BRUCHIDS AND LEGUME SEEDS: ADAPTATIONS AND ADAPTABILITY

Peter F. CREDLAND and Julie DENDY

Royal Holloway and Bedford New College,
University of London

Department of Biology,
Egham Hill, Egham,
Surrey, TW20 0EX, U.K.

Abstract:- Plant resistance has been recognized as a valuable means of pest control, forming part of the pest management triad in conjunction with chemical and biological methods. In the context of bruchid control in stored legume seeds, especially in subsistence agriculture, there is increasing interest in the use of crop cultivars with bruchid-resistant qualities. Resistant cultivars may even be perceived as the primary means of pest control as biological methods are in their infancy and chemical methods are too expensive or hazardous. However, such developments cannot be relied upon to solve pest problems and must be viewed in the totality of bruchid ecology and physiology if they are to make a significant contribution.

Just as insecticides act as powerful selecting agents, and insecticide resistance is a manifestation of adaptation, so do 'resistant' cultivars. Bruchid beetles in the field are usually mono- or oligophagous but the most important and cosmopolitan pest species can each utilize a wider range of hosts. This adaptability is a potential problem to any programme of bruchid control and is compounded by the variation between biotypes or populations of the same species.

The problems of assessing the quality of cultivars with individual populations of bruchid are illustrated by reference to one or two of the most important pests and the adaptation of populations to changes in host cultivars is discussed.

Introduction

The insects concerned; bruchids and bruchids

Only around 20 species in the family Bruchidae are commonly encountered as pests of the stored legume seeds which are cultivated and eaten by man (Johnson & Kistler, 1987). These species differ in many ways from the remaining 1300 species found living predominantly, but not exclusively, in leguminous seeds which are currently not of such importance. Whilst one can enter a long philosophical debate about Labeyrie's (1981) assertion that "there can be no such things as stored product insects - but there are insects which can invade and infest stored products", there is no doubt that there are stored-product pests and a recognizable field of study which is widely known as stored-product entomology (Prevett, 1990). For present purposes, we shall only consider those bruchids which can breed freely within stores without additional individuals from the field being required for the maintenance of their populations, and which can reproduce without access to any form of food as adults. Such features are typical of the pest species but most unusual or absent in the remainder. They may, furthermore, help to delineate between species which can invade or infest stores for a single generation and those which cause long-term, chronic damage terminated only by consumption of all the available host seed material, or by the application of an external agent such as an insecticide. It should therefore be appreciated that the subsequent observations and comments may apply to only a very small proportion of bruchid species and may certainly not be true of the family as a whole, particularly those members living in the field on their wild hosts. They do, however, relate to precisely those species which necessitate "stored-product protection", which is why they are relevant to current concerns.

The fundamental issues

With the exception of *Acanthoscelides obtectus*, the most important species of bruchid which infest stored legume seeds glue their eggs individually to partially dried host seeds. On hatching, the first instar larva penetrates the testa of the seed to which the egg was attached and spends the whole of its immature life within that same seed. The adult emerges and, in the store, does not feed before mating or oviposition.

Thus the resources available to an individual beetle and consequently its 'fitness' are determined primarily by the activities of its female parent, and the seed on which the egg is laid. Whilst it is obviously true that physical parameters such as temperature and relative humidity play a part in determining rates of development and survival, they are less easily controlled in subsistence agriculture than the other criteria which could provide avenues for effective control. It would be naive and foolish to ignore the importance of good cultural practice, nor should one diminish the significant part played by fumigants and other chemical insecticides in some situations. Traditional seed treatments, such as the use of natural oils, are also sometimes employed but, in every case, the seed itself has to be the weakest 'link' in the life history of the pests and is the universally available target.

The propositions which we wish to put forward have significant implications if bruchids are to be controlled either by the use of resistant varieties of seed or by biological methods. They are based upon work published in the last few years and also incorporate many of the ideas expressed in previous IWCSPP. This Conference is a most opportune time to draw these contributions together, highlighting both the outstanding problems and accumulated knowledge available to anyone seeking to control bruchids living in stored seeds.

