CONSERVATION BIOLOGICAL CONTROL: FROM THEORY TO PRACTICE

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INTRODUCTION

The literature of the last 50 years abounds with research papers and reviews of how floral biodiversity might affect the numbers and impact of indigenous natural enemies. However, it is only relatively recently that practical advice is available to any farmer who might wish to exploit such biodiversity in an economically viable fashion. "Practice" in the title of this paper is therefore used in the sense of actions that are practical and economical for a farmer to take; it does not necessarily mean that many farmers are taking such actions. Also the mosaic nature of agriculture in areas of less cultivated land, characteristic of much of northern Europe, provides more opportunities than would seem relevant to more diversity-impoverished environments such as the main agricultural belts of the United States. Hence this review has a strong European slant, although it is applicable to some areas in the United States, particularly the northeastern and northwestern parts of the country.

Over 35 years ago, probably the first comprehensive review (Fig. 1) of the relationships of crop pests and beneficial insects with uncultivated land (van Emden, 1965) was able to cite examples of all the components of Conservation Biological Control by Habitat Modification used in practice today. Some of these (on the left half of Fig. 1) had, even in 1965, already been known for a quarter of a century.

THE EARLY POINTERS FOR HABITAT MODIFICATION

The importance of nectar feeding by adult parasitoid wasps was shown in a striking way by Thorpe and Caudle (1938). They reported that parasitoids (*Pimpla examinator* [F.]) of the pine shoot moth (*Rhyacionia buoliana* Schiffermueller) showed entirely opposite responses to the odor of the host plant depending on their physiological state. Emerging females were repelled by pine oil, causing them to leave the forest and seek nectar plants outside. Once they had fed at flowers and their eggs had matured, the parasitoids were attracted by pine oil and so moved back to the trees.

Also by 1938, it was clear that some parasitoids had an obligatory requirement for a second species of host (an alternate host) in order to complete the annual cycle of generations. This had emerged from studies on the diamond-back moth (*Plutella xylostella* [L.]) in England (Hardy, 1938). The pest overwinters within a cocoon as a caterpillar, but the larval parasitoid *Diadegma fenestralis* Holmgren emerges in the fall and cannot utilize the mature diamond-back moth larvae for an overwintering generation. However, Hardy (1938) had no idea on what plant or in which caterpillar *D. fenestralis* overwintered. The mystery remained till 1960, when the late O. W. Richards by chance reared the parasitoid from a yponomeutid caterpillar (*Swammerdamia lutarea* [Haworth]) collected from hawthorn (*Crataegus monogyna* Jacquin) (O. W. Richards, unpublished).

In contrast to obligatory alternate hosts, other alternative prey/hosts are useful to natural enemies when their preferred food becomes scarce. Györfi (1951) demonstrated this for oak forests in Finland with and without ground vegetation. Outbreaks of gypsy moth (*Lymantria dispar* [L.]) were far more frequent in forests with a clean forest floor. Györfi studied a complex of seven species of parasitoids (Table 1), and found that the 45 species of caterpillar available as alternative hosts on the ground vegetation were necessary to sustain the parasitoids in years of gypsy moth scarcity, even though there were 34 alternative hosts in the canopy.

