

Zonocerus and Chromolaena in West Africa

A chemoecological approach towards pest management

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Summary

The variegated grasshopper, *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 Siam weed, *Chromolaena odorata* (L.) K. & R. (Asteraceae: Eupatoriaee), which, however, is not a food plant for *Zonocerus*. Knowledge of pharmacophagous utilisation of pyrrolizidine alkaloids (PAs) by *Zonocerus elegans* has suggested that flowers of *Chromolaena* which are attractive for and consumed by *Zonocerus variegatus* in a special manner do not have a nutritional function but rather serve solely as a PA-source. Field studies demonstrate that *Z. variegatus* is attracted to various PA-containing plants more strongly than to *Chromolaena* flowers, and pure PAs are also effective lures. In conclusion, *Zonocerus* seems to enjoy a non-nutritional association with *Chromolaena* which only provides PAs. These secondary plant compounds are stored and chemically protect the grasshoppers and particularly their diapausing eggs from predation and parasitism, and thus cause increased fitness and influence the population density of dry-season *Zonocerus*. Our ongoing behavioural, physiological and chemical studies strongly support this hypothesis and provide an example of the hidden and unpredictable effects which the introduction of a foreign plant can have on population dynamics of a native insect species and on (agro-)ecosystems. This knowledge on the pharmacophagous behaviour and its chemoecological context leads us to develop a PA-based bait to poison *Zonocerus* and/or infect the insects with pathogens and thus control them specifically in a way harmless to man and environment.

Résumé

Zonocerus et Chromolaena en Afrique de l'Ouest

Une approche chimio-écologique de lutte contre les animaux nuisibles

Le criquet puant, *Zonocerus variegatus* (L.) (Pyrgomorphidae), est un sauteriau africain polyphage, qui provoque - du moins pour ce qui est des populations de la saison sèche - de graves dégâts aux cultures et forêts dans certaines parties de l'Afrique de l'Ouest. Il semble que les fortes densités de population soient liées à la propagation d'une mauvaise herbe importée *Chromolaena odorata* (L.) K. & R. (astéracées: Eupatoriaee), l'herbe du Laos, qui ne sert cependant pas de nourriture à *Zonocerus*. Ce que nous savons de l'emploi de type pharmacophage fait par *Zonocerus elegans* des alcaloïdes de pyrrolizidine (AP) nous laisse supposer que les fleurs de *Chromolaena* qui attirent *Zonocerus variegatus* et qu'il consomme d'une manière particulière n'ont pas de fonction nutritive, mais servent seulement de source de AP. Des études réalisées sur le terrain ont montré que *Z. variegatus* était attiré par différentes plantes contenant des AP plus fortement que par les fleurs de *Chromolaena* et que les AP purs étaient des appâts efficaces. *Zonocerus* a donc un comportement pharmacophage par rapport à *Chromolaena* qui ne lui fournit que les AP. Ces composants végétaux secondaires sont emmagasinés par les sauteriaux qui s'en servent pour se protéger chimiquement eux-mêmes, ainsi que leurs oeufs en diapause, contre les ravageurs et parasites. Les AP améliorent ainsi sur la forme physique des sauteriaux et influent sur la densité des populations de *Zonocerus*. Les études comportementales, physiologiques et chimiques que nous poursuivons renforcent cette hypothèse et fournissent un exemple sur les effets cachés et imprévisibles que peut avoir l'introduction d'une plante sur la dynamique des populations d'un insecte indigène et sur des (agro-) écosystèmes. La connaissance du comportement pharmacophage et de son contexte chimio-écologique conduit au développement d'un appât à base de AP pour empoisonner *Zonocerus*, voire l'infecter à l'aide de pathogènes, et pouvoir ainsi le contrôler de façon sélective et sans risques pour l'homme et l'environnement (cf. Boppré and Fischer 1993).

Introduction

Siam weed (*Chromolaena odorata*) and the variegated grasshopper (*Zonocerus variegatus*) represent quite novel pest problems which at first sight do not seem interlinked. Here, we provide an overview of our ongoing chemoecological studies on *Zonocerus variegatus* which are aimed at understanding *Zonocerus*-plant relationships and utilising the knowledge gained for developing new ways to manage

pest populations of this grasshopper (see also Boppré 1991, Boppré et al. 1992).

Our studies are based on the fact that for many insects, plants represent much more than food sources because they not only utilise the plants' nutrients but also their noxious secondary compounds. These metabolites are believed to have evolved as defensive principles under the pressure of selective herbivory. However, many phytophagous insects exhibit behavioural and/or physiological adaptations to cope with certain plant defences; in a variety of cases these chemicals have meanwhile lost their repellent/deterrent effects and gained a new significance, e.g., serving instead as signals for host plant detection. Although some species are specialised to the extent of storing unconverted plant toxins for their own defence against predators, sequestration of secondary plant chemicals by insects is usually linked with feeding. There are, however, 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).