The propositions

Let us therefore consider a number of propositions relevant to bruchid control:

1) Species of bruchid which infest stored seeds are adaptable and can successfully utilize different species of host seed.

2) Geographically distinct populations, biotypes, of single bruchid species differ in terms of biological parameters.

3) Just as insects can be selected to produce populations resistant to insecticides, so 'enforced' development on atypical hosts or resistant cultivars of normal hosts will produce resistant populations.

4) As a consequence of biotype variation, the capacity to become resistant, i.e. to adapt, will vary from one population to another.

5) If populations differ in their capacity to adapt, it is imperative that new resistant cultivars are challenged with more than one bruchid population if their true value, or shortcomings, are to be appreciated.

6) Bruchids are probably no different from other insect pests of stored products in many of these respects, but as their primary hosts are of major significance in subsistence agriculture, where alternative means of control are limited, the significance of their adaptability and adaptation to biological control in its widest sense is of paramount importance.

Clearly, it is impossible to deal at length with each of these propositions in one contribution. We shall therefore not attempt to provide comprehensive justification for each one but merely to indicate where evidence for each is available or provide examples to support them. A more general background to our arguments, dealing with many of the theoretical aspects of host adaptation in herbivorous insects, has recently been provided by Via (1990), and we would commend this paper to those who want a broader perspective.

Results, evidence and discussion

1: Bruchids are adaptable.

Center & Johnson (1974), Southgate (1978) and Dobie (1981) are among many authors who have listed the numerous common, cultivated hosts of the primary pest species of bruchid. It is important to realise that the listed records do not generally include rare occurrences but that the species are found in these diverse hosts regularly, if not frequently. Center & Johnson (1974), and similar reports, also indicate the typically narrow host ranges of non-pest species. Furthermore, it is not uncommon for very unusual, even unique, records to be included in the host ranges of wild non-pest species in contrast to the situation pertaining to those which are pests. This widely recognized mono- or oligophagy in wild species but the polyphagy of those which infest stored seeds is a fundamental distinction between the two groups. Polyphagy may be taken as a clear illustration of the adaptability shown by the pest species and its origins have been demonstrated experimentally (Credland, 1990).

2: Biotypes vary in their biological parameters.

Populations of *Callosobruchus maculatus* differ in terms of fecundity, the number of larvae which survive to produce adults from similar seeds, adult weight (Credland *et al.*, 1986), and many other features such as larval food consumption (Credland & Dick, 1987) or the manner in which they distribute their eggs among the available hosts (Messina & Mitchell, 1989). Recently, differences in the allozyme frequencies of a number of metabolic enzymes have also been demonstrated between populations of *C.maculatus* (Abdel Gaber & Credland, unpubl. obs.). Thus, we deduce that variations between biotypes extend into numerous facets of their biology, many indicating genetic differences between the biotypes.

Similarly, there are important differences between populations of other pest species e.g. *Callosobruchus chinensis* (Fujii, 1968), *Acanthoscelides obtectus* (Huignard & Biemont, 1978) and *Caryedon serratus* (Robert, 1985).

In *Zabrotes subfasciatus*, a recent comparison of five biotypes from Colombia (two populations), Zimbabwe, Uganda and Mexico, revealed variation in a number of important parameters (Dendy & Credland, unpubl. obs.). For example, the percentage of adults emerging from seeds of *Phaseolus vulgaris* initially bearing comparable numbers of eggs, development period and the weights of newly emerged adults were significantly different among the biotypes, although not every biotype differed from every other in each respect (Fig. 1).

