

Opinion

A Conceptual Framework for Integrated Pest Management

Johan A. Stenberg^{1,*,@}

The concept of integrated pest management (IPM) has been accepted and incorporated in public policies and regulations in the European Union and elsewhere, but a holistic science of IPM has not yet been developed. Hence, current IPM programs may often be considerably less efficient than the sum of separately applied individual crop protection actions. Thus, there is a clear need to formulate general principles for synergistically combining traditional and novel IPM actions to improve efforts to optimize plant protection solutions. This paper addresses this need by presenting a conceptual framework for a modern science of IPM. The framework may assist attempts to realize the full potential of IPM and reduce risks of deficiencies in the implementation of new policies and regulations.

When Is It Integrated Pest Management?

Many national and intergovernmental bodies have firmly decided that the future officially endorsed paradigm for crop protection will be 'integrated pest management (IPM)'. For example, a European Union (EU) Directive [1] has obliged all professional plant growers within the Union to apply the general principles of IPM since 2014. Most textbooks define IPM as a holistic 'approach' or 'strategy' to combat plant pests using all available methods, with minimal applications of chemical pesticides [2,3]. The aim is not to eradicate pests, but to manage them, maintaining their populations below economically injurious levels [4,5]. Putting this vision into practice would reduce not only farmers', consumers', and the environment's exposure to toxic compounds, but also problems caused by pesticide-resistant pests.

Introduction of the IPM concept spurred intense exploration of various actions that could contribute to IPM programs. At the time of writing, a Web of Science search using the term 'Integrated Pest Management' returns around 50 000 hits, suggesting that IPM and associated issues have engaged an army of researchers. However, despite the expressed enthusiasm for IPM, most cropping systems still depend on heavy use of chemical pesticides [6], and IPM is still far from being efficiently researched or applied, probably because no holistic science of IPM has emerged as yet.

The founders of IPM recognized that integrating several methods to combat pests would require interdisciplinary research programs [4,5], but many interdisciplinary research programs with a claimed objective to study IPM actually focus on single plant protection methods. For example, entomologists, chemical ecologists, and plant breeders may apply an interdisciplinary approach to generate cultivars with high indirect resistance to pest insects, but this can hardly be considered IPM research as it focuses solely on one element of pest management (plants' intrinsic heritable resistance). More than one pest management action must be considered to meet the 'integrated' criterion of IPM. Thus, I propose that the science of IPM should be defined as the systematic study of the compatibility and optimization of actions associated with at least two pest management elements (Box 1 and Figure 1, Key Figure). In this opinion article, I first

Trends

Integrated pest management is globally endorsed as the future paradigm for crop protection, but in practice it just means that several pest management elements are combined – not integrated.

Different pest management elements interact with each other, having synergistic or antagonistic effects when used together. The emerging science of IPM systematically studies the compatibility and optimization of the involved elements.

Most interactions within IPM involve effects of plant resistance on other pest management elements. By contrast, biological control is affected by almost all other elements.

¹Department of Plant Protection Biology, Swedish University of Agricultural Sciences, 23053 Alnarp, Sweden
 @Twitter: @Stenberg_JA

*Correspondence:
 johan.stenberg@slu.se (J.A. Stenberg).
 URL: <http://www.slu.se/stenberg>.

Box 1. Definitions**The Concept of IPM**

A holistic 'approach' or 'strategy' to combat plant pests and diseases using all available methods, while minimizing applications of chemical pesticides.

The Science of IPM

The systematic study of the compatibility and optimization of simultaneously implemented actions associated with at least two pest management elements of the IPM pyramid.

describe the individual elements of ecologically based IPM, and then map research routes to identify optimal combinations of actions for successful IPM.

The Individual IPM Elements**Intrinsic Heritable Plant Resistance**

Wild plants have evolved traits that help them resist pests and pathogens either directly or indirectly [7–9]. Direct defenses – such as secondary metabolites [10], trichomes [11], and wax layers [12] – directly defy attackers, making the plant less detectable, attractive, edible, or susceptible to infection. Indirect defenses, by contrast, attract and reward the natural enemies of pests, thereby engaging them as 'bodyguards' [13,14]. Plant traits involved in indirect defenses include odors (often pest induced) that attract natural enemies to infested plants [8], and nectar that rewards and sustains attracted natural enemies of pests [15].