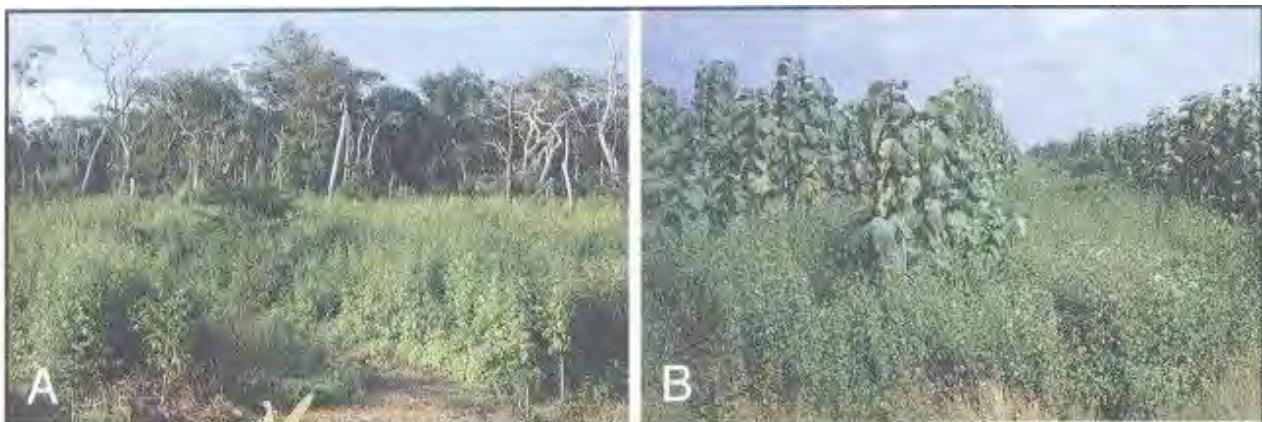
Pyrrolizidine alkaloids (PAs) are a large group of secondary plant metabolites, and pharmacophagy with respect to PAs is being investigated in numerous butterflies and moths (Lepidoptera), some flea beetles (Coleoptera: Chrysomelidae: Gabonia) and chloropid flies (Diptera: Chloropidae). The Lepidoptera, for example, use PAs as precursors for the bio-synthesis of male intraspecific signal compounds (pheromones) and/or store these plant metabolites for their own defence; *Creatonotos* spp. (Arctiidae) even make use of them as morphogens which regulate the growth of the male scent organs (for reviews cf. Boppré 1986, 1990, 1995).

Pharmacophagy also occurs in grasshoppers of the genus *Zonocerus*. The present article concentrates on the pharmacophagous relationship between *Zonocerus* and plants containing pyrrolizidine alkaloids, considering in particular the introduced weed *Chromolaena odorata*.

The Siam weed, *Chromolaena odorata*

(Plate 1)

Chromolaena odorata K. & R. (*Eupatorium odoratum* L.) (Asteraceae: Eupatoriaee) is a perennial shrub native to the tropical Americas. Following its introduction into India, *C. odorata* has invaded Southeast Asia from whence it subsequently reached Africa. In its new habitats it spreads quickly, forming dense thickets of a height of up to two meters which flower once a year during the dry season. It has become a major weed which seriously interferes not only with natural vegetation but also with forestry, pastures and plantation crops. 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. The need to control Siam weed has been recognised: there is a Network on Biological Control and Management of *Chromolaena odorata* with a secretariat at the University of Guam, International Workshops are being held, and the International Organisation for Biological Control of Noxious Animals and Plants (IOBC) is establishing a global *Chromolaena* working group. For recent synoptic accounts on *Chromolaena odorata* see, e.g., Audru et al. (1988), Cruttwell McFadyen (1989), Ambika and Jayachandra (1990), and Boppré et al. (1994).



