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Breeding for inducible resistance against insects – applied plant breeding aspects

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Many of the pre-requisites necessary for breeding plants with inducible resistance to pests are no different from breeding for constitutive resistance. In both cases it is necessary to have resistance genes giving high enough yield gains from pest protection, efficient selection methods and means of introducing resistance genes into agronomically acceptable plant material. In addition, resistance traits need to be neutral or positive to non-target organisms. In inducible resistance, there is also the need for proper timing and specificity of induction. Tentatively the ideal inducible resistance is triggered by specific cues which rapidly induce specific resistance traits with long duration relative to the sensitive period of the crop and which give a systemic plant response. It takes knowledge to develop appropriate selection methods for resistance and in the case of inducible resistance we also need knowledge about how the inducing factors are operating. Inducing cues may come from insect activities on the plant (e.g. feeding, oviposition), from neighbouring plants or from manmade chemical formulations of elicitors. Plant selections can be based on plant damage levels, insect numbers, insect responses, plant resistance traits and/or molecular characteristics of the plant genome.

Breeding for insect-inducible resistance to insects has been applied in the form of rapidly induced highly specific resistance in insect - crop combinations where there are gene-for-gene relationships, such as with the Hessian fly and the Russian wheat aphid in wheat. To my knowledge there are no examples of traditional breeding where less specific types of resistance; induced by insects, by neighbouring plants or by chemical formulations; have been deliberately bred into commercial cultivars. It is likely that the accumulating knowledge about the mechanisms of induced resistance will find applications in cultivars produced by genetic engineering.

Key words: induced plant resistance, pests, herbivores, mechanisms, selection

Introduction

In nature, plants within a population generally vary in resistance levels in relation to a certain pathogen or pest. Without any deeper knowledge about the underlying mechanisms humans have exploited this, first during domestication of crops by selecting the healthy, high yielding plants as seed sources for the next generation, and since the beginning of the 2000th century by goal-oriented breeding of arable crops for resistance to pests and pathogens. Studies of mechanisms and regulation of plant resistance is now a large and still expanding field of biological research, the results of which can be applied in plant breeding. In the following sections I will highlight some of the central principles of breeding for resistance with special emphasis on breeding for induced resistance against a major pest group, insects.

Resistance mechanisms

Plant resistance to insects, i.e. inherited plant characteristics that reduce the effects of insect attack, can be explained by three principally different mechanisms (Fig. 1). Compared to a susceptible plant, the resistant plant is less used by the insects as an egg-laying and feeding site (**antixenosis**/non-preference), less suitable for the insects as a host (**antibiosis**) or less injured by the pest (**tolerance**). This plant-focussed classification of explanations for resistance was proposed by R. Painter (1941). Nowadays many ecologists (e.g. Karban & Baldwin 1997) define plant resistance from the herbivore's point of view and therefore exclude tolerance in the definition of resistance. However, the aim with breeding and deployment of resistant cultivars is to reduce damage to the crop be it mediated by any of antixenosis, antibiosis or tolerance. In a resistant plant all three mechanisms may be operating or just one or two of the three. From a sustainability point of view it is preferable to have all three mechanisms functional in a resistant cultivar. For an insect to overcome resistance based on both antixenosis and antibiosis it takes at least two kinds of adaptations for instance.

The host selection behaviour of insects has been studied in quite some detail and much is now known about which types of plant characters are important for host choice in herbivorous insects. Before as well as after coming in contact with a plant, insects respond behaviourally to its morphology (colour, shape, size, texture), and often most important of all, to its chemistry (Fig. 1). However, it is a great task to determine which of all plant chemicals may explain an antixenosis reaction.

Also in antibiosis, plant chemical compounds play a key role. Many of the so called secondary compounds are toxic to non-adapted insects. Besides, the water content or the composition of nutrients in the plant diet may be sub-optimal, thereby slowing down the growth of young insects. Another type of antibiosis is when mechanical plant barriers (e.g. sticky or ordinary hairs) interfere with insect activities and increase insect mortality rates.