Unfortunately, many resistance traits have been lost during the domestication of crops [16,17]. There are several reasons for this, but most importantly resistance was not prioritized during the 20th century when pest problems could be solved with cheap chemical pesticides. By contrast, direct defense traits were often selected against as they interfered with the taste and texture of the crop. Indirect defenses were rarely consciously selected against, but were ignored due to lack of awareness of their importance.

While both direct and indirect defense traits have been widely lost from modern cultivars, recent research has shown that important traits remain in wild crop relatives [18–20]. Thus, one of the most important tasks for resistance breeders will be to find and utilize the natural variation in these traits – especially indirect defense traits – in wild crop relatives, and transfer them to future cultivars to improve crops' intrinsic resistance to pests and pathogens.

The multigene nature of most resistance mechanisms constitutes a challenge for successful breeding. Fortunately, increasing resistance is now a priority, and new technologies for targeted genome editing such as clustered regularly interspaced short palindromic repeats (CRISPR)/Cas [21] will aid this aim, but a major challenge will be to develop cultivars with enhanced resistance to several pests [22]. The most realistic strategy may be to improve indirect defenses by enhancing recruitment of generalist natural enemies, which can combat diverse pests [19].

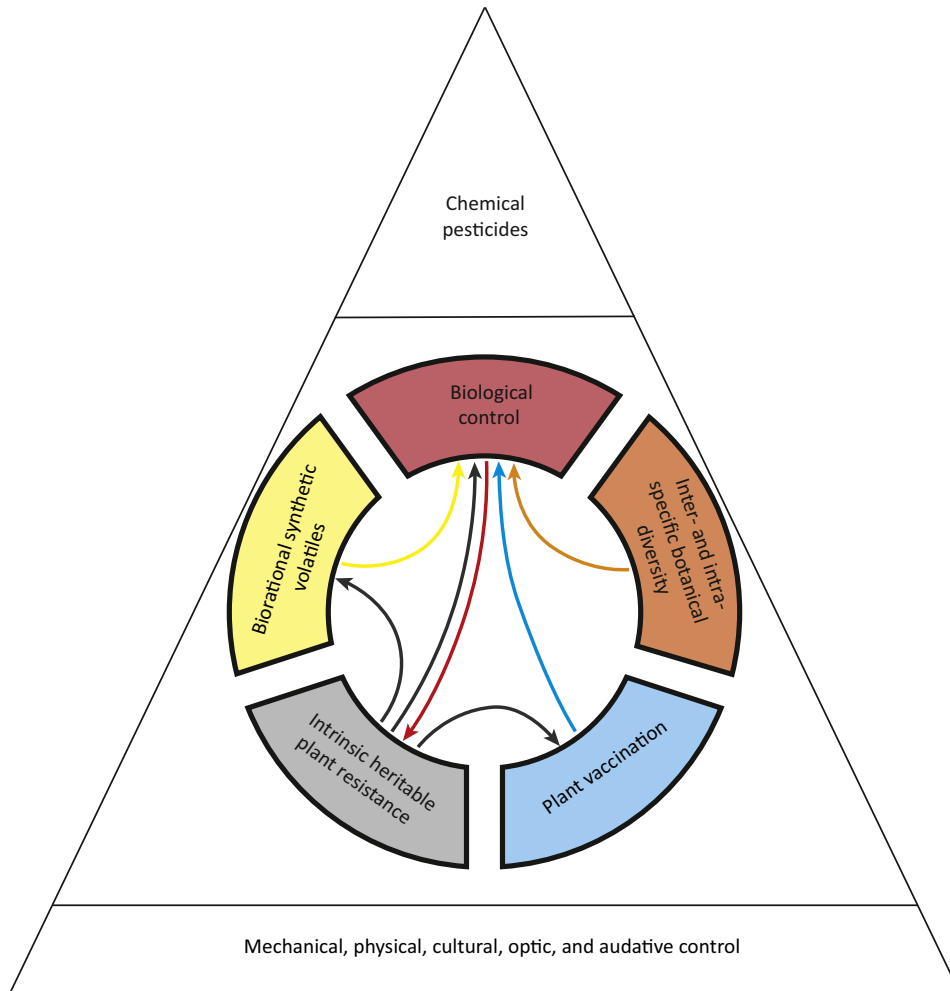
Plant Vaccination

Plants frequently respond to pest attacks by inducing direct and indirect defenses that efficiently counter both the currently attacking pest and pest species that may attack later. This process can be regarded as 'plant vaccination' if the defense-inducing organism is relatively harmless and the induced defense makes the plant resistant to a more detrimental pest [23].

Plants can also be vaccinated by exposure to factors that induce a 'primed' state, in which they respond more rapidly and strongly to subsequent pest attacks [24–26]. A major advantage of

Key Figure

The Integrated Pest Management (IPM) Pyramid Showing the Most Important Pest Management Elements



Trends in Plant Science

Figure 1. The base tier of the IPM pyramid consists of abiotic actions that can be applied before or immediately after planting and may continue until harvesting. Then follows a circular tier consisting of important elements that can be classified as ‘ecological’ and form the basis for ecology-based IPM. Finally, the top tier of the pyramid includes chemical pesticides that should only be applied when necessary, if the more basal IPM elements fail to keep pest populations under the economic threshold. Arrows denote particularly important interactions between the ecological elements. These seven interactions are key research areas that require elucidation to integrate the elements and realize the full potential of IPM.