A



C



E

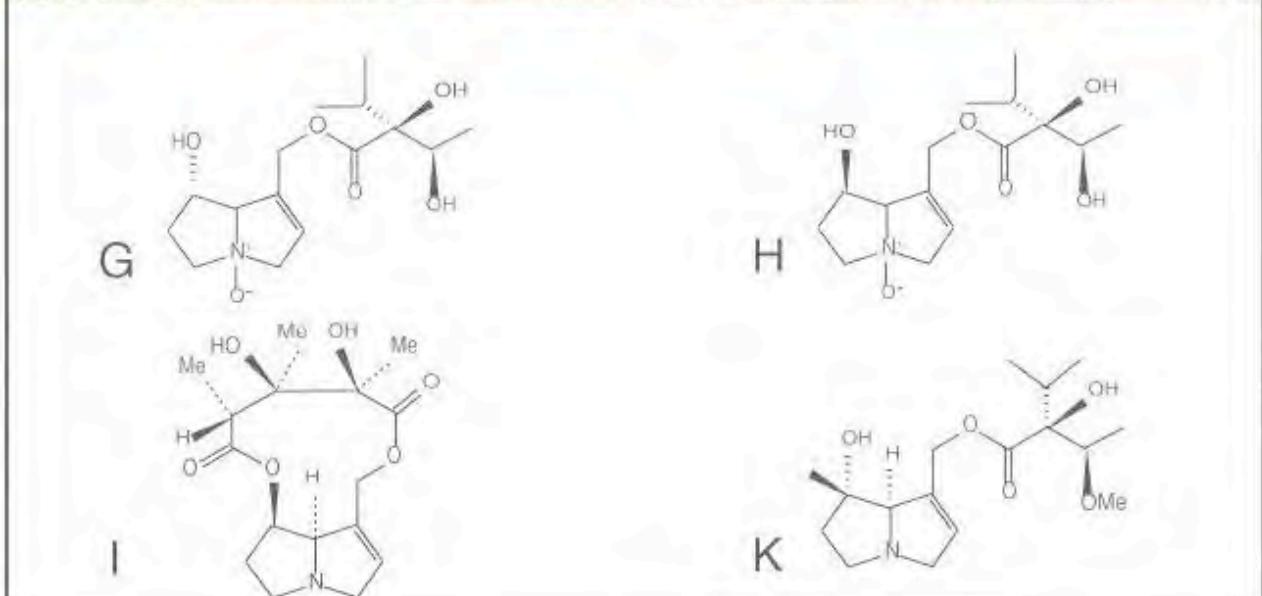


Plate 1. **A, B** Regularly mown but quickly regrowing bushes of *Chromolaena odorata* near a natural forest (A) and in a teak (*Tectona grandis*) plantation (B) near Bohicon, Benin. **C** Undisturbed growing thicket of *C. odorata* in bloom. **D** Inflorescences of *C. odorata* (centre: mature flower heads with conspicuous stigmata). *Crotalaria* sp. (E) and *Heliotropium indicum* (F), plants containing pyrrolizidine alkaloids. **G-K** Molecular structures of pyrrolizidine alkaloids: rinderine (G), intermedine (H), monocrotaline (p, heliotrine (K) (G and H as N-oxides)

The variegated grasshopper, *Zonocerus variegatus* (Plate 2)

Zonocerus variegatus (L.) (Orthoptera: Pyrgomorphidae) is an aposematic grasshopper with polyphagous feeding habits. It feeds not only on a wide variety of plants (for a comprehensive list of references see Chiffaud and Mestre 1990), it appears to require a mixed diet for proper development. Apparently very few plants - including Citrus and cassava (*Manihot esculenta*) - fulfil the nutritional requirements for good survival of the grasshoppers. (Cassava, however, produces noxious cyanogens, and *Zonocerus* can only utilise this plant through group attack which circumvents the plant's defence; Chapman 1985).



Plate 2. **A** Pair of long-winged *Zonocerus variegatus* (males guard females until termination of egg-laying). **B** Aggregation of hoppers of *Z. variegatus* on tips of *Chromolaena odorata* plants. **C-G** *Z. variegatus* damaging banana (*Musa* sp.; O), maize (*Zea mays*; D), leaves (E) and bark (F) of teak (*Tectona grandis*), and cassava (*Manihot esculenta*; G)

Zonocerus is univoltine. Eggs are laid at special sites where hundreds of male and female adults aggregate- The eggs hatch 6-8 months after oviposition, and in Southern Benin, for example, the grasshoppers occur in two distinct and alternating populations, the wet-season (from March/April to September/October) and the dry-season population (from October/ November to March/April). For synoptic accounts on *Zonocerus* see, e.g., Chapman et al. (1986) and Chiffaud and Mestre (1990).