Tolerance is not as well defined and understood as the other two resistance types. When tolerance is manifested as no or low yield penalty after insect attack, the explanation may be that plant resource allocation is directed to those plant parts that we harvest, e.g. seeds, at the expense of others, e.g. roots. Tolerance is considered durable as it does not put any pressure on the insect to adapt. The insect does as well on a tolerant host as it does on a susceptible host.

The characteristics of plants commonly change over time so that the plant is more acceptable and suitable as a host at certain developmental stages than at others. If phenology of the pest and phenology of the plant is always out of phase, such age-dependant **pseudo-resistance** may also efficiently protect the plant from damage.

Inducible resistance

Apart from developmentally related changes in plant characteristics, plant characters also change depending on the special environment of the plant. Inducing agents may be abiotic or biotic and the plant responses may affect a broad or narrow range of organisms associated with the plant. Plant responses causing resistance to an herbivore may be more or less rapidly induced, may last for hours, days, weeks and even years, and responses may be localized to the site of induction or expressed also in other plant parts. The same type of plant characteristics that function as constitutive resistance factors may also be inducible. Often the induction just causes an increase in an existing trait, such as increased hairiness in hairy plant surfaces (Baur et al. 1991, Dalin & Björkman 2003) or increased levels of glucosinolates (e.g. Agrawal et al. 2002) or proteinase inhibitors (e.g. Green & Ryan 1972) in a plant already containing such compounds. In other cases plants produce new compounds as a response to the induction, e.g. phytoalexins or pathogenesis related (PR) proteins (Kogan & Paxton 1983, van Loon & van Strien 1999).

Certain plant traits may also favour the natural enemies of an herbivore resulting in **indirect defense** of the plant. Those plant traits may be constitutive, but there are also examples of induced plant traits that are attracting natural enemies (Dicke & van Loon 2000).

Breeding for inducible resistance – pre-requisites

There are certain criteria that need to be fulfilled for a successful breeding programme aimed at improved induced resistance. Many of these considerations are no different from those when breeding for constitutive resistance.

Resistance genes

First of all, to be able to breed for a certain trait there must be genes giving variation for that trait. Genetic variation for induced resistance to herbivorous arthropods has been shown in various plant species such as grapes (English-Loeb et al. 1998), cucumber (Agrawal et al. 1999a), barley (Hays et al. 1999), soybean (Underwood et al. 2000), wild radish (Agrawal et al. 2002), wild mustard (Fabbro & Steinger 2004) and wheat (Weng et al. 2005).

At the functional level induction must result in definitely reduced damage to the crop compared to the normal situation. This means that the induced traits must be efficient as resistance factors to the target herbivore. In addition, the induced response must not increase plant susceptibility to other herbivores (cf. Agrawal & Sherriffs 2001), pathogens and abiotic conditions, nor negatively affect non-target herbivores or natural enemies of the herbivores. Neither can the mounting of induction be so costly to the plant so that its yield will be as low as if it was fully susceptible. However, one of the advantages often claimed for induced resistance compared to constitutive is that it saves plant resources, since it is raised when needed. To have maximum out of this temporal resistance then, it is essential that the induction is rapid because most of our important arable crops are annual or biennial and infestations by pests are commonly short but intense. Several of the examples of resistance bred into crops may actually be of that rapidly induced type and not a result of constitutively expressed plant characters. There are strong indications for that in studies of cecidomyids (Subramanyam et al. 2006) and homopterans (Boyko et al. in press). For the breeder, it is of less importance whether the resistance is induced or not in those cases. Nevertheless, knowledge about the mechanisms can help in developing efficient selection tools for the resistance.

Selection methods

Another type of pre-requisite for breeding inducible resistance into crops is that the induced response must be possible to select for, with high precision and at reasonable economical costs. Ideally, selection should be made in the field and be based on improved yield under influence of pests and pathogens, their natural enemies, normal abiotic conditions and field management procedures. However, for such evaluations it is necessary to have a large number of genetically uniform plants, for replicated trials, and for tests in several locations. Replicated trials are essential since insect responses to resistance traits are often quantitative rather than qualitative and especially since insects tend to have clumped distributions for other reasons than plant qualities (e.g. higher densities in field edges). Furthermore, herbivorous insects are often very sensitive to plant developmental stage, something which complicates comparisons of plants which differ in developmental rate.