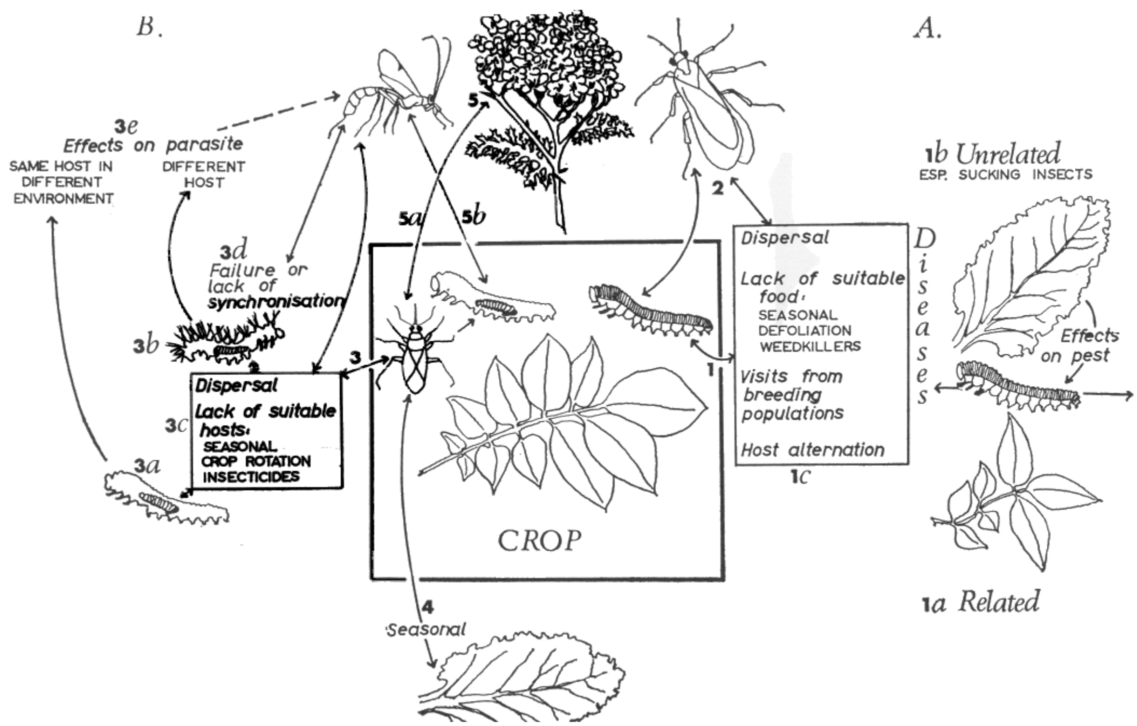

Figure 1. Biological relationships between uncultivated land and both pest (*A*) and beneficial (*B*) insects. Injurious species feed on both crop and related (1*a*) or unrelated (1*b*) wild plants for a variety of reasons (1*c*). Pests (2), predators (5*a*) and parasitoids (5*b*) may also feed at flowers (5). Beneficial insects may also utilize alternate (3*d*) or alternative (3) prey, again for several reasons (3*c*). Such alternative food may affect the physiology of the natural enemy (3*e*). Sometimes, carnivorous insects may feed phytophagously on plants outside the crop (4). From van Emden (1965).

Table 1. Alternative hosts of the main parasitoids of *Lymantria dispar* (L.), condensed from Györfi (1951)

Parasitoid	Number of alternative hosts	Number on ground flora
Ichneumon dispar Poda	7	0
Pimpla instigator (F.)	21	10
Theronia atalantae (Poda)	16	10
Apanteles fulvipes (Haliday)	27	19
Apanteles liparidis (Bouché)	3	2
Apanteles porthetriae (Muesebeck)	4	4
Apanteles melanoscelus Ratzeburg	1	0
TOTAL	79	45

The importance of the right microclimate (usually humidity) for beneficial insects was already noticed over 60 years ago by Taylor (1940), who attributed the scarcity of pest antestia bugs (*Antestiopsis* spp.) in neglected coffee plantations to the effect of shade in maintaining humidity favorable to their natural enemies.

In spite of these early pointers available by the time of van Emden's (1965) review, there was no movement towards implementing such concepts on farms for many years, for these reasons:

- Insecticides were considered effective, and the problems associated with them were not sufficient to change farmers' attitudes;
- The focus of biological control was firmly on the classical approach of importation;
- Farmers were not prepared to encourage weeds on their land;
- The idea of "biodiversity" was considered too complex to be useful in practice.

Today, however, instead of titles like "The role of uncultivated land in the biology of crop pests and beneficial insects" (van Emden, 1965), it is possible to write headings such as "The practical exploitation of plant diversity" (in van Emden and Peakall, 1996). This has come about partly because floral diversity is now being introduced on farms for reasons unconnected with biological control (see later), but also because there has been a breakthrough in thinking. It has been realized that diversity and community stability (including lack of pest outbreaks) are not causally related, and it is therefore pointless to hope to mimic naturally evolved diversity. Rather, just one small element of habitat modification (such as the provision of just one plant species) might achieve the desired enhancement of biological control (Way, 1966; van Emden and Williams, 1974).