Although there are several early reports on serious damage caused by *Zonocerus*, only recently have the grasshoppers begun to pose serious and growing problems (cf. FAO 1990). In Nigeria, for example, *Zonocerus* has reached pest status only about 20 years ago (cf. Modder 1986) but only the dry-season populations seem to have much higher population densities than the wet-season ones, and only they cause serious damage to various arable crops (e.g., cassava, maize and cotton) as well as to plantation trees (e.g., teak and Citrus) (cf. Chiffaud and Mestre 1990). This situation has been assumed to be due to deforestation, increasing agriculture, and - in particular - to intensified cultivation of cassava, which is in full foliage long into the dry season when most other potential host plants have dried up (Bernays et al. 1975; cf. Chapman et al. 1986). The pathogenic fungus *Entomophaga grylli* is an important mortality factor only under wet conditions. However, Toye (1974) has suggested that there may be a correlation between the increased dry-season populations of *Zonocerus* and the spread of *Chromolaena odorata*, but without offering any clue regarding possible causal links-

The gregarious hatchlings and early instar hoppers of *Zonocerus* feed on *Chromolaena* foliage in part, and they like the tips of *Chromolaena* as roosting sites, forming dense overnight aggregations on them (Plate 2 B). While this plant provides many of the habitat needs of the insect, it is not an adequate nutritional source permitting normal development (see, e.g., Bernays et al. 1975). Nevertheless, *Zonocerus* is strongly attracted to flowers of *Chromolaena*, which the grasshoppers consume in large numbers (cf. Modder 1984a, 1986; Fischer and Boppre 1994). However, hoppers fed exclusively with *Chromolaena* flowers from the fourth instar on failed to become adults (Chapman et al. 1986). If *Chromolaena* is nutritionally inadequate for *Zonocerus*, why do the insects become a pest preferentially where the foreign weed occurs?

[go to next section of this publication](#)

[go to previous section of this publication](#)

Zonocerus, pyrrolizidine alkaloids (PAs) and Chromolaena

Zonocerus elegans (Thunb.), a species closely related to *Z. variegatus*, is known to be attracted to withered plants containing pyrrolizidine alkaloids (PAs), as well as to pure PAs, and to take up these secondary plant substances (Bopp et al. 1984). Bernays et al. (1977) reported that *Z. variegatus* sequesters and stores PAs from *Crotalaria retusa* (Fabaceae). The wide host range of *Zonocerus* includes several additional PA-plants such as *Heliotropium* (Boraginaceae), as well as *Emilia* and *Ageratum* (Asteraceae) (for references see Chiffaud and Mestre 1990, Chapman et al. 1986).

Our field studies in Benin revealed that *Z. variegatus* is not only attracted to *Chromolaena* flowers (cf. above). Dried parts of various PA-containing plants, extracts of these plants, and certain pure PAs also provide very effective lures for hoppers as well as adults of both sexes; roots of *Chromolaena* exhibit great stimulatory capacity, dry foliage, however, is not attractive (see below).

Among the variety of plant genera containing PAs, many species of the Eupatoriaee have been found to possess several PAs (cf. Smith and Culvenor 1980; Mattocks 1986). Altogether, the knowledge summarised briefly above suggests that flowers of *Chromolaena* contain PAs and might provide a novel, rich and most readily available although temporally restricted source of PAs for dry-season populations of *Zonocerus*, perhaps influencing its population dynamics to a greater extent than the indigenous PA-plants, which are usually quite rare or only contain small amounts of PAs (see below).

Secondary chemistry of *Chromolaena odorata*

Biller et al. (1994) provided for the first time detailed chemical analyses proving that *Chromolaena odorata* indeed contains a mixture of PAs with rinderine and intermedine as major components plus ⁷O- angeloyl-retronecine, ⁹O-angeloyl-retronecine and acetyl-rinderine, all occurring exclusively as N-oxides (see Plate 1 G,H). In the ecological context, the distribution of PAs in *Chromolaena* is particularly interesting: while the foliage is devoid of PAs, the highest concentrations occur in the roots (ca 1 µmol/g dry weight) and in the mature inflorescences (ca 2 µmol/g dry weight). Moreover, there are great differences in the PA-content of flowers in different developmental stages; as the florets mature and stigmata and style arms appear, the PA-content increases. These chemical data precisely match the results of behavioural studies (see below).

A special manner of consumption* of *Chromolaena* flowers by *Zonocerus*

* We talk about "consumption" and not of "feeding" because the latter word implies uptake of nutrients

The attractive power of inflorescences is highest when they have mature florets showing two-lobed stigmata, and the stigmata are preferred organs for starting the consumption of flowers (Modder 1984a, 1986; see Fig. 1 and Plate 3A,B).