Thus, in most cases it is most realistic to start selections in breeding materials segregating for resistance under controlled conditions in the greenhouse or in the laboratory. Designing appropriate tests where conditions are optimised for distinguishing resistant genotypes from more susceptible ones takes knowledge about the background of resistance. In both constitutively expressed and induced resistance, selections for resistance can be made in bioassays with insects on plants, comparing plant yield, insect numbers, plant symptoms, antixenosis, antibiosis or tolerance (cf Fig. 1). Determining effects specifically of induced resistance in such bioassays, demands genetically homogenous plant material to enable comparisons of the same genotype at induced and not induced status, and in replicated trials. However, it takes many plant generations to achieve such non-segregating test lines by traditional breeding. Doubled haploid technique, an alternative method of producing non-segregating lines, is very useful and now available for various crops (Maluszynski et al. 2003).

If the resistance is of the induced type, it is also necessary to make sure that the conditions for induction are fulfilled. When the resistance is induced by other factors than the insect itself one must make sure to include those in the test and to have the right timing for induction and testing. Probably there is always a background of induced plant responses outdoors since the plant in the field continuously interacts with microbes, herbivores and abiotic stressors (e.g. wind, UV-light, drought). Consequently, if selections for resistance are only made in a protected environment like the greenhouse or the laboratory, there is a risk that plants with a high potential to be induced by such agents are no more excelling than others. On the other hand, plant genotypes inducing resistance by non-specific inducers might invest as much energy in defense reactions as constitutively resistant ones.

If the induced resistance trait has been identified, resistance selection can be based on analyses for that. This makes the selection more precise compared to selection methods based on insect responses, where environmental effects on the target insect that are not related to the plant resistance may confuse. Furthermore it is not necessary to have the insect at hand (except in cases where it is necessary to induce the trait by insect attack), which reduces costs for keeping insect cultures and allows selections as soon as there are new plant materials ready for testing.

Non-relevant environmental effects on the plant resistance trait itself can also be a problem for precise selections. Selection by molecular markers is a further step closer to the genetic causes for resistance. This is an attractive method also for other reasons. Markers for various different traits can be screened simultaneously and tests can be made without having the pest insects at hand. Development of specific genetic markers for inducible resistance might actually be easier than development of markers for constitutive resistance. If the inducible genes are present on microarrays for c-DNA analysis, they may be identified as up- or down-regulated genes in the induced plant compared to the non-induced plant. Even so, many genes are expected to change in their expression levels due to induction and there is the challenge to sort out which are of importance for the resistance reaction and which are not.

Compatibility – gene transfer

Apart from genetic variation and efficient selection methods for induced resistance, practical breeding requires that the trait must be possible to introduce in agronomically acceptable plant material. Unfortunately it is difficult to find high levels of resistance to insects in cultivars currently used in agriculture and horticulture. Often one has to use more primitive sources such as wild relatives of our crops. Thus, it takes many back-crosses to regain all the necessary quality characters of a crop. If the resistance is depending on many genes it may be very resource demanding to keep all the genes in the breeding material. Furthermore, there may be hybridization problems, if the source is more distantly related. However, modern techniques can be used to overcome this problem, at least partly. By somatic hybridisation, genomes from two related but different species can be merged (Glimelius et al. 1991). More recent and more useful is the technique of transferring single genes from almost any organism by transformation. One advantage with this technique is that no unwanted genes are transferred. (In the case of somatic hybridisation between a crop and a non-crop species, many unwanted plant characters are introduced.) Another advantage is that the gene expression can be made very specific, by use of promoters that are only active in certain plant tissues or under certain conditions. Knowledge about genes and gene regulation in induced resistance may yield both new genes and new gene regulators to be introduced in crop plants by transformation. And since the transferred DNA is normally well characterised, plant selection in the breeding material can be based on DNA markers without the need of always having the insect present for bioassays.

Inducing agents and examples of induced resistance mechanisms

There are many physical and biological environmental factors that may influence levels of plant resistance to insects (Kogan & Paxton 1983). Here resistance-inducing factors of insect-, plant- and artificial origin are discussed.

