Chemoecological studies reveal causes for increased population densities of *Zonocerus* (Orth.: Pyrgomorphidae) and offer new means for management*

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O.W. Fischer and M. Boppré.
Forstzoologisches Institut der Albert-Ludwigs-Universität, D-79085 Freiburg i.Br., Germany

Summary. Grasshoppers of the genus *Zonocerus* sequester pyrrolisidine alkaloids (PAs) not only from certain nutritional host plants but also independent of dietary requirements. Storage of PAs serves protection of the insects from antagonists, and thus acquisition of these secondary plant chemicals modulates the grasshopper's population dynamics. Flowers of the introduced weed *Chromolaena odorata* (Asteraceae) represent a novel and inexhaustible resource of PAs – but only for populations in the dry-season. Evidence is provided that better performance related to the presence of *Chromolaena* is a reason that dryseason populations became a serious pest in coincidence with the spread of the weed. The chemoecological knowledge on the *Zonocerus*-PA relationship permits the development of selective baits, and with environmentally sound and cost-efficient application of insecticides the species can be lured to its doom. Multiple means of employing PA baits within integrated pest management (IPM) concepts are possible, i.e., strategies of population management can be tailored according to actual demands and conditions. Apart from fighting the grasshopper in individual farms, a general reduction of *Zonocerus* populations is suggested to lower mean levels of abundance in areas with frequent upsurges; this could be done by combining PA baits with mycoinsecticide technology.

Résumé. Les sauteriaux du type *Zonocerus* séquestrent les alcaloïdes de pyrrolicidine (AP) de certaines plantes hôtes non seulement à des fins nutritionnelles, mais également pour des raisons d'un tout autre ordre, les AP emmagasinés par les insectes leur servant à se protéger de leurs ennemis. Ces composants chimiques végétaux secondaires influent ainsi sur la dynamique des populations de sauteriaux. Les fleurs de la plante introduite dite Herbe du Laos, *Chromolaena odorata* (astéracées) constituent une source de AP renouvelable et inépuisable – toutefois uniquement pour ce qui est des populations de la saison sèche. Etant donné que les performances des insectes s'améliorent grâce à la présence de *Chromolaena*, il existe une corrélation certaine entre la pullulation de *Zonocerus* durant la saison sèche et la propagation de *Chromolaena odorata*. La connaissance du rapport chimio-écologique entre *Zonocerus* et les AP permet la mise au point d'appâts sélectifs attirant les sauteriaux vers de insecticides non destructeurs de l'environnement et rentables économiquement. Il existe de multiples moyens d'employer des appâts à base de AP selon les concepts de la lutte intégrée, c'est-à-dire qu'il est possible d'adapter les stratégies de contrôle des populations aux besoins et conditions existants. A part la lutte contre les sauteriaux menée au niveau des exploitations agricoles, il sera utile de réduire de façon générale les populations de *Zonocerus* afin d'abaisser les taux moyens d'abondance dans les zones fréquemment infestées. Ceci pourra être réalisé en associant les appâts à base de AP à la technologie des mycoinsecticides.

Introduction

The variegated grasshopper, *Zonocerus variegatus*, is extremely polyphagous and more than 60 arable crops, including cassava, maize and cotton, as well as plantation trees such as teak and *Citrus*, have been reported to be vulnerable to damage by this species. (For synoptic accounts on *Zonocerus* see, e.g. Chapman et al. 1986 and Chiffaud and Mestre 1990.) *Z. variegatus* occurs all over West Africa, and in this large and diverse region its pest status varies considerably according to different climatic conditions, to plants cultivated and to land use systems. To date, no reliable data on economic losses caused by *Zonocerus* are available (see below), but locally and temporarily serious damage certainly occurs, necessitating management.

Due to an apparent linkage between the population dynamics of *Zonocerus* and the introduction and continuing spread of *Chromolaena odorata* in Africa (see below), an increase of problems with *Zonocerus* in both agriculture and silviculture is foreseeable (cf. FAO 1990).

Here, we report on ecological characteristics of *Zonocerus variegatus*, in particular on the influence of plant secondary chemistry on its population dynamics, and in consequence we suggest management means to be implemented in IPM concepts tailored to specific demands and conditions.