Figure 1. Sketches of flower heads of *Chromolaena odorata* with mature florets and prominent stigmata (left) and of remains of flower heads after attack by *Zonocerus variegatus* showing various degrees of consumption of florets and ovaries (Drawn after video recordings and photograph.), cf. Plate 3B

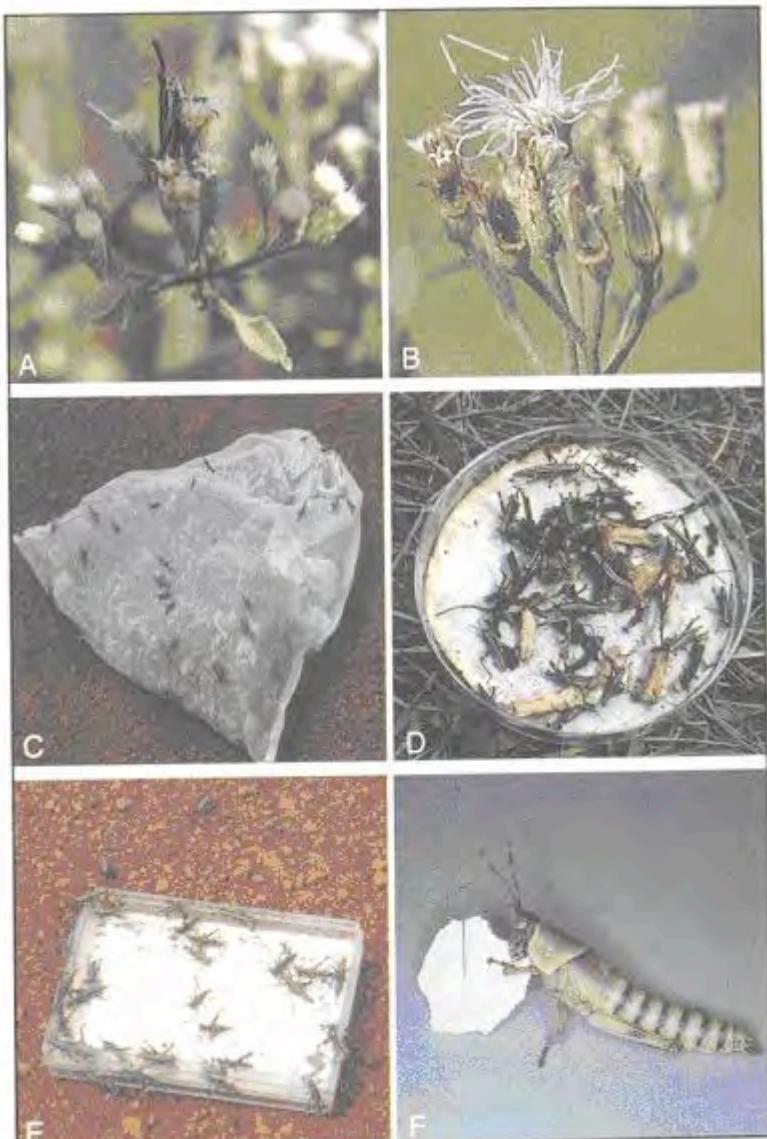


Plate 3. **A** A hopper of *Zonocerus variegatus* feeding on stigmata from flower heads of *Chromolaena odorata*. **B** Flower head of *C. odorata* in full bloom exhibiting stigmata (arrow) and remains of flower heads after attack by *Z. variegatus* (cf. Fig. 1). Hoppers of *Z. variegatus* attracted to and feeding at remoistened dry roots of *C. odorata* (**C**) and *Heliotropium indicum* (**D**) and at a dish containing pyrrolizidine alkaloids purified from *Crotalaria scassellatii*. **F** Adult *Z. elegans* consuming a fibreglass disc impregnated with pure pyrrolizidine alkaloids in the laboratory

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; it ingests the entire set of florets of a *Chromolaena* flower but leaves the bracts alone as far as possible; i.e., in order to get access to the PA-rich ovaries in these small capitulae the grasshoppers eat only a small fraction of the surrounding bracts and consume the entire inner parts of the capitula, leaving the remaining bracts, obviously carefully avoiding parts not containing PAs. „Feeding“ by *Zonocerus* thus results in characteristic remains of *Chromolaena* flowers. Incidentally, what looks like a great reduction in seed production does not seem to reduce the reproductive success of *Chromolaena* significantly.

Sequestration of *Chromolaena*-PAs by *Zonocerus*

We were able to demonstrate (Biller et al. 1994; O.W. Fischer, A. Biller, M. Boppre, T. Hartmann unpubl.) that extracts of field-caught specimens of dry-season populations of *Zonocerus variegatus* contain four PAs in all stages and in both sexes as well as in eggs: rinderine (major PA) and intermedine (as in *Chromolaena*), lycopsamine and echinatine (not found in *Chromolaena*, but structurally only slightly modified), all quantitatively as N-oxides. The amounts of PAs stored can be as much as 5 mg/individual. PAs are not present in specimens raised indoors on PA-free plants but appear if they have been fed with flowers or roots of *Chromolaena* or with respective extracts. Evidently, *Zonocerus* transforms two of the plant PAs into their isomers (cf. Biller et al. 1994).