SOME EXAMPLES OF DIVERSITY OUTSIDE THE CROP

Diversity Outside the Crop Planned for Biological Control

Sotherton (1984) found high densities of adult Carabidae overwintering in the grass banks outside cereal fields. Such banks are characteristic of British agriculture, particularly along roadsides as part of woody hedgerows. The predatory beetles sought the well-drained yet humid conditions provided by these banks. As a result of this work, simple "beetle banks" have been designed – narrow raised strips of light soil sown with a suitable grass species (usually *Dactylis glomeratus* L.). These strips can be accommodated under the post and wire fencing around the field and can accumulate densities of overwintering carnivorous beetles as high as 1,500 per m^2, rather higher than found in natural banks.

The importance of flowers to attract beneficial insects for adult feeding, particularly hover flies (Syrphidae) and larger parasitoids (Ichneumonidae and Braconidae) is now fully recognized, and border strips of flowers are sown for this purpose. A particularly rich pollen source is American buckwheat (*Phacelia tanacetifolia* Bentham) (Gurr *et al.,* 1998). This plant has the added advantage of being an annual with nonhardy seeds; frosts in winter would therefore prevent any unintentional spread of *P. tanacetifolia* as a weed.

A novel approach to using alternative insect hosts for parasitoids of cereal aphids has been proposed by Powell (2000). This approach exploits the fact that the aphid sex pheromone attracts the parasitoids at times and in situations where it is not responded to by aphids. Some of these parasitoids can utilize aphid hosts on nettles and grasses adjacent to the crop. The parasitoids can be concentrated there when they leave the cereal fields in the fall by placing pheromone sources among the weeds. In the spring, to overcome any tendency the parasitoids might have to remain constant to the weed-feeding aphids or the weeds themselves, pheromone lures could be placed in the cereal crop to attract the parasitoids back into the crop.

Occasionally, an alternative host plant can be used as a selective trap for pests to increase the natural enemy: pest ratio on the crop. Such a selective trap crop for wheat stem sawfly (*Cephus cinctus* Norton) was a 15 to 20 m wide strip of sterile brome grass (*Bromus sterilis* L.) around wheat fields in Canada some 30 years ago (cited by van Emden, 1977). The grass arrests many of the arriving sawflies, which oviposit in the grass. The larvae bore into the stems but are unable to complete their development so produce no subsequent generation of sawflies. However, parasitoids in the larvae do emerge safely and move onto the wheat. The grass is in effect a factory that converts pest biomass into parasitoids.

A final example of diversity outside the crop planned for biological control, and an example of an obligatory alternate host, is the famous recommendation to plant blackberries near Californian vineyards (Doutt and Nakata, 1973) . This promotes biological control of the grape leafhopper (*Erythroneura elegantula* Osborn) by the egg parasitoid *Anagrus epos* Girault. This parasitoid has to have an overwintering generation in leafhopper eggs, but its host *E. elegantula* overwinters as an adult. The blackberry leafhopper *Dikrella californica* Osborn, by contrast, does overwinter as an egg and provides a suitable alternate host. Later it became apparent that leafhoppers on some of the trees in the vineyard environment were more effective in providing the necessary eggs overwinter. More recently still, commercial plantings of French prune trees (*Prunus domestica* L.), which support another leafhopper (*Edwardsiana prunicola* [Edwards]) that overwinters as an egg, are seen as potentially most useful in promoting *A. epos*, though the practice has not been widely adopted by growers of vineyards (Murphy *et al.,* 1998).

Diversity Outside the Crop for Reasons Other than Biological Control

In Europe, some diversity outside crop areas has been introduced as a result of food overproduction and public pressure for more environmentally benign agriculture, particularly to conserve bird populations in farmland. In the United Kingdom, government subsidies are available for several schemes aimed at encouraging farmers to use land for conservation rather than production. Areas of diverse vegetation are thus appearing on farms. It seems only reasonable to suppose that they will make a valuable contribution to biological control by providing alternative hosts and nectar sources for beneficials.

One of these schemes is "Set-aside," which in 2002 (DEFRA, 2002a) provided payment for taking out of production land previously used for cereals, oilseeds, proteins, linseed, flax (for fiber), or hemp (for fiber), but excluded land that was already being used for plantation crops, woodland, or pasture in 1991. The minimum set-aside is 10% of the relevant crop area, and minimum blocks must be 0.3 ha with a minimum width of 20 m. Farmers are obliged to adhere to strict management rules, including a prohibition on any form of cash return from the land. The area committed to set-aside can be managed in various ways. For example, it may be left to recolonize with plants naturally, it may be sown with a wildflower mix, or be used for non-commercial woodland.