(a)

(b)

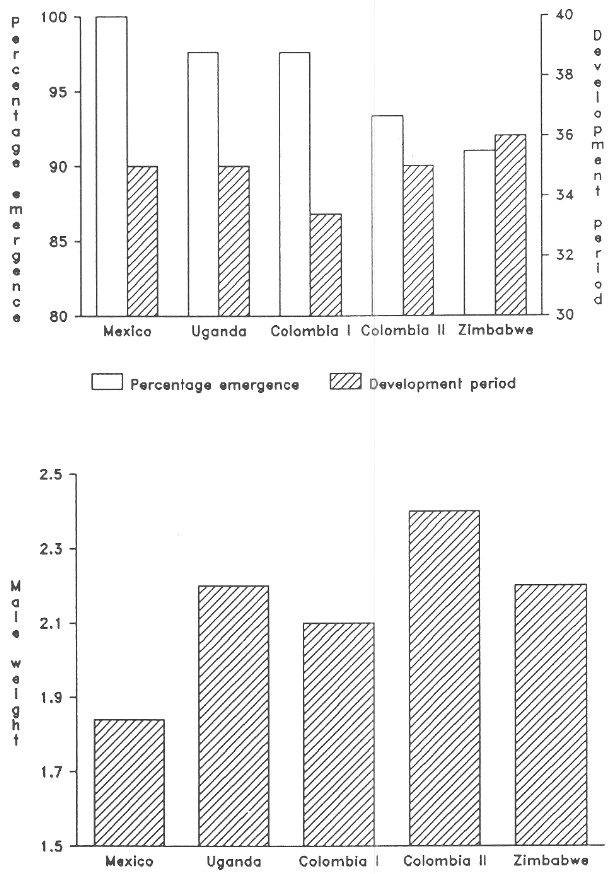

FIGURE 1. The percentage emergence and development periods (a) and the mean live weights of male adults at emergence (b) of 5 biotypes of *Zabrotes subfasciatus* developing in the Calima cultivar of *Phaseolus vulgaris.*

These differences between biotypes reared on the same hosts provide the clearest experimental evidence of important distinctions between them but are dependent on detailed and often tedious study in the laboratory. Their relevance, in practical terms, can be exhibited most readily by the simple expedient of challenging several biotypes with a single, uniform, alternative host. When a number of biotypes of *Callosobruchus maculatus* were challenged with whole green lentils, *Lens culinaris,* which are a host for some local populations but are not grown in many areas where the beetle is to be found, there were marked discrepancies in the capacity of the biotypes to lay eggs, for the larvae to develop and in the development periods (Credland, 1990). Comparable differences were observed when biotypes of the same species were first reared on a novel 'resistant' cultivar, TVu2027, of the cowpea, *Vigna unguiculata*, the most common host (Dick & Credland, 1986a).

Similarly, when three biotypes of *Zabrotes subfasciatus* were reared on three different cultivars of their primary host species, *Phaseolus vulgaris*, there were conspicuous differences in the performance of each and, furthermore, it was not always possible to predict how any one biotype would respond from the performance of any other (Dendy & Credland, unpubl. obs.). For example (Fig. 2), a greater percentage of the larvae of the Zimbabwe biotype survived to produce adults in a commercial red kidney bean (RKB) than in the variety Calima from Colombia, whereas the opposite was true in a Ugandan biotype and there was no difference in a biotype from Colombia.

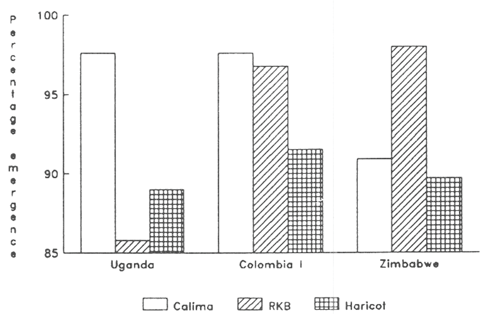

FIGURE 2. The percentage emergence of 3 biotypes of *Zabrotes subfasciatus* developing on 3 cultivars of *Phaseolus vulgaris*.