priming is that the defenses are not turned on until needed, thus reducing the associated metabolic costs. In nature, priming and/or defenses can be induced by various biotic or abiotic factors, including herbivore-induced plant volatiles [27], egg deposition [28], heavy metal stress [29], and soil microbes [30]. One interesting opportunity discussed by Pineda *et al.* [30] is to transplant ‘healthy soil’ with beneficial microbes for priming or inducing defenses of crop plants.

In other cases, seeds or plants can be treated before sowing or planting, thus providing the grower with resistant material from day one. For example, tomato plants grown from jasmonate- and β -aminobutyric acid-treated seeds reportedly have stronger induced defenses than controls against both arthropod pests and pathogenic fungi [31]. Challenges for future research include the development of techniques that provide defenses against several pests simultaneously and improve the consistency of priming responses. To meet this objective, better understanding of the molecular mechanisms involved in priming defenses to targeted pests is required.

Inter- and Intra-Specific Botanical Diversity

The importance of biodiversity for ecological processes can hardly be overstated [32,33]. *Inter alia*, monocultures are highly sensitive to pests and often severely damaged by outbreaks [34]. There are several reasons for this sensitivity. The first is lack of intraspecific botanical variation: a genetic monoculture has no variation in resistance genes, so all plants in it will be potentially susceptible to any pest capable of establishing a colony in or on one of them. Thus, resistance can be significantly improved simply by using several varieties in a field. For example, increasing the genotypic biodiversity of rice in China has reduced frequencies of rice blast by 94% and increased yields by 89%, relative to those of genetic monocultures [35]. Accordingly, the temptation to use a single cultivar because it has high pest resistance is counterproductive – mixtures almost always provide higher cropping security than single cultivars, even when they include cultivars with low resistance [36].

Another reason for monoculture's pest sensitivity is their lack of interspecific botanical diversity: single-crop systems do not benefit from any 'associational resistance' [37] – that is, reduction in plants' detectability by, and vulnerability to, pests linked to growth in communities with other plant species. Although interspecific diversity *per se* may reduce pest problems, the effect can be greatly improved by consciously combining plant species with attracting and repelling traits. The 'push-pull' concept (which combines use of a repellent plant around a crop and a 'trap crop' some distance from it) is to date the most successful approach to protect crops from arthropod pests using interspecific botanical diversity [38].

Although a convincing body of literature shows that increases in inter- and intra-specific botanical diversity reduce pest problems, it is still unclear which of these two factors is most important, and should be prioritized.