Another of several alternative incentives is the "Countryside Stewardship Scheme," which makes grants to "improve the natural beauty and diversity of the countryside, enhance, restore and recreate targeted landscapes and historical features….." (DEFRA, 2002b). Farmers enter into 10-year agreements to manage land in an environmentally beneficial way in return for an annual payment, and capital grants are available for projects such as replacing or laying new hedgerows and tree plantings.

SOME EXAMPLES OF DIVERSITY INSIDE THE CROP

Diversity Inside the Crop Planned for Biological Control

The grassy ridges known as "beetle-banks" at the edges of cereal fields (see earlier) have the disadvantage that beetles move only short distances into the crop in the spring. The concept has therefore been extended to siting such "beetle-banks" as 1.5 m wide "predator conservation strips" at 200 m intervals across fields, but leaving gaps at the ends for machinery to turn (Thomas and Wratten, 1988). The strips can be created afresh whenever a farmer wishes to change the direction of cultivation. The costs are only about 0.5% of yield. This compares with gains of 5% of yield from increased predator efficiency and with spray costs of 2.5% of yield. A further step is to sow nectar plants such as American buckwheat on the strips to combine two elements of habitat modification (overwintering sites for predators and attraction of predators and parasitoids for nectar feeding).

Viticulturists in Switzerland have recently been faced with the withdrawal by industry of virtually all their permitted insecticides and, one imagines in some desperation, they have turned to Conservation Biological Control by sowing flowering "mini-meadows" between the rows of vines. The provision of flowers and alternative prey has been very successful, particularly in the moister areas of the country, at keeping pests below their economic thresholds (Boller, 1992).

Steep increases in the cost of winter feed for farm animals have caused farmers in Europe to consider undersowing food crops with an animal forage crop. Powell (1983) has examined the potential for undersowing wheat with rye grass for improving biological control of aphids on the wheat. Once the grass has been colonized by the aphid *Myzus festucae* Theobald, which does little damage to the forage, the parasitoid *Aphidius rhopalosiphi* De Stefani Perez is released. In this way a parasitoid population is already established on the grass to attack the grain aphid *Sitobion avenae* (F.) when it invades the wheat crop in the spring.

Diversity Inside the Crop for Reasons Other than Biological Control

Intercropping two food crops is an age-old agricultural practice probably developed for more productive subsistence farming and to obtain some weed control by covering the bare soil between rows of an upstanding crop with a spreading crop plant species. The selection of the two species to be intercropped is therefore not made on the basis of possibilities for Conservation Biological Control, although the effects of intercropping on the latter have been the focus of much debate and theorizing in the literature. A brief review is given by Gurr *et al.* (1998). Table 2 presents a summary of the effects of intercropping on insects.

Some years ago on arable farms in the United Kingdom, populations of the gray partridge (*Perdix perdix* L.) were in serious decline (Potts, 1986). This decline was attributed to the reduction caused by herbicides and insecticides in the amount of insect food available to the chicks at the crop edge. In cereals, the edge rows yield less than the rest of the crop, and farmers have found it economic to sacrifice yield there still further in return for higher partridge populations and the associated income from shooting rights. Although grass-killing herbicides still need to be sprayed at the field edges to prevent incursion from serious grass weeds, farmers valuing the income from partridges will shut off the outside boom to leave an unsprayed 6 m strip when applying insecticides or herbicides for broad-leaved plants. Rands (1985) showed such practice increased partridge brood size two to six fold, compared to areas where the whole field was sprayed. The visual result is very impressive in terms of floral diversity; flowers abound and there are many potential alternative hosts for beneficial

Table 2. Overview of intercropping effects on insect pest populations (from van Emden and van Huis,1992).

Colonization and Establishment	
Visual effects	Olfactory effects
Crop background	Masking host plant
Phenotype	Masking host insect*
Wider spacing	Repellent chemical stimuli*
Camouflage	
Population Development and Survival	
Microclimate	Natural enemies
Humidity, shade*	Favorable habitat*
	Alternative host/prey*
	Supplementary food*
Feeding	Dispersal
Quality	Trapping
Confusing olfactory stimuli	Physical interference
	Loss of dispersing individuals

* Intercropping effects that are relevant to conservation biological control.

insects on the weeds and cereals. A similar profusion of weeds and flowers is seen where an unsprayed "buffer zone" at the edges of crops is imposed on farmers by legislation. Buffer zones can vary considerably in width; their aim is to protect sensitive adjacent environments such as watercourses and nature reserves from pollution, particularly by herbicides. This practice is relevant for agriculture in developing as well as in developed countries.