The information conveyed is principally also valid for *Z. elegans*, which inhabits South and East Africa; it is much less studied, but with respect to its biology and ecology it is most similar to *Z. variegatus* (Wickler and Seibt 1985).

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Factors affecting population dynamics of *Zonocerus variegatus*

Seasonality

Generally, the variegated grasshopper is univoltine (egg diapause: six to eight months; six larval instars of approx. One to three weeks each; adult life-span approx. Two months), but under certain climatic conditions it may occur in two distinct and alternating population peaks (e.g. in Benin). Interestingly, dry-season populations seem to achieve much higher densities than wet-season ones, and serious damage happens in dry seasons only (Anonymous 1977; Page 1978).

Antagonists

Conclusive studies on the role of antagonists on population dynamics as well as on influences of abiotic factors are missing. *Zonocerus* appears well protected, and comparatively few predators are known (Chapman and Page 1979). Upon disturbance, older larvae and adults eject large amounts of repulsive secretion (pyrazines; W. Francke, personal communication); also, secondary compounds from certain plants are stored for protection (see below). Reported predation by lizards, mantids, spiders, solifuges and tettigonids (e.g. Page 1978; Chapman 1962) apparently has little impact on *Zonocerus* populations, as does the nematode *Mermis* (Matanmi 1979) and the phorid fly *Megaselia* (Gregorio and Leonide 1980).

The pathogenic fungus *Entomophaga grylli* is considered to be an important mortality factor under wet conditions (Toye 1982; Chapman and Page 1979), and the parasitic fly *Blaesoxipha filipjevi* (Sarcophagidae) sporadically affects adults at oviposition sites and causes female *Zonocerus* to lay only one egg pod (Taylor 1964; Chapman et al. 1986).

Zonocerus-plant relationships

Zonocerus not only feeds on a wide variety of plants (refs in Chiffaud and Mestre 1990) but appears to require a mixed diet for proper development; therefore considerable movement between plants occurs: *Zonocerus* may leave a plant and change to another species even though there is still plenty of food. Our own observations support those of McCaffery and Harris (unpublished, quoted by Chapman et al. 1986): "A consequence of nymphal mobility is a continual turnover of the insects in any one area such as a field of cassava; e.g. a complete turnover of the population in a 100 m2 cassava field may occur within 10 days."

Feeding experiments have revealed that very few plants – in particular cassava (*Manihot esculenta*) – fulfil the nutritional requirements of the grasshopper. Insects reared on cassava develop most quickly, gain most weight and produce most eggs (Bernays et al. 1975; Iheagwam 1979; McCaffery et al. 1978). Although many cassava varieties produce noxious cyanogens (Bernays et al. 1977a; McCaffery 1982), *Zonocerus* can utillise this plant through group attack, which circumvents the plant's defences by exhausting its protective devices (Chapman 1985).

Intensified cultivation of cassava and the use of non-cyanogenic varieties apparently is one factor responsible for increasing densities of dry-season populations. A number of native herbs and creepers which mediate good performance are annuals which are not available in the dry season; cassava, however, remains in full foliage deep into the dry season when most other potential host plants have dried up (Bernays et al. 1975; cf. Chapman et al. 1986).

Although he could not provide evidence of a possible link, Toye (1974) has suggested that the increased dry-season populations of *Zonocerus* might be related to the spread of the introduced weed *C. odorata*. Because *Chromolaena* is nutritionally inadequate for *Zonocerus* (see below), it has long been a puzzle as to how this plant influences this grasshopper's population dynamics.

Zonocerus' relationship to pyrrolizidine alkaloids (PAs)

Zonocerus sequesters pyrrolizidine alkaloids from plants and stores them for its defence (Bernays et al. 1977b; Biller et al. 1994; O.W. Fischer, unpublished data). To non-adapted animals, vertebrates as well as invertebrates, PAs act as a taste deterrent, and PAs protect not only the plants producing these secondary chemicals from being eaten but also adapted insects which gather them from plants and store them (refs. in Boppré 1986, 1995).

Sources of PAs are found among the many host plants of the grasshopper: *Crotalaria* (Fabaceae), *Heliotropium* (Boraginaceae), *Emilia*, *Ageratum* (Asteraceae) and others. (For occurrence of PAs see, e.g. Smith and Culvenor 1980; Rizk 1991; Hartmann and Witte 1995.) Thus, as with many insects, for *Zonocerus* plants may represent much more than food sources because they not only utilise the plants' nutrients but also their noxious secondary compounds.