Biorational Synthetic Volatiles

A developing pest control strategy is to use 'biorational' substances, which have low toxicity to nontarget taxa and include various volatiles such as insect pheromones [39] and plant volatiles [40] (or derivatives of these compounds) that influence pests' behavior. To date, sex pheromones have been the most frequently applied, often in efforts to disrupt mating of insect pests. This involves dispensing relatively large amounts of sex pheromones in plantations, thereby suppressing males' abilities to find female conspecifics for mating [39]. A disadvantage of mating disruption is that it cannot be used curatively. However, it is efficient, environmentally friendly, and relatively inexpensive. Other important uses of pheromones include mass trapping [41] with either male- or female-produced pheromones, and herbivore repellence using alarm pheromones [42]. However, recent findings indicate the presence of relatively high intraspecific variation in pheromone blends among pest populations [43]. Thus, further study of the population specificity of lures' efficacy, and the feasibility of developing pheromone blends for local populations, is required. Synthetic plant volatiles have been used less extensively, and usually as parts of push-pull systems [40,44]. However, recent research suggests that plant volatiles significantly influence the strength of insect herbivores' responses to pheromones [45]. Thus, future use of plant volatiles may be most significant as part of blends with pheromones.

Biological Control

Biological control, or biocontrol, is the use of living organisms to reduce the population density or impact of pests [46,47]. It is one of the oldest nonchemical control methods used in agriculture [47]. Arthropods are mainly controlled using predators, parasitoids, and pathogens, while plant pathogens are mainly combated using antagonistic microbes. Often viewed as the cornerstone of IPM, biological control is probably the most well-researched element of the IPM concept, and root of some of the most innovative practical applications. For example, 'flying doctors' (inoculated bees) are being used as vectors for high-precision applications of microbial biological control agents to flowering crops infected with pathogenic fungi [48]. Similarly, for 20 years insecticidal proteins associated with the bacterial biological control agent *Bacillus thuringiensis* have been expressed by transformed *Bt* crops [49].

Most of the intrinsic problems associated with biological control appear mainly in open areas with arthropod agents, which in some cases can emigrate from the plantation leaving the pest behind, attack each other (intraguild predation) rather than the target pest [50], or attack nontarget prey [51]. A problem mainly associated with microbial agents is that pests can evolve resistance [52,53]. As we will see, some of these problems can be solved by combining biological control with actions associated with other IPM elements.

IPM Research: Strategies for Integrating the Elements

As the objective of IPM is to optimize combined effects of actions associated with the elements reviewed above, the science of IPM should elucidate interactions between these actions and formulate strategies to optimize the interactions' synergy (Figure 1). Seven such interactions (research areas; described below) are identified in this paper, and visualized in Figure 1. Particularly important research questions are presented in the Outstanding Questions section.

Optimization of Intrinsic Heritable Plant Resistance for IPM

Interactions with Plant Vaccination

In general, effects of priming and induction are strongly dependent on plant genotype [54]. For example, *Hordeae* grasses such as wheat, barley, rye, and oats can be vaccinated against a range of herbivores using *Epichloë* microbes via alkaloidal secondary metabolites [55]. However, effects of *Epichloë* may be either positive or negative, depending on plant genotype [55]. These findings provide breeders with new opportunities to optimize effects of plant vaccination, but show that neglect of this issue at the breeding stage may severely impair results of vaccination. The paucity of knowledge about and guidelines for breeding to facilitate plant vaccination against pests constitutes a major obstacle, which will require investments in basic molecular research. On the more positive side, new genetic resources from wild crop relatives, and novel genome editing technologies, provide hope for progress in this area.

Interactions with Biorational Synthetic Volatiles

Recent research has shown that defensive plant semiochemicals can make herbivore sex pheromones either less or more attractive to conspecifics. More specifically, herbivorous cotton leafworms are only reportedly attracted to mating sites by sex pheromones in the presence of certain combinations of host volatiles, and single plant defense compounds (such as 4,8-dimethylnona-1,3,7-triene) can strongly suppress pheromone signals [45,56]. These discoveries open up new opportunities for breeders to modulate plants' profiles of volatiles that interact with sex pheromones, thereby signaling to herbivores that a crop plantation is an unsuitable mating site or facilitating mass trapping with pheromone traps. Realization of these possibilities will require more knowledge of interactions between plant volatiles and pheromone signals, and thus new creative collaborations between crop breeders and insect chemical ecologists. Future attempts to transform crops to release pest alarm pheromones [57] may also

benefit from considering plant semiochemicals, as overall pheromone and plant volatile profiles may be the ultimate determinants of pest behavior.