Thus, whenever populations of a single bruchid species from different localities have been compared in a standard assay, it has been found that they exhibit differences in a number of parameters which affect the rates at which their populations increase. Laboratory studies on unspecified biotypes may indicate the kind of situation or changes to be anticipated in the field but, without due attention being paid to the biotype actually studied, they cannot be expected to accurately predict events which will occur. Similarly, observations made in one field location cannot be taken as representative of those which may occur elsewhere, even if climatic conditions and the host seed cultivar are the same.

3: Resistant cultivars or atypical hosts produce resistant populations.

There are very few studies of the effect of rearing more than one generation of bruchid on an atypical host or a resistant cultivar of a normal host species. Where such studies have been conducted, they have shown that in each case a population rapidly becomes 'fitter' in the new situation in either behavioural (Wassermann & Futuyma, 1981), or both behavioural and physiological characteristics (Credland, 1990).

Biotypes of *Callosobruchus maculatus* which had not previously been reared on lentils in the laboratory, and had probably not encountered them in the field because of their origins, generally laid small numbers of eggs on them and few of the larvae survived to adulthood when first encountering them in an experimental assay. Furthermore, development was much slower than on cowpeas, their normal host. When two such biotypes were reared for a year or more (12+ generations) on lentils, there was a very marked increase in fitness in both cases (Credland, 1990). Thus enforced utilization of an abnormal host, for the biotypes tested, led to the rapid evolution of populations which overcame those factors in lentils which had previously restricted 'fitness' and, ultimately, population growth.

genetic changes in behavioural than physiological responses to hosts, such as Wassermann & Futuyma (1981) noted in their experiments with *Callosobruchus maculatus*. Many other examples can be found in the reviews of Futuyma & Peterson (1985) or Via (1990).

It is well known that many insects in stores can be controlled by fumigation or, indeed, by the use of other chemical methods. However, in subsistence agriculture where the cost of materials and their application are of paramount importance, such procedures are of limited value even if the expertise for their appropriate use is available. The use of 'resistant' seeds in which the development of insect pests is interrupted is obviously a most attractive alternative. It is critically important in this context that the limitations are recognized and that appropriate steps are taken to consider the implications of what is happening.

Any host seed imposes evolutionary pressures on an insect attempting to utilize it as a source of nutrient and/or protection. There is a huge volume of literature dealing with this subject, of which a significant part deals with the family Bruchidae. Whether the interaction of seed and beetle is strictly a coevolutionary process matters less than the appreciation that beetles in the field have few hosts and those which are pests have rather more. As conventional biological wisdom would lead one to expect, bruchids are well adapted to their primary hosts and may have sophisticated means of utilizing their environment (e.g. Rosenthal, 1983). Where such hosts are grown and stored by man, significant loss of human resources will occur.

It is the adaptability of the common pest species of bruchid which both increases host range and limits the value of new cultivars bred primarily for resistance to bruchids. For the reasons already mentioned it is reasonable to expect, and all the evidence indicates, that further hosts may be attacked and that reliance upon resistant seeds can, at best, offer only short term advantages. This will be most apparent if resistance is monofactorial, a property likely to be especially true of genetically engineered cultivars.

Mallet (1989) has argued that "using insecticides in turn until resistance evolves to each gives almost the same total control period as a planned rotation", involving these same chemicals. Thus, rotational use of control measures provides no better management of resistance than the straightforward sequential use of compounds which has been conventional practice. "A mixture of insecticides, on the other hand, can delay the evolution of resistance by several orders of magnitude compared with a rotation" (Mallet, 1989). By analogy, one would therefore anticipate that a new cultivar, whose resistance was dependent on a number of different factors operating essentially simultaneously, would delay the bruchids' use of such seeds much more effectively than one which was based on only one abnormal characteristic. Biologically, one is then demanding adaptation of several parameters simultaneously and even the adaptable bruchid is faced with a serious challenge!