Although sequestration of secondary plant chemicals by insects is usually linked with feeding, there are so-called pharmacophagous insects that search for specific secondary compounds directly, consume them independently of food uptake and use them to increase their fitness (Boppré 1984, 1995). For example, pharmacophagy with respect to PAs is known for numerous butterflies and moths (Danainae, Arctiidae and others), some flea beetles (*Gabonia*) and chloropid flies which are attracted to dry parts of PA plants, and also to the pure compounds. The Lepidoptera, for example, gather PAs for use as precursors for the biosynthesis of male pheromones and/or store these plant metabolites for their own defence; *Creatonotos* spp. (Arctiidae) even make use of them as morphogens which specifically regulate the growth of the male scent organs (for reviews on PA pharmacophagy see Boppré 1986, 1990, 1995).

For *Zonocerus*, dry parts of various PA plants, extracts of these plants as well as certain pure PAs provide very effective lures for all stages of both sexes; the insects take up PAs and store them (Boppré and Fischer 1993, 1994; Boppré et al. 1984; O.W. Fischer and M. Boppré, unpublished data). Therefore, *Zonocerus* is PA pharmacophagous; it utilises a variety of plants for obtaining nutrients ("grocer's shops"; e.g. *Manihot*), others for obtaining nutrients plus PAs ("supermarkets"; e.g. *Heliotropium*), and yet others solely to accumulate these secondary compounds ("pharmacies"/"drug stores"; dry parts of PA plants); the latter case can only be recognized experimentally. The pharmacophagous behaviour not only affects the insects' population dynamics and provides an explanation for the puzzling role of *Chromolaena*, but it also enables the development of a bait to lure and concentrate *Zonocerus* (see below).

The special role of Siam weed, Chromolaena odorata, *for Zonocerus*

C. odorata K. & R. (*Eupatorium odoratum* L.) (Asteraceae: Eupatoriae) is a perennial shrub native to the tropical Americas. Following its introduction into India, *C. odorata* invaded South-East Asia from whence it subsequently reached Africa in the late 1930s and became a dominant weed in the 1970s. In its new habitats it spreads quickly, forming dense thickets of up to two metres in height which flower once a year during the dry season. It has become a major weed which seriously interferes not only with forestry, pastures and plantation crops but also with natural vegetation (e.g. Ambika and Jayachandra 1990; Goodall 1995). In favour of its invasive traits is its apparent chemical protection: vertebrate herbivores avoid it entirely, and there seem to be only a few adapted insect phytophages. (For synoptic accounts on *C. odorata* see, e.g. Audru et al. (1988), Cruttwell McFadyen (1989), Ambika and Jayachandra (1990) and M. Boppré, unpublished data.)

Although young hoppers of *Zonocerus* frequently aggregate overnight on the tips of *Chromolaena* plants and feed sporadically in small amounts, this plant is not adequate for normal development (Bernays et al. 1975; McCaffery et al. 1978). The flowers are consumed on a large-scale (Modder 1984), but they alone do not suffice as food (see Chapman et al. 1986).

Why then does the insect become a pest preferentially where the foreign weed occurs?

Modder (1984, 1986) reported that flowers of *Chromolaena* are attractive for all instars of *Zonocerus*; the attractive power of these inflorescences is highest when florets mature and show stigmata, which are preferred organs for starting consumption (Modder 1984, 1986). Interestingly, such flowers are not consumed entirely, as one might expect and as the grasshoppers do with flowers of other plants; rather *Zonocerus* is quite choosy; young hoppers select the stigmata, older ones and adults ingest the entire set of florets of a *Chromolaena* flower but leave the bracts alone as much as possible (Boppré and Fischer 1994, and Fig. 1 therein), i.e. in order to get access to the ovaries within these small capitulae.