Interactions with Biological Control

Intrinsic heritable plant resistance affects not only pests but also beneficial organisms like biological control agents. For example, predatory bugs used for biological control often suck plant sap, or nectar whose quality affects the performance and biological control efficacy of the predators [19,58,59]. By contrast, parasitoids are exposed to the plant material that their herbivorous hosts consume, and are thus indirectly affected by plant-resistance traits [16,60]. In addition, physical plant defenses such as trichomes are known to affect biological control agents [11]. While these examples show that plant traits affect biological control agents, it is still largely unknown how plant resistance ultimately affects plant damage in the presence and absence of biological control [61,62]. Predators, parasitoids, and pathogens may be differently affected by different kinds of plant-resistance traits, allowing crop breeders to design cultivars suitable for specific biological control agents [62].

Plant volatiles too could be used to improve biological control, and a breeding strategy for this purpose has been published elsewhere [19]. However, important problems remain to be solved. For example, attraction of biological control agents to volatile-emitting crops still works best at small scales [63]. To make indirect defenses more relevant, we need to understand how to attract (and retain) sufficient numbers of biological control agents to, for example, large maize fields.

Optimization of Plant Vaccination for IPM

Interactions with Biological Control

Research on plant vaccination in IPM contexts is limited [64]. A potential risk is that when basal plant defenses are induced or primed, not only pests but also beneficial organisms, like their predators, will also be exposed to the defenses [65]. However, in the few studies that have investigated effects of plant vaccination on predation, positive effects on predation rates have been detected. For example, induction of cotton defenses can induce omnivorous thrips (*Frankliniella occidentalis*) to switch from feeding on host cotton plants as pests to feeding on herbivorous spider mite eggs [66]. In addition, two recent studies found that plant-feeding predators can be used to vaccinate plants, as the predatory bug *Macrolophus pygmaeus*, which is often used as a biological control agent, can induce proteinase inhibitor (PI) activity and accumulation of transcripts of the PI-II gene in tomato [67], consequently reducing pest pressure [68]. Thus, some biological control agents could theoretically be introduced to plantlets in nurseries for vaccination and then hitch-hike with the plants to the final growing areas to provide biological control services. Apart from these intriguing results, possible synergies between plant vaccination and biological control have been almost completely unexplored, and are wide open for new idea-based research.

Optimization of Inter- and Intra-Specific Botanical Diversity for IPM

Interactions with Biological Control

A favorite topic for many IPM researchers is the optimization of plant diversity for biological control. To date, this is probably the most intensively investigated area of IPM, having produced important practical applications such as intercropping [69], flower strips [70], and various types of habitat management [71]. The idea behind this IPM approach is to add plant-based food, shelter, and alternative prey to biological control agents, while maintaining the direct associational resistance to pests as described earlier. Functional botanical diversity is often obtained by adding companion plants carrying floral or extra-floral nectar [19]. For example, a recent multicountry multiyear study showed that planting nectar-producing plants around rice fields increased the abundance of predators and parasitoids, while pest populations were reduced

[72]. Interpreting results of these studies is not straightforward, partly because generally they do not show causal relationships (only correlations) between increases in botanical diversity, improvements in biological control, and reductions in pest densities. Thus, there is often only speculative understanding of the mechanisms responsible for the beneficial effects. In addition, interventions at very local scales (e.g., mixed intercropping) [73] to landscape scales [74] can reportedly have beneficial habitat effects, but further research is needed to identify the optimal spatial scale of botanical diversification to favor biological control agents [71]. As yet, almost all IPM research regarding effects of botanical diversity on biological control has solely focused on interspecific diversity. However, botanical diversity could also be manipulated at the plant trait [75] or plant genotypic level [76–78]. The mechanisms whereby intraspecific plant diversity affects biological control agents are unknown, but could involve effects on pests [78]. For example, variation in pest development time, which can be enhanced by mixing resistant and susceptible cultivars, can suppress predator–prey cycles and mitigate pest outbreaks [79]. To date, interspecific and intraspecific crop diversity has not been simultaneously manipulated in any published study, leaving abundant opportunities for future IPM research to explore the optimal taxonomic level(s) of diversity.