There are a number of deductions of practical importance which can be made from our knowledge of bruchids and their interactions with hosts. First, the mono- or oligophagy of non-pest species may be attributable to the complex of allelochemicals present in wild legume seeds (Liener, 1982); therefore, it is not surprising that traditional native cultivars which have some resistance are difficult to "dissect" biochemically in order to identify *the* resistance factor. Secondly, if bioassays are to be used to 'isolate' or identify resistance factors, they must be sufficiently discriminating to separate the effects of each. This demands not only careful procedures allied to detailed analysis, but also an appreciation of the biotype variation among the beetles which may be encountered. Finally, to release a new resistant cultivar based on a single factor may not justify the expense in its creation, in the longer term. Hilder *et al.* (1990), in considering the genetic engineering of crops for insect resistance, concluded that a "multi-mechanistic resistance package" consisting of a pyramid of resistance factors is the appropriate goal for plant breeders;

Similarly, rearing two biotypes of *C.maculatus* on a 'resistant' cultivar of cowpea, TVu2027, showed that there was a rapid increase in fitness expressed as both enhanced larval survival and an increased developmental rate as each generation passed (Dick & Credland, 1986b).

Thus we conclude that, at least in the case of *C.maculatus*, which appears to be the only bruchid species currently subjected to the type of experiment under consideration, there is an undoubted 'adaptation' to new hosts.

4: Biotypes vary in their capacity to adapt to resistant hosts.

The two biotypes of *Callosobruchus maculatus* which were reared on lentils for protracted periods differed in their adaptations to these 'new' hosts (Credland, 1990). Similarly, the biotypes reared for several generations on 'resistant' cowpeas differed in the rates or extent of adaptation (Dick & Credland, 1986b). Thus, although adaptation may be a common phenomenon it is not possible to extrapolate from the form which it takes in one biotype to another. As has previously been argued (Credland, 1990), this variation may be critical to the capacity of a bruchid species to expand its geographical and host ranges. Only where a biotype with the requisite adaptability enters a new area or encounters a new host can it be expected that a permanent extension of the species' range will occur.

5: New host cultivars must be tested with several biotypes.

Publications dealing with the bioassay of well established, newly collected or newly bred cultivars using one or another species of bruchid beetle are extremely numerous. However, except for the work already cited, we know of not a single case where more than one biotype of the bruchid species concerned has been employed. This is despite the obvious, though unstated, objective of utilizing the data to illustrate that one or another of the accessions has some resistant property which may be of value to plant breeders or growers outside the area in which the tests were conducted. Such publications may usefully eliminate susceptible varieties but cannot be taken to *prove* that any variety is resistant to the bruchid species as a whole.

Where it has been collected in any systematic way, all the evidence points to the fact that reliable bioassays must always employ a known, identified biotype and ideally involve more than one. Clearly there are practical limitations in the use of multiple biotypes in every test but, ultimately, this is an essential and not merely a desirable step. It actually reflects the real biological world to which the bioassay results will be related and not the simplified model which would be more convenient, and cheaper, but on which dependence may ultimately lead to far greater wastage of effort and resources.

6: Importance of adaptation and adaptability in subsistence agriculture.

Bruchids are not unique in their capacity to utilise a variety of hosts and to adapt to new ones. For example, Gould (1979) showed that the mite, *Tetranychus urticae*, could rapidly adapt to a new host, cucumber, which initially caused high mortality. He concluded that "that a single herbivore population may contain the genetic variation necessary for rapid adaptation to a plant community containing a previously marginal host". Furthermore, "adaptation to one marginal host caused a somewhat general expansion of host plant range". Holloway & Mackness (1988) provided an extreme example by demonstrating that some populations of *Sitophilus oryzae* could survive on toxic legumes, a totally different family of plants to that normally utilized. The very non-specific means of detoxifying legume toxins suggests that such transitions may be more common than is normally accepted. It may also imply that changes at the physiological or biochemical level may be less easily detected than changes at the behavioural level. This would neatly explain the more rapid ironically they were really arguing for a reconstruction of the type of resistance which is probably found in most wild resistant hosts.