Insect induced resistance

Breeding for resistance to the cecidomyid Hessian fly (*Mayetiola destructor*) in wheat began already in the early 1900s (Smith et al. 1999). In this case the resistance is of the gene-for-gene type with many biotypes of the herbivore differing with respect to with which resistance genes they are compatible and not. So far, thirty-two resistance genes have been identified by classical genetic studies (Sardesai et al. 2005). While these genes/alleles are involved in recognition of avirulent midge genotypes there are others subsequently induced which result in plant traits causing the death of the insect. A recently isolated lectin-coding gene, *Hfr*-1, is up-regulated more by the presence of avirulent than virulent larvae in three wheat genotypes, each carrying a different resistance gene involved in recognition (Subramanyam et al. 2006). The same lectin gene was not up-regulated by mechanical damage, the bird cherry-oat aphid nor barley yellow dwarf virus. If the product of this gene is a major determinant of the mortality of Hessian fly larvae in wheat, this is an example of a rapidly and specifically induced resistance trait which already has been exploited in plant breeding. The fact that avirulent larvae of the Asian rice gall midge (*Orselia oryzae*) induce resistance to a virulent midge biotype (Bentur & Kalode 1996) suggests a similar induced mechanism in rice bred for resistance to *O. oryzae*. Certain aphid species provide more examples of this avirulence/resistance gene-for-gene relationship between insect and plant. Plant genes involved in recognition of putative avirulence proteins from the Russian wheat aphid (*Diuraphis noxia*) have been characterised in wheat along with many plant genes regulated upon aphid feeding attempts (Boyko et al. in press). Thus, this and the similar aphid – host relationship between the greenbug (*Schizaphis graminum*) and its small grain hosts (e.g. Hays et al. 1999) might be other examples of rapidly and specifically insect induced resistance that is already used in breeding for resistance.

Insect induced responses with action towards a broader spectrum of herbivores are perhaps more widely recognised as "induced resistance". Wound induced systemic increase of a proteinase inhibitor (PI) in solanaceous plants is a classical example of this phenomenon (Green & Ryan 1972). Knowledge about this and other PIs has been applied in genetic engineering of plants for improved insect resistance. For example, a gene for a potato proteinase inhibitor, driven by its wound-inducible promoter, has been introduced in rice where it has been shown to increase resistance to a stem borer (Duan et al. 1996). There are also many other examples of PI genes from various sources that have been combined with constitutive promoters and transformed to crop plants like tobacco (Hilder et al. 1987, De Leo et al. 2001), oilseed rape (De Leo et al. 2001) and strawberry (Graham et al. 1997). In the future, we may well see new applications where inducible resistance is turned into constitutive by combinations of natively inducible genes with constitutive promoters.

Plant induced resistance

Plant damage may not only result in induced responses in the damaged plant itself but also in responses by neighbouring plants (Rhoades 1983, Baldwin & Schultz 1983, Bruin & Dicke 2001). In addition, also undamaged plants may, via volatile elicitors, influence neighbouring plants so that these become more resistant to herbivores (Ninkovic et al. 2006). Such effects have been found in both inter- and intra-specific plant communications and is part of the phenomenon called **allelobiosis**. A recently launched project (see www.plantcommistra.com) aims at thorough characterisation of allelobiosis in barley. The volatile cues behind allelobiotic effects are being identified and the responding plants are investigated for plant induced responses in terms of gene activities and metabolic end products, as well as effects on aphids and their natural enemies. Many breeding lines, modern barley cultivars and wild barleys are currently being screened for allelobiotic effects, because the capacity to induce and respond is known to be highly genotype-specific. Moreover, it is known that only certain combinations of inducer and responder give rise to allelobiosis and there are also indications of that allelobiosis is more pronounced in ancient material. If, however, yield effects of allelobiosis prove to be significant in existing modern cultivars, the results are directly applicable as cultivar mixtures. In parallel, continued breeding efforts will still be needed since yield levels are continuously raised as new cultivars are released on the market. The breeding goal is therefore to improve both inducing and responding capacities in modern barley germplasm, probably using molecular and/or biochemical markers as tools for plant selections.