Perhaps paradoxically, the development of herbicide-tolerant crops may provide an opportunity for increasing diversity within the crop to provide insect food for partridge chicks and also for beneficial insects. This possibility is exemplified by genetically modified (GM) sugar beet (Dewar *et al.*, 2000). Because non-GM sugar beet is peculiarly sensitive to herbicides, the United Kingdom sugar beet crop is managed to be weed-free, with intensive use of pre-emergence herbicides. Thus it is only in GM crops that weeds can be allowed to persist till the danger of competition with the crop forces the use of the herbicide to which the GM crop is tolerant. This is likely to be late enough for the early weed diversity to be of value.

Schemes such as Set-aside and Countryside Stewardship, mentioned earlier as providing financial incentives for diversity outside the crop, also apply to within-crop areas. Thus one can now see large "islands" of diverse vegetation inside intensively managed and heavily sprayed arable fields, providing rich and diverse resources for farmland birds (and incidentally also for beneficial insects) in the middle of crop monoculture (Fig. 2).

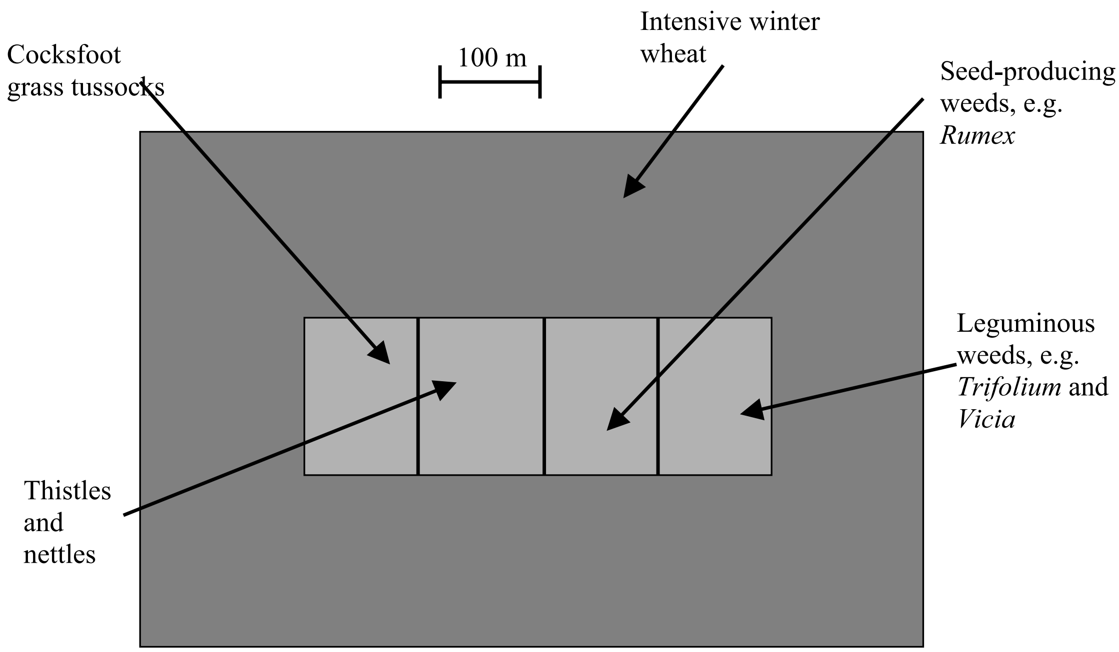

Figure 2. Example of a Countryside Stewardship scheme on an intensive arable farm in Cambridgeshire, United Kingdom.

CONSERVATION BIOLOGICAL CONTROL IN RELATION TO INSECTICIDES

Background

A quite different approach from Habitat Modification to the conservation of biological control is the protection of biological control agents when insecticides have to be used. This was termed "integrated control" in the late 1950s (Stern *et al*., 1959), with chemical control being integrated with biological control in such a way as to cause minimum disruption to the latter. However, all the early examples of integrated control show far more than this definition suggests. van Emden (1974) has argued that, in each case, chemical control improved the otherwise inadequate biological control. This proactive use of pesticide to conserve biological control is beautifully illustrated by the work of Wheatley (1963) in coffee plantations in Kenya. One remarkable aspect of Wheatley's control of coffee loopers was that he used the ultra broad-spectrum DDT as a selective insecticide. It was simply painted around the trunks of the coffee trees. Whenever biological control on the trees was losing impact, natural pyrethrum at a knock-down rather than at an acute toxic dose was sprayed in the canopy. The dislodged insects separated when they recovered into those (like the caterpillars) that could only regain the foliage by passing over the DDT band, and the many adult beneficials that would fly back.

