly, further study on armyworm epidemiology should concentrate on two points: 1) validation of some of the laboratory results obtained in the present study (see Chapter 5) under field conditions while simultaneously assessing the effects of plant age, rainfall and natural enemies on fitness, and 2) the dry season phenology of the African armyworm. Both points are likely to

increase our understanding of the observed drought-outbreak relationship in this species. Until we know the underlying mechanism of this relationship, long-range forecasts of outbreaks are unlikely to be improved. Though the occurrence of armyworms during the first months of the short rainy season in Kitui District was always correctly predicted in the years 1988 to 1991, based on the rule of thumb that outbreaks only develop after years that have been relatively dry and warm, a more reliable anticipation of the severity of an armyworm season might be obtained.

The fact that a first generation of probably *solitaria* phase caterpillars might have gone unnoticed in the lower, eastern part of Kitui District in both 1988 and 1991 indicates that the pheromone trap network in this area is still too dispersed to monitor all armyworm activity. As moth numbers founding such a first generation can be expected to be very low, a relatively high density of traps is likely to be required. If initiated by localized off-season rain, an increase in trap density is also needed. Such rain can be expected to be most prevalent and intense in the lower, eastern part of Kitui District, where heating of the air is certainly more intense than in the higher, western part where most of the sampling areas were located that were used in the present study.