Artificially induced resistance

Artificial induction of plant defence by elicitor applications has been tried in many crops to control many different pathogens (Vallad & Goodman 2004). Signal compounds were functional analogues of salicylic acid. The results are somewhat disappointing since although there has often been a considerable reduction in disease rates after elicitor applications, a proportionally raised yield compared to yield of untreated controls has not been realised. Generally there has been greater yield increases as a result of conventional pesticide treatments (Vallad & Goodman 2004). Similarly, after chemical induction with jasmonic acid aimed at improved resistance to insects there has been an herbivore-reducing effect of induction without any realised yield increase (Agrawal et al. 1999b, Thaler 1999). Partly these results might be explained by plant allocation of resources to induced plant defense reactions at the sacrifice of yield. However, Vallad & Goodman (2004) believe that it is possible to minimize negative induction effects on agronomic traits by breeding, since genetic variability for costs of induced responses has been found (Agrawal et al. 2002). Experimental application of elicitors is a fairly simple technique and it would certainly be worth trying to make selections in breeding materials grown under the influence of plant defence elicitors, aiming at new varieties optimised for less costly but efficient artificially inducible resistance traits. This kind of resistance might best be employed for crops where the key pest has periodical and predictable outbreaks. An example is the bird cherry-oat aphid (*Rhopalosiphum padi*) in Scandinavia where plant resistance is not needed every year and where egg frequencies on the winter host can be used as a general predictor of the coming attack rates in cereals.

Breeding for improved inducible resistance by chemical elicitors can be made by traditional methods but genetic engineering can substantially increase the efficiency of the breeding process. Transgenic resistance provides the possibility to combine inducible promoters with resistance genes that are regulated differently in the native organism. Transgenic broccoli in which an inducible promoter from tobacco promotes expression of *Bacillus thuringiensis* (Bt) toxin after induction with a salicylic acid analogue has been evaluated with regards to resistance against *Plutella xylostella* (Bates et al. 2005). In this case, however, timing of induction was critical because it took 2-3 days to reach maximum Bt concentration. Furthermore, leaves produced after the induction became successively less toxic indicating that repeated applications with inducer might be necessary. A third complication was that there seemed to be endogenous control of the promoter by compounds in the broccoli plants, something which might be avoided using a promoter which is not of plant origin.

In some cases mechanical damage by feeding insects has been shown to increase resistance against further insect damage, but it is probably not worthwhile mimicking this by making artificial damage in order to induce resistance in crops. The conclusion is reached partly because the damage may in itself reduce yield and partly because some mechanical damage is present anyway, in the form of wind damage, insect damage etc. In addition it has been shown that for induction of strong, specific resistance effects, larval regurgitants can be more effective than mechanical damage alone (Felton & Eichenseer 1999). Some of the compounds in insect saliva that are responsible for such induction are known. If those compounds could be produced cheaply in large amounts and applied to fields in a simple way, this might be another application worth trying and subsequently improve by breeding for optimum efficiency.

Conclusions

Tentatively the ideal inducible resistance requires specific cues for induction which rapidly induce specific and efficient resistance traits with long duration relative to the sensitive period of the crop and which give a systemic plant response. Breeding for some of those resistance characteristics has taken place in the form of rapidly induced highly specific resistance in insect - crop combinations where there are gene-for-gene relationships, such as with the Hessian fly and the Russian wheat aphid in wheat. To my knowledge there are no examples of traditional breeding where less specific types of resistance; induced by insects, by neighbouring plants or by chemical formulations; have been deliberately bred into commercial varieties. One of the proposed advantages with induced resistance compared to constitutive is the reduced costs to the plant, thus adding to the yield gain from resistance. However, there is no conclusive evidence for this, so far. It is likely that the accumulating knowledge about the mechanisms of induced resistance will find applications in cultivars produced by genetic engineering.

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Figure 1. Schematic view of the causes for plant resistance to pests. The steps in the ladder represent different levels of understanding. Plant traits causing resistance may be constitutive or induced.

Yield

Amount of pest or symptom

Insect behaviour – “antixenosis”
Insect performance – “antibiosis”
Plant tolerance

Plant morphology, anatomy, chemistry
Plant allocation of resources

Plant genetic constitution