Certain plant material but also several pure PAs not only emit volatiles to attract the insects (see below) but also provide phagostimulants: *Zonocerus* eagerly takes up plant material, pure chemicals and almost any substrate (paper, cloth, fibre-glass) impregnated with appropriate plant extracts or compounds. From laboratory tests with *Z. variegatus* we know that the 'hunger for PAs' is enormous in all stages of this species; grasshoppers take up several milligrams in their adult stage (M. Boppre and O.W. Fischer unpubl.). Ingested free-base PAs are converted into their N-oxides, stored and eventually transferred into the eggs (O. W. Fischer et al. unpubl.).

Since *Chromolaena* only flowers during the dry season, it is only the specimens of dry-season populations which have access to an 'inexhaustible' source of PAs provided by the introduced weed. Indeed, in chemical analyses of wet-season grasshoppers (when *Chromolaena* is not flowering) and grasshoppers from north of Benin (where *Chromolaena* is absent) we found different PAs, but these do not show the pattern of *Chromolaena* and originate from other PA-plants, including *Heliotropium* and *Ageratum* (O.W. Fischer et al. unpubl.).

Specificity of attraction* to sources of PAs (Plate 3)

* For further details see Fischer & Boppre (1994)

General observations. - All stages (hatching to adult) of *Zonocerus* are strongly attracted to a variety of natural and artificial sources of PAs. This behaviour is not sex-biased. Visual cues facilitate orientation, which is, however, primarily olfactory. Certain PA-sources can lure hoppers and adults over distances of several meters upwind, and flying of adults over greater distances towards baits has been recorded, too. As with other activities (cf. Kaufmann 1965), responses to PA-baits are best when the temperature is above 23° C and when there is full sunshine (see also Boppre et al. 1984; Modder 1984b, 1986).

Of course, in all tests on the attraction of artificially offered PA-sources there is competition with naturally occurring ones. Attractive baits might well fail in stands of flowering *Chromolaena* plants, while in areas devoid of PA-sources several hundred grasshoppers can be lured within two hours.

Zonocerus preferentially feeds on vertically standing plants (cf. Kaufmann 1965), and hung up 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 up it.

There is no indication that attraction to PAs is temporally restricted in such a way that the 'hunger for PAs' terminates after ingestion of a certain amount of these plant substances, i.e. *Zonocerus* are attracted to PAs during their entire life independent of the amount of PAs already ingested. In laboratory tests where pure PAs had been offered ad libitum, we could not recognise any consistent pattern in PA-uptake, except that on the average females took up larger amounts than male specimens.

Attraction to withered plants. - Only withered or dried, entire plants of *Heliotropium indicum* are effective, but its foliage, roots and unripe seeds offered separately also cause *Zonocerus* to leave their roosting or feeding sites and visit these baits. Fresh foliage and roots are not attractive unless mechanically damaged, and the attractive power of dry plant material can be increased by chopping and/or re-moistening it with water (see below). Compared to *Heliotropium*, dry material of any part of *Crotalaria* spp. and *Ageratum conyzoides* shows only a much reduced attraction, and foliage of

[go to previous section of this publication](#)

Implications

Zonocerus grasshoppers are thus pharmacophagous; they utilise a great variety of plants for obtaining nutrients ('grocer's shops') and solely use plants containing pyrrolizidine alkaloids for gathering these secondary compounds ('pharmacies', 'drug stores'). In conclusion, the puzzle of the coincidence of the spread of *Chromolaena* and the pest status of *Zonocerus* seems to be explicable by the following hypothesis: *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 predators or parasitoids (e.g., larvae of Mylabris beetles), thus giving rise to the increased fitness and population density 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.

To date, there is only circumstantial evidence in favour of this idea. However, the hypothesis is in agreement with all known facts. To non-adapted animals, vertebrates as well as invertebrates, PAs are taste repellent, and PAs thus protect not only plants producing these secondary chemicals from being eaten but also adapted insects which gather them from plants and store them. As in other insects sequestering PAs, *Zonocerus* is aposematic in appearance and has very few known natural enemies; Chapman and Page (1979) stated that the „virtual absence of mortality in the eggs is unusual for acridids”, and we assume a relation to the storage of PAs. Unfortunately, because most reports in the literature on *Zonocerus* do not provide sufficient details on environmental conditions (presence of plants, season, etc.), many published data cannot be (re)interpreted in relation to our knowledge on PA-sequestration in these grasshoppers.