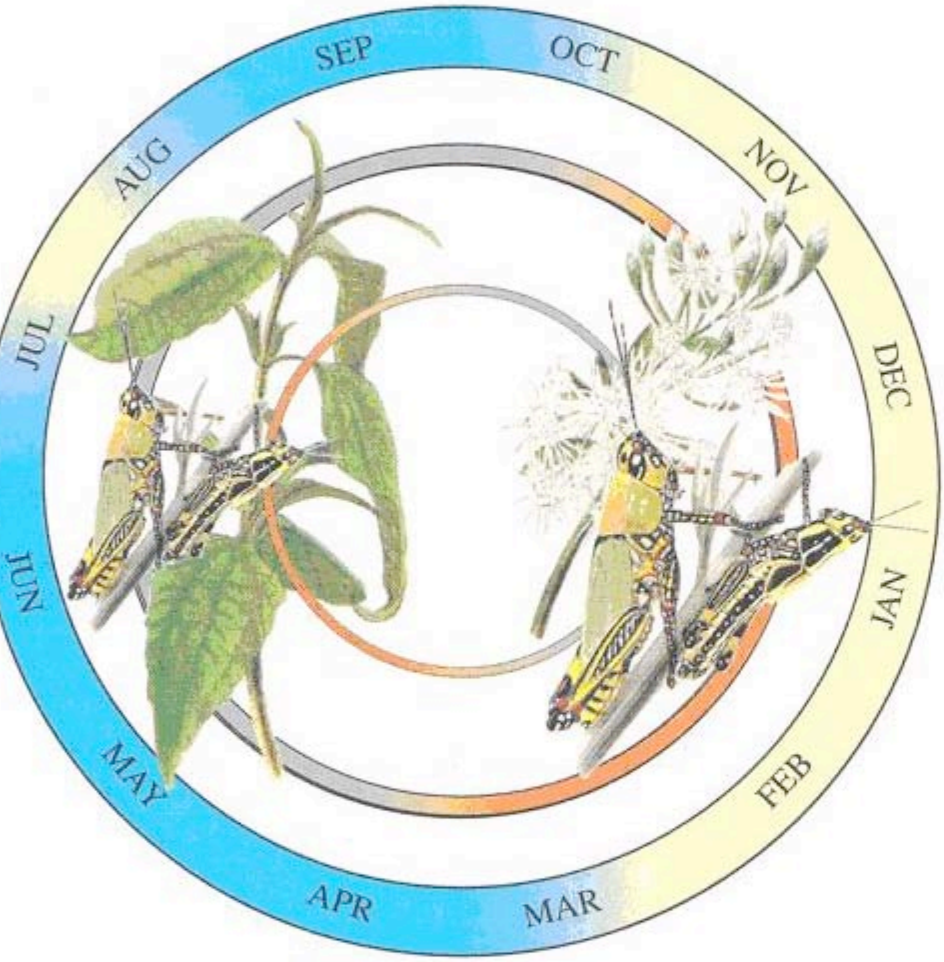
Flowers of *Chromolaena* can be used to lure *Zonocerus* (Modder 1984, 1986), but its foliage does not elicit any response. However, roots of Siam weed exhibit strong attractive power, particularly if chopped into pieces, dried and re-moistened (see below and Boppré and Fischer 1994; O.W. Fischer and M. Boppré, unpublished data).

Biller et al. (1994) provide detailed chemical analyses showing that *C. odorata* produces a mixture of PAs with rinderine and intermedine as major components plus 7*O*-angeloyl-retronecine, 9*O*-angeloyl-retronecine and acetylrinderine, all occurring exclusively as nitrogen oxides. In the ecological context, the distribution of PAs in *Chromolaena* is particularly interesting: highest concentrations occur in the roots and in the mature inflorescences with a maximum in the unripe ovaries. The foliage is devoid of PAs. (Non-PA secondary chemicals represent the anti-herbivorous mechanism of the foliage.) Moreover, as the florets mature and stigmata and style arms appear, the PA content increases.

These chemical data precisely match the results of the behavioural studies mentioned above. Also, the insects have been shown to store PAs from *Chromolaena* and transfer them into the eggs (Biller et al. 1994; O.W. Fischer, unpublished data; cf. Boppré 1991; Boppré et al. 1992). Thus, for dry-season populations of *Zonocerus* flowers of *Chromolaena* provide a novel, rich and most readily available – although temporally restricted – source of PAs.

In conclusion, the puzzle of the coincidence of the spread of *Chromolaena* and the increased abundance of *Zonocerus* seems to be explicable by the following hypothesis (cf. Boppré 1991): *Zonocerus* enjoys a non-nutritional association with *Chromolaena*, which provides PAs; these secondary plant compounds are stored and chemically protect the grasshoppers and particularly their diapausing eggs from antagonists, thus giving rise to the increased fitness and higher densities of certain (e.g. dry-season) populations of *Zonocerus*. Without *Chromolaena*, i.e., either before its introduction or in areas where it is absent or in the wet season when *Chromolaena* does not bloom, PAs often seem to be a limited resource restricting the grasshoppers' reproductive success.