If what has been said appears a council of despair or hopelessness, we would not agree. We foresee no insuperable problems in the development of seeds resistant to bruchids but merely emphasise that laboratory studies and an appreciation of fundamental biological phenomena provide a sound strategic basis which must not be overlooked. "An understanding of the mechanisms of pest evolution is therefore an essential step in the development of improved and more durable management strategies and deployment methods" (Via, 1990). Recognition of these conditions can, and will, provide a useful if not a permanent answer to 'the adaptable bruchid'.

Acknowledgements - We are greatly indebted to the Natural Resources Institute of the Overseas Development Administration for their financial support which enabled a significant part of this work to be undertaken and the authors to attend the meeting in Bordeaux.

References

Center, T.D. & Johnson, C.D. (1974) Coevolution of some seed beetles (Coleoptera: Bruchidae) and their hosts. *Ecology*, **55**: 1096-1103.

Credland, P.F. (1990) Biotype variation and host change in bruchids: causes and effects in the evolution of bruchid pests. In *Bruchids and legumes: economics, ecology and coevolution* (eds Fujii, K., Gatehouse, A.M.R., Johnson, C.D., Mitchell, R. & Yoshida, T.), Kluwer Academic Publ., Dordrecht. Pp. 271-287.

Credland, P.F. & Dick, K.M. (1987) Food consumption by larvae of three strains of *Callosobruchus maculatus* (Coleoptera: Bruchidae). *J. stored Prod. Res.*, **23**: 31-40.

Credland, P.F., Dick, K.M. & Wright, A.W. (1986) Relationships between larval density, adult size and egg production in the cowpea seed beetle, *Callosobruchus maculatus*. *Ecol. Ent.*, **11**: 41-50.

Dick, K.M. & Credland, P.F. (1986a) Variation in the response of *Callosobruchus maculatus* (F.) to a resistant variety of cowpea. *J. stored Prod. Res.*, **22**: 43-48.

Dick, K.M. & Credland, P.F. (1986b) Changes in the response of *Callosobruchus maculatus* (Coleoptera: Bruchidae) to a resistant variety of cowpea. *J. stored Prod. Res.*, **22**: 227-233.

Dobie, P. (1981) Storage. In *Pest control in tropical grain legumes*. Centre for Overseas Pest Research, London. Pp. 37-45.

Fujii, K. (1968) Studies on interspecific competition between the azuki bean weevil and southern cowpea weevil. III. Some characteristics of strains of two species. *Res. Popul. Ecol.*, **10**, 87-98.

Futuyma, D.J. & Peterson, S.C. (1985) Genetic variation in the use of resources by insects. *A. rev. Ent.*, **30**, 217-238.

Gould, F. (1979) Rapid host range evolution in a population of the phytophagous mite *Tetranychus urticae* Koch. *Evolution*, **33**, 791-802.

Hilder, V.A., Gatehouse, A.M.R. & Boulter, D. (1990) Genetic engineering of crops for insect resistance using genes of plant origin. In *Genetic engineering of crop plants* (eds Lycett, G.W. & Grierson, D.), Butterworths, London. Pp. 51-66.

Holloway, G.J. & Mackness, M.I. (1988) The evolutionary adaptation of enzyme systems in *Sitophilus oryzae* fed on toxic legumes. *Ent. exp. appl.*, **48**, 165-172.

Huignard, J. & Biemont, J.C. (1978) Comparison of four populations of *Acanthoscelides obtectus* (Coleoptera: Bruchidae) from different Colombian ecosystems. *Oecologia*, **35**, 307-318.

Johnson, C.D. & Kistler, R.A. (1987) Nutritional ecology of bruchid beetles. In *Nutritional ecology of insects, mites, spiders, and related invertebrates* (eds Slansky, F. & Rodriguez, J.G.), J. Wiley & Sons, New York. Pp. 259-282.