Of course, the hypothesis given above does not imply that the novel source of PAs - flowers of *Chromolaena* - is the exclusive cause for increased and harmful dry-season populations, and it does not rule out that the increased cultivation of cassava and lack of pathogens are additional factors supporting dry-season populations of *Zonocerus*. However, our general finding that pyrrolizidine alkaloids influence the population dynamics of *Zonocerus* might also explain the occasional local occurrence of huge population densities in areas where there is only one grasshopper population per year and/or where there is no Siam weed: large populations of other PA-containing plants such as *Heliotropium indicum*, which can be quite common on disturbed land, provide PAs just as well as flowers of *Chromolaena* do.

Pest management of *Zonocerus*

To date, to control *Zonocerus*, egg sites are mechanically destroyed or hoppers are sprayed with synthetic insecticides. However, Modder (1986) has suggested an integrated pest management concept, 1 phase of which involves the relation of *Zonocerus* to *Chromolaena*. Nymphs and adults are to be trapped with *Chromolaena* inflorescences or - if available - with volatile chemicals extracted from them; a combination of insecticide plus *Chromolaena* attractant and phagostimulant would attract and poison the grasshoppers (Modder 1986). Although we agree with Modder's final conclusions and add knowledge on chemical ecology which leads to more effective biotechnological means of management of *Zonocerus*, we disagree with several of his arguments.

Assuming that *Chromolaena* has no relevance to populations of *Zonocerus*, Modder (1986) 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; Boppre et al. 1994).

Our finding that the roots of *Chromolaena* are powerful attractants for *Zonocerus* permits farmers of small cassava or maize fields to lure *Zonocerus* with chopped roots of *Chromolaena* (or, e.g., *Heliotropium*), thus concentrating these insects for subsequent destruction, mechanically or with the aid of fire. The advantages are that roots are available all year and that *Zonocerus* can be lured independently of *Chromolaena* being in bloom (which would also compete with root baits).

This simple technique to concentrate *Zonocerus* can also be used in combination with more sophisticated (i.e. efficient) means to kill the grasshoppers: i) considering that these lures also stimulate feeding, impregnation of roots with orally acting insecticides would reduce labour and work without regular inspections for longer periods; ii) instead of employing such an attracticide, it would be possible to combine PA-lures with a pathogen in a way so that the grasshoppers would infect themselves without consuming bait material and - preferably - also distribute the pathogen within the population.

Since root baits can be highly variable, we aim to develop a standardised bait based on PAs which is formulated in such a way that it provides a persistent source of the attractive principle. Such a lure is expected to act as a kind of hyper-normal stimulus, reducing competition with natural sources of PAs and acting over longer distances.

Independent of the technology used, in the long run it will be advisable to use any such device not only to protect selected farms but also to install it at egg-laying sites in the neighbourhood of farmland in order to reduce the offspring of the grasshoppers and thus avoid high population densities in future seasons.

Lastly, it should be emphasised that all the possibilities for managing *Zonocerus* briefly discussed above are highly specific for these grasshoppers - although sources of PAs are very attractive for a variety of insect taxa (see Introduction). These other species usually are absent or rare in areas where *Zonocerus* poses a problem, and if needed, they could be intentionally kept off harmful PA-baits of any kind by simple mechanical means.

Prospects for further studies on *Zonocerus*

Apart from finalising the development of means based on volatile degradation products of pyrrolizidine alkaloids and noxious for *Zonocerus*, additional studies are required for a full understanding of the biology of this grasshopper and its relation to *Chromolaena*, including further details on the sequestration of PAs, demonstration of protection of eggs, etc. Our studies will also include experiments designed to investigate whether PAs solely influence the grasshoppers' protective devices or if the plant chemicals have additional roles. PAs might, for example, influence egg production. Taylor (1972) has reported that wet- season *Zonocerus* lay significantly fewer eggs than dry-season ones. On first sight, this contradicts what one would expect, since egg production relates to the availability and quality of food (cf. Page 1978), and this seems to be better in the wet season. Perhaps PAs somehow influence egg production. Having found that PAs regulate the growth of androconial organs in *Creatonotos* moths organ specifically and in a direct dose relation (references in Boppre 1990), for us such a finding would be no surprise.