This explains why *Zonocerus* appears as a pest preferably where *Chromolaena* occurs, also why we have to envisage increasing problems with this grasshopper for the future. However, it does not imply that the novel source of PAs – flowers of *Chromolaena* – is the sole reason for increased and harmful dry-season populations, and it does not rule out that the increased cultivation of cassava, deforestation and/or lack of antagonists are additional factors favouring an increase in dry-season *Zonocerus* populations. In any case, *Chromolaena* appears to influence population dynamics to a greater extent than the indigenous PA plants, which are usually quite rare or contain small amounts of PAs. However, particularly high population densities can of course also be triggered by indigenous PA plants. For example, an outbreak of *Zonocerus elegans* in 1987/88 in Tanzania where no *Chromolaena* occurs seems to be correlated to preferred feeding on *Ageratum* (Nyambo 1991). *Ageratum* is a common weed containing PAs similar to those in *Chromolaena* (Wiedenfeld and Röder 1991), but it is less competitive and much less persistent in comparison with *C. odorata*.



Zonocerus variegatus (L.) (Pyrgomorphidae) is a polyphagous African grasshopper. In parts of West Africa its dry-season population has reached pest status, apparently in coincidence with the spread of the introduced weed *Chromolaena odorata* (L.) K. & R. (Asteraceae: Eupatoriae), which, however, is not a food plant for *Zonocerus*.
Zonocerus sp. sequester pyrrolizidine alkaloids (PAs) not only from certain nutritional host plants but also independent of dietary requirements. Storage of PAs serves to protect the insects from antagonists, and thus aquisition of these secondary plant chemicals modulates the grasshopper's fitness. Flowers of *Chromolaena odorata* represent a novel and inexhaustable resource of PAs, but only for populations in the flowering season, and there is evidence that better performance related to the presence of *Chromolaena* is a reason that dry-season populations became a serious pest in coincidence with the spread of the weed.
The figure illustrates the two distinct and alternating populations of the univoltine *Zonocerus variegatus* in southern Benin. Outer circle: seasons (yellow: dry; blue: wet). Central circle: high abundance of dry-season *Zonocerus*; inner circle: low abundance of wet-season *Zonocerus*; orange: occurrence of larvae/adults; grey: eggs. Flowers of *Chromolaena* bloom in December and January only.
The chemoecological knowledge of *Zonocerus* and *Chromolaena* demonstrates the risk of introduction of foreign plants in (agro-)ecosystems by providing an example of the hidden and unpredictable effects secondary plant chemicals - even those which are not required for nutrition - may have on the population dynamics of insects. It also permits the development of selective baits as a new means for management, and with environmentally sound and cost-efficient application of insecticides, the species can be lured to its doom.

On the pest status of *Zonocerus variegatus*

Z. variegatus is a polyphagous species, and high population densities potentially may become harmful to a large number of cultures. In the literature, this insect is generally regarded as a serious pest. To date, hardly any data on damage to crops are available (see, e.g. Baumgart 1994), although the need for proper evaluation of its pest status as a basis for developing economically appropriate control strategies has often been recommended (e.g. Toye 1982). A recent questionnaire inquiry by J.A. Timbilla et al. (unpublished) at institutions in 36 African countries has provided only little data on damage and costs for control, respectively. However, the great attention this grasshopper receives is reflected in the publication of more than 250 papers within the past 60 years; for sure, this is not based on academic interest but underscores its economic importance. "There is a consensus among entomologists that, at least in some countries, the insect has changed in the last 15 – 20 years from a spasmodic, generally minor pest to a more regular and relatively major problem" (Chapman et al. 1986).