Labeyrie, V. (1981) Ecological problems arising from weevil infestations of food legumes. In *The ecology of bruchids attacking legumes (pulses)* (ed. Labeyrie V.), Junk, The Hague. Pp. 1-15.

Liener, I.E. (1982) Toxic constituents in legumes. In *Chemistry and biochemistry of legumes* (ed. Arora, S.K.), Oxford & IBH, New Delhi. Pp. 217-257.

Mallet, J. (1989) The evolution of insecticide resistance: have the insects won? *Trends in Ecology & Evolution*, **4**, 336-340.

Messina, F.J. & Mitchell, R. (1989) Intraspecific variation in egg-spacing behaviour of the seed beetle *Callosobruchus maculatus*. *J. Insect Behav.*, **2**, 727-742.

Prevett, P.F. (1990) Stored-product entomology - the challenge of the next decade. *Bull. ent. Res.*, **80**, 3-6.

Robert, P. (1985) A comparative study of some aspects of the reproduction of three *Caryedon serratus* strains in the presence of its potential host plants. *Oecologia*, **65**, 425-430.

Rosenthal, G.A. (1983) A seed-eating beetle's adaptations to a poisonous seed. *Sci. Am.*, **249**, 164-171.

Southgate, B.J. (1978) The importance of the bruchidae as pests of grain legumes, their distribution and control. In *Pests of grain legumes: ecology and control* (eds Singh, S.R., Van Emden, H.F. & Taylor, T.A.), Academic Press, London. Pp. 219-229.

Via, S. (1990) Ecological genetics and host adaptation in herbivorous insects: the experimental study of evolution in natural and agricultural systems. *A. rev. Ent.*, **35**, 421-446.

Wassermann, S.S. & Futuyma, D.J. (1981) Evolution of host plant utilization in laboratory populations of the souther cowpea weevil, *Callosobruchus maculatus* Fabricius (Coleoptera: Bruchidae). *Evolution*, **35**, 605-617.

LES BRUCHES ET LES GRAINES DE LEGUMINEUSES
ADAPTATIONS ET ADAPTABILITE

Peter F. CREDLAND et Julie DENDY

Royal Holloway and Bedford New College,
University of London.
Department of Biology,
Egham, Surrey, TW20 OEX, U.K.

RESUME

La résistance des végétaux est reconnue comme étant un bon moyen pour éliminer les ravageurs. Elle forme une des branches d'une triade, les autres étant les méthodes chimiques et biologiques. Dans le contexte de l'élimination des bruches dans les stocks de graines de légumineuses, particulièrement dans l'agro-alimentaire, l'emploi de cultures résistantes aux bruches présente un intérêt croissant. Ces cultures résistantes peuvent même être perçues comme étant le premier moyen de lutte, étant donné que les méthodes biologiques ne sont pas encore arrivées à un stade avancé et que les méthodes chimiques sont dangereuses et trop chères. Cependant, on ne peut compter sur de telles percées technologiques pour résoudre le problème et celles-ci doivent être perçues dans la totalité de l'écologie et de la physiologie des bruches si elles veulent apporter une contribution suffisante.

Les cultures résistantes sont comme les insecticides qui agissent comme de puissants agents de sélection et contre lesquels la résistance apparaît comme une manifestation d'adaptation. Les coléoptères des champs sont souvent mono ou oligophages mais les espèces de ravageurs les plus importantes et les plus cosmopolites peuvent maintenant utiliser une plus grande variété d'hôtes. Cette adaptabilité est un problème potentiel pour tout programme d'élimination des bruches et elle se complique des variations entre les biotypes ou entre les populations des mêmes espèces.

On illustrera, par référence à un ou deux des ravageurs les plus importants, les problèmes que pose l'estimation de la qualité des cultures en rapport avec les populations de bruches et on discutera de l'adaptation des populations aux changements dans les cultures d'hôtes.