Optimization of Biorational Synthetic Volatiles for IPM

Interactions with Biological Control

Although pheromones presumably evolved because of their ability to trigger behavioral responses in conspecifics, they can sometimes be exploited by other organisms [80,81]. If predators and parasitoids use herbivore pheromones to locate their prey [82], mass release of sex pheromones to disrupt mating could also disrupt biological control. However, most predators and parasitoids tend to target immature stages of their prey (either eggs or larvae), which do not produce sex pheromones. Thus, in most cases biological control of herbivores will not be affected by the use of synthetic sex pheromones, but the possible utility of other herbivore pheromones in biological control measures should be further explored. For example, aphid alarm pheromones [80] have two known biological effects: (i) disrupting aphid feeding on their host plants, and (ii) acting as kairomones, attracting natural enemies of the aphids [57,83]. Thus, transforming crops to release aphid alarm hormones is a promising strategy. In a recent study, the parasitoid *Aphidius ervi* spent more time foraging on a hexaploid variety of wheat following transformation of the plant, enabling it to release the aphid alarm pheromone (E)- β -farnesene [57], but this did not suppress aphid infestations in the field. A complicating factor is that aphid alarm pheromones are considered short-range cues agents [84], which may have little ability to attract natural enemies from far away. However, combining pheromones with plant volatiles, which often have longer ranges, may be an effective strategy. Furthermore, predators and parasitoids can quickly learn to disregard dishonest signals [85]. Therefore, future research should investigate the possibilities to release aphid alarm pheromones solely after aphid attack, to guide predators and parasitoids specifically to damaged plants.

Optimization of Biological Control for IPM

Interactions with Intrinsic Heritable Plant Resistance

A major problem in modern agriculture is that pests rapidly evolve counter-resistance to previously resistant cultivars [86–88]. Recent research suggests that crop breeders' arms races with pests can be supported by biological control agents [89]. The theoretical background for biological control-aided durable resistance was laid out already 25 years ago when Gould *et al.* [90] suggested that biological control agents that decrease the differential pest fitness between resistant and susceptible cultivars should delay the evolution of counter-resistance in the pest. This hypothesis was tested in experiments with *Bt* broccoli expressing Cry1Ac, herbivorous diamondback moths, and predatory lady beetles [89]. As predicted, the herbivore evolved counter-resistance to *Bt* broccoli much more slowly in the presence of lady beetles.

The possibilities to increase the durability of crop resistance to pests by applying inherent resistance-enhancing measures in combination with biological control are intriguing, but have received far too little attention by IPM researchers. Both evolutionary modeling and manipulative experiments are needed to increase our understanding of the interactions involved, and the circumstances needed to prolong resistance via biological control.

Concluding Remarks and Future Perspectives

Holistic IPM involving all action levels is probably unattainable, and we are currently not anywhere near obtaining complete and optimal programs for research or applications. However, great progress can be made if the seven research areas outlined above are prioritized.