Before these ideas, conservation of biological control agents under a pesticide regime was limited to the use of selective compounds, rather than the selective use of ones that had a broad spectrum of toxicity. One selective compound already widely used 40 years ago was the toxin of the bacterium *Bacillus thuringiensis* Berliner, selective for Lepidoptera. At that time there was hardly a hint that the sprayer would one day be replaced by the GM plant as the means to deliver the toxin. However, the high kill of the pest achieved is potentially damaging to the pest's biocontrol agents, which could present a problem should the pest develop tolerance to the toxin. On the other hand, generalist natural enemies and enemies of minor pests of the crop are likely to benefit from the reduction in insecticide on the *B.t.* crop.

The ideas of integrated control as an approach to Conservation Biological Control were not followed up for many years. As with Habitat Modification, there was no real need to reduce the use of insecticides, and the focus of biological control remained on importation. Also, farmers and even scientists had grown up with the belief that insecticides could only damage biological control. Today, however, the integration of pesticides into pest management is fully accepted (van Emden and Peakall, 1996), with the important central idea that the number of natural enemies killed as a result of applying insecticide is relatively unimportant. What matters is that the ratio of natural enemies to pests should have increased after the application.

Improvements in natural enemy/pest ratios can be achieved in many ways (reviewed by van Emden and Peakall, 1996), even with broad-spectrum toxins. An example applicable to many crops is "band-spraying," in which only alternate sprayer swathes are treated each time it is necessary to apply an insecticide. Particularly with synthetic pyrethroids, many natural enemies are disturbed by the spray and fly to the unsprayed swathes. A more crop-specific example is the idea of treating aphids with a very ephemeral insecticide after lady beetles (Coccinellidae) have laid their eggs, yet while the progeny are still protected within the egg from insecticides (Morse, 1989). Since the lady beetles lay eggs in proportion to the abundance of their prey, this timing maximizes the number of hatching coccinellid larvae while reducing the number of the prey they are required to control.

CONCLUSIONS

In relation to both approaches to Conservation Biological Control briefly reviewed here, Habitat Modification and improving the natural enemy/pest ratio, the concepts were well articulated by scientists 40 years ago as theoretical contributions to improve biological control. The two ideas that (1) trying to copy natural diversity is not desirable and (2) the relative proportion of pests and natural enemies killed by insecticides is the key to pesticide selectivity, soon produced practical suggestions for implementing Conservation Biological Control.

There is still considerable reluctance among farmers to follow this path, but ways of improving biological control by indigenous or released natural enemies are increasingly being requested by farmers in Europe and willingly tested by them. It is not that these farmers are philanthropists and have suddenly developed a greater environmental conscience; it is that there are strong forces pushing them in that direction:

- Environmental lobbies, especially the host of bird lovers, are putting pressure on both governments and farmers to halt what is perceived as a reduction in biodiversity, especially of farmland birds, attributed to high-input agriculture. As a result, governments are introducing financial incentives such as the Countryside Stewardship Scheme to increase biodiversity on farms;

- The media have successfully fueled an unreasonable distaste for insecticides in the public. Increasingly, houses in farming communities are being purchased as second or retirement homes by town-dwellers with little understanding of agriculture and a strong dislike of witnessing spraying activity locally.

- Also as a reaction to public demand, supermarkets, which in many countries control over 80% of fresh produce sales, are imposing integrated crop management protocols on farmers who wish to be suppliers.

- New pesticide safety standards are forcing the retesting of older products, and agrochemical companies are finding it easier to withdraw compounds from sale than to reregister them. Many crops now suffer from an acute shortage of permitted insecticides, especially with the lengthy delays in the approval of new compounds. This shortage of pest control materials has made farmers more aware of the dangers of pest resistance when relying on just one or a few compounds, and they are seriously seeking more sustainable solutions to their pest problems.

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