Obtaining reliable data – not only on quantitative but also on qualitative economic losses as well as on additional injuries such as transmission of bacterial (CBB) and viral (OMV) diseases by *Zonocerus* (Terry 1978; Givord and Den Boer 1980; Nkouka et al. 1981) – is probably difficult because of the many crops affected differently, the peculiar habits and bionomics of the grasshopper and the different agricultural systems involved. Dispersal of *Zonocerus* obstructs both assessment of damage and control: *Zonocerus* is not only polyphagous but usually requires changes in its diet for proper performance (cf. above); in consequence, high population densities may be found on a field, but damage does not become serious because this grasshopper leaves a host although it still provides plenty of food. We do not know of any other pest insect with such a trait. Movements related to changes of host plants has also been reported by Nwana (1984), who found that the insect stays longer in unweeded fields than in weeded ones, which is likely due to diversity of hosts.

Although the question is open under which circumstances control actions are justified and at which expenditure, there are many situations necessitating management of *Zonocerus*. Also, it is beyond doubt that there is great spaciotemporal variation. Thus, the goal must be a pest management concept permitting tailoring of means according to local conditions with respect to population density and also to availability of control means. In particular, prophylactic actions are required which have to be conducted at a community level (see below).

Current means and concepts for controlling *Zonocerus*

Various conventional control methods, i.e., use of insecticides, pathogens and mechanical means, are applicable to *Zonocerus*. Costly and environmentally hazardous spraying of synthetic chemicals are mainly applied, although IPM approaches have been advocated repeatedly (Anonymous 1977; Page 1978; Toye 1982). The most recent one by Modder (1986) consists of mechanical exposure of egg pods, spraying of insecticide on roosting nymphs and trapping nymphs and adults with flowers of *Chromolaena* (hoping to eventually find "the volatile chemical substance from the inflorescenses" and use this with insecticide after the flowering season and before egg laying).

Modder’s (1986) concept is quite acceptable, but we disagree with his idea of protecting *Chromolaena*. Assuming that *Chromolaena* has no relevance to populations of *Zonocerus*, he believes it would be better to preserve *Chromolaena* in order to distract nymphs away from economically important plants. This opinion provokes contradiction apart from the erratic assessment of Siam weed on the fitness of *Zonocerus*: on the one hand, because the grasshoppers require nutrients not provided by *Chromolaena*, they cannot be confined to the weed; on the other hand, *C. odorata* is ecologically and economically harmful in many ways, e.g. through suppression of succession of natural vegetation and in being a fire hazard (e.g. Ambika and Jayachandra 1990; Crutwell McFadyen 1989; M. Boppré, unpublished data).

Management of pest populations of *Zonocerus* in view of PA pharmacophagy

The chemoecological knowledge on the relationship of *Zonocerus* to plants containing pyrrolizidine alkaloids, in particular the attractive and phagostimulatory power of PAs, can be utilised for developing a bait for IPM purposes (cf. Boppré et al. 1984; Boppré 1991; Boppré and Fischer 1993, 1994). Of course, as with other cases employing lures (e.g. pheromone baits used in the control of moth pests), there is competition between man made lures and natural ones. A major peculiarity has to be observed in addition: PAs are not required to maintain the life of *Zonocerus*, rather these secondary plant compounds are utilised supplementarily. Thus, the motivation of the insect to search for PAs is secondary compared with ordinary feeding behaviour or any sexual activities, and *Zonocerus* responds to sources of PAs less "automatically" than does a male moth to female sex attractants; an *instant* response cannot necessarily be expected.

Stimuli involved in locating sources of PAs

Although *Zonocerus* is pharmacophagous with respect to PAs and attracted by dry plants of various species and also by pure PAs (which proves that indeed only PAs and not any other secondary plant chemicals lure the insect), it is unable to discriminate between intact, living PA-containing plants and plants devoid of PAs over a distance. This is because in living plant tissue PAs are confined to cell vacuoles, which prevents detection without physical contact; also, PAs are large molecules with insufficient volatility for olfactory perception. However, *Zonocerus* is capable of perceiving PAs with its gustatory (contact-chemo)receptors on the mouth parts and can thus only detect intact PA plants upon contact; PAs then act as phagostimulants. (It is interesting to note that in combination with the "good taste" of PAs, *Zonocerus* accepts higher doses of insecticides; i.e., repelling properties of pesticides are reduced.) However, when plants are mechanically damaged (e.g. by phytophages) or if they wither and wilt, PAs get exposed to the outside environment; and – as with pure PAs – the atmospheric conditions trigger their disintegration into a variety of derivatives, some of which are volatile and perceivable by olfactory receptors located on the insects' antennae. A major initial step in derivatization is hydrolysis, and therefore the attractive power of dry plant material can be increased by chopping and re-moistening it with water. Also, the identical response of *Zonocerus* to a variety of PA sources containing different PAs can be explained by the existence of a common volatile derivative (for details on the "PA odour" see M. Boppré, unpublished data).