The concept of strategic control aims at controlling outbreaks that are critically in terms of the potential they have in generating upsurges in following generations. The very first outbreaks of a season in the primary outbreak areas are definitely 'critical' in this sense. They consist of *gregaria* phase caterpillars, which can severely damage crops when densities are high enough. If it is true, as some of the observations in the present study indicate (Chapter 2), that these caterpillars constitute the second generation and not the first, the question should be addressed whether it is possible to control the first generation of *solitaria* phase caterpillars such that no outbreaks develop. An additional reduction of the area over which control would be required might be achieved. As mentioned above, a more detailed monitoring network is a first prerequisite to locate the first generation. Whether the *solitaria* phase caterpillars can subsequently be eliminated sufficiently, remains to be seen.
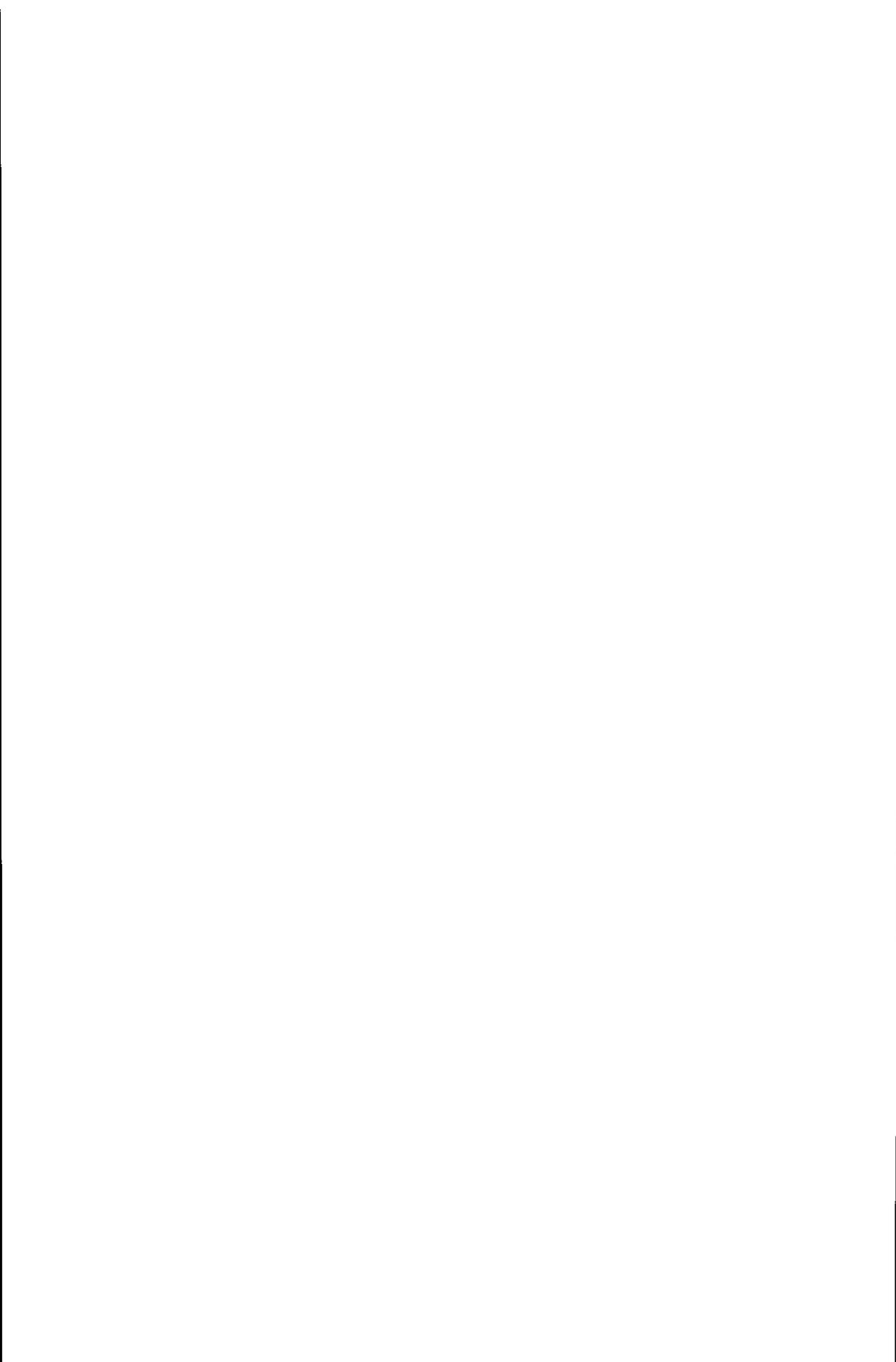
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Johannes Antonius Marie Janssen was born on February 10, 1964 at Roermond. He grew up in a cattle-dealer's family in the village of Linne (Limburg, the Netherlands). In 1982 he graduated from the 'Bisschoppelijk College Schöndeln' at Roermond. In the same year he started his biology study at the Wageningen Agricultural University. He passed the first year examination (propaedeutic exam) with honours in 1983. During his graduate studies he was involved in research projects at the departments of Entomology, Plant Physiology and Theoretical Production Ecology. Thanks to grants from the Dutch Ministry of Agriculture, Nature Management and Fisheries and the 'Stichting Landbouwhogeschoolfonds' he could study during seven months at the University of California, Berkeley and Riverside. His attention was primarily focused on the biology of plants, their enemies (the insects) and friends (the parasites of the enemies). During his study, he was employed as a teaching assistant at the above mentioned Wageningen Agricultural University departments as well as at its department of Plant Taxonomy. The Master of Science was obtained in January 1988.

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Het in dit proefschrift beschreven onderzoek werd door hem uitgevoerd in de periode 1988-1992 vanuit de vakgroep Entomologie van de Landbouwuniversiteit te Wageningen, waaraan hij aanvankelijk als tewerkgesteld erkend gewetensbezwaarde en aansluitend als toegevoegd onderzoeker was verbonden. In de genoemde periode verbleef hij jaarlijks enige maanden in Kitui District, Kenya, voor het verrichten van veldwerk onder de auspiciën van het 'Regional Armyworm Project' van de 'Desert Locust Control Organization of Eastern Africa'. Daarnaast voerde hij een deel van het onderzoek uit op de vakgroep Bodemkunde en Plantevoeding van de Landbouwuniversiteit te Wageningen.

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