Regrettably, so far, we have only had opportunities to investigate three dry- season populations of *Zonocerus variegatus* for quite short periods in Benin, i.e. our knowledge is quite limited. Other localities with different vegetation, climatic conditions, etc. need to be considered, as does the closely related species *Z. elegans*. While this is not relevant for the goal of managing *Zonocerus* by baiting, for other, additional ways of biocontrol one needs to know much more on the biology of the species of this genus. Their polyphagy makes them potentially most dangerous for agriculture; Chiffaud and Mestre (1990) list 62 cultivated plants attacked by *Zonocerus*. At present, damage caused by this grasshopper is judged quite inconsistently in the 25 West African countries where *Zonocerus* occurs. However, experts have recognised its increasing relevance and at the same time our insufficient knowledge on its biology and ecology (FAO 1990). To prepare for future situations research on *Chromolaena* also must be intensified. For instance, in East Africa *Zonocerus variegatus* and *Z. elegans* occur sympatrically in part, and to date both are unobtrusive;

Chromolaena has not yet invaded this part of the continent. Based on our present knowledge, we must anticipate an increasing economic importance of *Zonocerus* grasshoppers.

General consequences

Provided our hypothesis on the effect of *Chromolaena* on population sizes of *Zonocerus* is correct, it provides an example of the effect secondary chemicals of plants not used for nutrition can have on population dynamics of insects. Similar non-nutritional phenomena might exist in many other insect-plant relationships but have not yet been recognised. In addition, it is an example of a significant although inconspicuous role an introduced plant can have on (agro-)ecosystems; perhaps many other introduced plants affect certain insects by increasing or decreasing their fitness only via secondary compounds.

[go to next section of this publication](#)

Chromolaena does not modify the grasshoppers' behaviour at all. However, roots of Siam weed exhibit strong attractive power, particularly if chopped into pieces and dried; this can be further increased by re-moistening (see below). Flowers of *Chromolaena* release attractive stimuli best if their stigmata are conspicuous (Modder 1986).

The absolute amounts of material needed for a good bait cannot be given. On the one hand, in general there is variation in the quantities of secondary compounds contained in plants; on the other hand, its treatment (intensity of chopping, mode of drying, duration of exposure, number of moistenings) greatly determines the release of its attractive volatiles (see below) - and also its durability. Nevertheless, amounts as little as 2-5 g of roots suffice to lure *Zonocerus*.

Attraction to raw extracts of plant material. - Experiments on the behaviour-modifying chemicals have shown that methanol extracts of attractive plant material contain the stimuli necessary for both attraction and consumption. While extracts of only a few grams of roots of *Heliotropium* or *Chromolaena* provide good lures, for flower extracts from *Chromolaena* quite large amounts are needed; this agrees with the chemical data on the concentrations of PAs in different plant parts (see above).

Attraction to pure PAs. - Mixtures of PAs extracted and purified from *Crotalaria scassellatii* (major components axillarine and axillaridine), but also individual compounds including monocrotaline and heliotrine (Plate 1 I,K), lure *Zonocerus*. Although in plants PAs usually occur as N-oxides, the respective free bases are also attractive. Thus, whereas tests with plants are no more than an indication that PAs and not any other secondary plant chemicals are indeed the lures, the tests with pure chemicals definitely prove that PAs alone are responsible for attraction.

The attractive principle released from sources of PAs. - As stated above, the attractive power of plant materials is species and organ specific but is also greatly influenced by treatment. In choice tests, plant material and raw extracts are in general more attractive than pure PAs. Nevertheless, there is no evidence that additional chemicals acting synergistically are required. Rather, all observed effects are explicable by considering degradation products of PAs to act as airborne stimuli for the insects:

PAs are large molecules with insufficient vapour pressure to exhibit the volatility necessary for detection by the chemoreceptive organs of the insects. In living plant tissue PAs are confined to cell vacuoles and thus have no contact with the outside environment. When plants wither and wilt, but also if they are mechanically damaged, PAs get exposed and the atmospheric conditions trigger disintegration into a variety of derivatives, some of which are volatile. Isolated PAs are quite stable molecules; however, they are susceptible to hydrolysis, and the chemical environment of decomposing plant cells might especially promote their derivatisation. Details on the attractive principle released from sources of PAs will be published elsewhere (M. Boppre and S. Schulz in prep.; cf. Boppre and Bogner 1989). It is not a volatile derivative but intact PAs which seem to cue gustatorially the uptake of these compounds.

In summary, dry but not living PA-plants are attractive, moistening of dry plant material increases attraction, and pure PAs are weaker lures than plant material. Differences observed in the luring capacity of different PAs (and their N-oxides) are no longer puzzling if one considers the different readiness of individual PAs to degradation. In this light, seeming discrepancies such as, for instance, PAs of *Crotalaria scassellatii* being very stimulative in laboratory experiments but weak lures in the field, can be related to quantitative differences in the release of attractive compound.

[go to next section of this publication](#)

[go to previous section of this publication](#)

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