PA baits – versatile tools

Attraction with flowers of *Chromolaena* is the simplest way of baiting *Zonocerus*; however, their attractivity quickly fades, and inflorescences are only available once a year for a few weeks (moreover at a time when there is heaviest competition with flowering stands of *Chromolaena*). PA baits made up from roots (or foliage, in case) of PA plants provide a year-round alternative. Other PA-pharmacophagous insects are usually rare or absent in areas where *Zonocerus* is present and can if necessary be kept off PA baits by simple mechanical means. Thus, such simple baits represent versatile tools with high specificity to concentrate *Zonocerus* for killing and for monitoring purposes, respectively. (Monitoring of later instars and adults is otherwise difficult, because they do not congregate at the tips of foliage as do early hoppers.)

For control with PA baits, insects can be lured to the poison instead of the poison being brought to the insects; this permits environmentally safe reduction of populations with a minimum of insecticide. Apart from spraying insecticides on insects gathering at baits, combinations of PA bait and insecticide (attracticides) can be produced which work maintenance-free for more or less long times. Depending on the demand, attracticides employing PAs offer a menu of options which permit tailoring of the most appropriate control strategy:

Types of PA baits/attracticides to lure *Zonocerus*

There are two general types of attracticide applications (O.W. Fischer and M. Boppré, unpublished data):

- Baits for mechanical trapping and for use in combination either with pathogens or stomach-acting pesticides, utilising both the attractive and the phagostimulatory power of PAs; require regular re-moistening (necessary for emission of the volatile derivatives).

type of PA source	comments
• mechanically damaged leaves of PA plants (spp. of fades *Heliotropium*, *Crotalaria* and others)	easily obtainable; available all year; attractivity after a few days but can be regained by moistening

• dried, chopped and re-moistened roots of PA-plants (spp. of *Heliotropium*, *Chromolaena* and others)	easily obtainable; available all year; attractive for weeks if stored dry; attractivity can be regained after years by re-moistening

- Baits for mechanical trapping and for use in combination either with pathogens or pesticides which act upon contact. The attractive material is confined in polyethylene bags which act as dispensers for slow and continuous release of "PA odour"; regular re-moistening in this case is not necessary, but the dispenser needs to be protected from being eaten by the insects.

type of PA source	comments
• dried and chopped parts of PA-plants (spp. of *Heliotropium*, *Crotalaria*, *Chromolaena* (roots only))	easily obtainable; available all year; attractive for weeks if stored dry; attractivity can be regained after years by re-moistening
• methanolic raw extracts of PA plants1, 2 (including spp. not occurring in the habitats of *Zonocerus*!)	easy to produce with simple laboratory equipment; can be standardized; shelf-life of many years
• purified extracts of PA plants 1, 2 (including spp. not occurring in the habitats of *Zonocerus*!)	easy to produce with laboratory equipment; can be standardized; shelf-life of many years
• pure PAs1, 2, 3 (e.g. heliotrine, monocrotaline axillarine, retrorsine) extracted from plant material	best for standardizing, requires professional production; shelf-life of many years

1Applied on substrates such as cardboard, filter paper, glass fibre filters, sponge clothes or any other material.
2Combination with stomach-acting insecticides is possible but would be a waste.
3Although in plants PAs usually occur as nitrogen-oxides, the respective free bases are attractive.

At present, neither PA baits nor attracticides employing PAs are commercially available, but it is hoped that these will eventually be manufactured locally in a standardized way.

As indicated above, the attractive power of the various kinds of baits differs, varying and fading more or less quickly; therefore, absolute amounts of material needed for a good bait cannot be given. However, 5 – 10 g of dry PA-plant material and 200 mg of pure PAs, respectively, have given good results (O.W. Fischer and M. Boppré, unpublished data).