Most previous ecology-based IPM research has focused on integrating botanical diversity with biological control, while measures intended to enhance plant resistance, vaccination, and pheromone-based manipulations have been mainly treated (if considered at all) as nonintegrated supplements. While integrating diversity/biocontrol is very important, most of the seven classes of IPM interactions clearly involve effects of, or on, plant resistance. Thus, there are many unexplored opportunities to improve IPM through breeding, but also numerous challenges. IPM researchers have paid relatively little attention to the roles of plant genetics as yet, but this must change if IPM is to reach its full potential. Plant breeders, in turn, should be encouraged to participate in future IPM programs to a greater degree. The optimal solution may not always be to maximize plant resistance, but to optimize it from a holistic IPM perspective. Breeders should benefit from the IPM framework, because (for example) efficient biological control can help to enhance the durability of plant resistance by weakening natural selection for counter-resistance in pests [89,90]. Furthermore, due to the dependence of effects of actions at other levels on plant breeding programs, breeders inevitably bear high responsibility for the outcome of IPM programs, and must consider the suitability of their cultivars within prevailing IPM frameworks. As plant resistance affects phenomena associated with most other IPM elements, in many cases mathematical modeling will be required to identify the optimal level of resistance. Recent modeling to elucidate the optimal resistance for biological control in a system consisting of a host plant, a specialist herbivore, and an omnivorous predator has demonstrated the utility of the approach for managing the complexity of IPM [58].

A burning issue is whether or not to accept transformed plants in IPM programs. Previous studies often dismissed the use of genetically modified (GM) crops [91], while a more recent paper clearly states a perceived need to apply modern breeding techniques [92]. Breeding to realize complex IPM solutions, often involving combinations of several plant resistance traits, will be almost impossible using only classical breeding techniques. Thus, parts of the IPM community may need to adjust their ideology to achieve functional and sustainable holistic solutions.

Another conclusion that can be drawn from the IPM pyramid is that biological control is the most sensitive element to actions at other levels. Whatever is done to combat pests will almost certainly also affect any biological control agents. This offers abundant potentially valuable opportunities for novel synergistic measures as the effects of modulating plant resistance, vaccination, and pheromone treatments on biological control have received particularly little attention. In these contexts, mathematical modeling will also likely play important roles in elucidating optimal solutions as it will be frequently too difficult, or expensive, to construct full-factorial experiments covering all relevant IPM elements.

As many national and intergovernmental bodies have already formulated regulations prescribing IPM [1], the research community has a major responsibility to address the complex scientific problems that must be resolved to realize its full potential. Integration of actions at all of the

Outstanding Questions

Intrinsic heritable plant resistance

(i) Integration with 'plant vaccination'

Which plant genes, traits, and mechanisms enable some plant genotypes to respond strongly to priming/induction stimuli, while others respond weakly?

(ii) Integration with 'biorational synthetic volatiles'

Which plant semiochemical mixtures and single compounds interfere with herbivore pheromone signals? Can plants be transformed to release optimal blends of herbivore pheromones and semiochemicals?

(iii) Integration with 'biological control'

Which direct and indirect plant resistance traits affect the performance and efficiency of biological control agents? Do predators, parasitoids, and microbes respond differently to focal plant traits?

Plant vaccination

(iv) Integration with 'biological control'

Does plant vaccination affect the performance and efficiency of biological control agents? To what extent can biological control agents be used to vaccinate plants?

Inter- and intra-specific botanical diversity

(v) Integration with 'biological control'

What are the optimal temporal and spatial scales to manipulate botanical diversity to favor biological control? Which plant traits mediate functional diversity? What is the optimal level (trait, species, or cultivar) to manipulate botanical diversity to favor biological control?

Biorational synthetic volatiles

(vi) Integration with 'biological control'

To what extent can biological control agents exploit different kinds of pest pheromones? Can the attraction of natural enemies from a distance using alarm pheromones be improved by adding plant semiochemicals to the volatile blend?

Biological control

(vii) Integration with 'intrinsic heritable plant resistance'

elements within the ecological domain will require intense assiduous basic research, but will probably provide numerous strong synergistic effects that will increase the sustainability of agriculture. Recent breakthroughs highlighting important effects of plant resistance traits on pheromone signaling [45] and biological control agents on plant vaccination responses [67,68] are just two examples showing that new scientific understanding is laying foundations for rapid advances in IPM. The new science of IPM has the intrinsic capacity to enable efficient and sustainable food production to feed the world's increasing population, and replace a large proportion of currently used toxic pesticides. The proposed conceptual framework is intended to assist efforts to realize this vision.

To what extent can biological control agents increase the durability of plant resistance by delaying the evolution of counter-resistance in pests? Which factors maximize this beneficial effect of biological control on pest evolution?

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Supplemental Information

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