Zonocerus is susceptible to numerous insecticides including, BHC and fenitrothion (Anonymous 1977; Oyidi 1984), but also to various chitin synthesis inhibitors as well as to natural products such as dennetia oil (Iwuala et al. 1981) and neem (e.g. Olaifa and Adenuga 1988; Baumgart 1994); with respect to fungal pathogens, recently good success with *Zonocerus* has been obtained with *Metarhizium flavoviride* (Douro-Kpindou et al. 1995) but other mycoinsecticides are worthwhile testing, too.

As with other activities of *Zonocerus* (cf. Kaufmann 1965), responses to PA baits are best when the temperature is above 23 °C and when there is full sunshine (see also Boppré et al. 1984; Modder 1984, 1986). The chemically mediated congregation of *Zonocerus* at PA baits can be facilitated by visual cues. The grasshoppers are attractable by linear vertical patterns (cf. Kaufmann 1965), and hanging PA baits are more attractive than ones placed on the ground. When we combined a lure on the ground with a stick in its vicinity, the majority of grasshoppers attracted jumped onto the stick and climbed it.

There is no indication that attraction to PAs is restricted in such a way that the "hunger for PAs" terminates after ingestion of a certain amount of these plant substances; i.e., *Zonocerus* is attracted to

PAs during its entire life independent of the amount of PAs already ingested. In laboratory tests where pure PAs had been offered ad libitum, no consistent pattern in PA uptake could be recognized, except that on the average females took up larger amounts than did males (O.W. Fischer, unpublished data).

Further prospects for future IPM of *Zonocerus*

The two *Zonocerus* species are peculiar grasshoppers with respect to their biology and their appearance as pests in agriculture and forestry, and there cannot be any "one and only" recipe to combat high population densities. Rather, it is necessary to have an IPM concept which provides toolkits for selection and combination of the most appropriate control strategy in a given situation, considering population densities and instars occurring, and also availability of technical equipment, labour, pesticides etc. To date, this requirement is met to a great extent.

For implementing the most environmentally sound and cost-efficient means, farmers must be trained by plant protection services to properly assess the potential threat and take preventive measures against *Zonocerus* upsurges before they cause damage. The uncommon traits of this insect require action many months in advance, e.g. survey and marking of egg-laying sites and combatting early instar hoppers weeks before late instars and adults can cause damage. Because of the tendency to host-switching and the dispersal behaviour of *Zonocerus*, it is difficult in most cases to predict areas which might eventually be affected; in consequence, pest management should be conducted at the community level.

Baiting Zonocerus for infection with pathogens

An appealing concept in *Zonocerus* control has its goal in a general reduction of population sizes in areas where the risk for damage is high for one reason or another; i.e., the objective should be to lower the mean level of abundance so that fluctuations above the economic threshold are reduced or eliminated. We are working on the development of a simple and cheap device which attracts the grasshoppers with a persistent PA source and infects them with specific fungal spores while they are (unsuccessfully) trying to gather PAs. Due to the movements of hoppers (see above) over weeks, part of the population will be infected and disseminate the pathogen to conspecifics (cf. Thomas et al. 1995). Such a device with which control is self-perpetuating would have to be given to communities and co-operatives for distribution in their areas at low density and at times when young hoppers appear.

General conclusions

A plant – cassava – introduced to Africa as a crop with high resistance to grasshoppers (Schaefers 1978) nowadays contributes to increased population densities of dry-season *Zonocerus*, and these populations are, in turn, supported by another introduced plant – *Chromolaena*. This case nicely illustrates the uncertainties of establishing foreign plants in (agro-)ecosystems. Moreover, it provides an example of the effect secondary chemicals of plants not required for nutrition and in any case gathered independent of food may have on the population dynamics of insects. Similar non-nutritional phenomena might exist in many other insect-plant relationships but have not yet been recognized. Also, the relations of *Zonocerus* to plants exemplifies that detailed basic knowledge on chemoecological interactions may lead to environmentally sound ways of pest management by employing secondary plant metabolites in simple formulations – just as in traditional medicine – or in a more "high-tech style".

Finally, the knowledge on storage of PAs by *Zonocerus* makes us note that it is not advisable to use these grasshoppers as food items for humans or domestic animals. According to the literature, it is not rare that *Zonocerus* are eaten and even sold on local markets in West Africa (see, e.g. Page and Richards 1977; Koman 1983). To vertebrates, including humans, many PAs are toxic; usually they do not cause instant harm but have hepatotoxic, carcenogenic and other effects (e.g. Huxtable 1990).

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