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USING GREEN *VACCINATION* TO BRIGHTEN THE AGRONOMIC FUTURE

Estrella Luna, P3 Institute for Translational Plant and Soil Biology, Animal and Plant Sciences Department,
The University of Sheffield, Wester Bank S10 2TN, Sheffield, UK

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Estrella Luna

Abstract

Crop plants host a variety of pests and diseases that can ultimately reduce agricultural productivity. Current methods of pest and disease control depend largely on pesticides. However, the use of chemicals alone is increasingly regarded as unsustainable due to the development of resistance and the introduction of stricter European regulation. There is a need, therefore, to reduce their use and to pursue the development of new Integrated Pest (and disease) Management (IPM) strategies. Research that focuses on the role that the plant's immune system can play against these biological threats provides another potential source for future IPM strategies. Plants have sophisticated ways to defend themselves effectively and some stimuli can augment their innate immune capacity to resist future diseases. This phenomenon is known as priming of defence. Studies, mainly in the model plant *Arabidopsis thaliana*, have unravelled the molecular and physiological mechanisms of this apparent plant '*vaccination*'. This article describes recent findings and provides the ingredients for the "right formulation" in order to integrate green *vaccination* as a tool for the second green revolution.

Introduction

The world population is growing and meeting food demands will require an increase in agricultural productivity estimated at around 70% (Godfray *et al.*, 2010). During the 1950s and 60s, there was a similar requirement to increase agricultural productivity, a need that was addressed by the "green revolution". This change in crop production methods led to increased food production, which was supported by the introduction of new crop varieties, infrastructure, agricultural policies and synthetic fertilizers and pesticides (Royal-Society, 2009). Although the main goals of the green revolution were achieved, it also brought unexpected consequences, such as dramatically increasing the use of non-renewable energy sources and chemical fertilizers and pesticides that can have a negative impact on the environment. Decades after the green revolution, there is still an ever increasing need to intensify agricultural production. However, this second green revolution needs to rely on a challenging sustainable intensification of agriculture.

Despite current control measures, weeds, pests and pathogens claim up to 40% of our major crop yields. Without control measures, crop losses could amount to as much as 80% (Oerke&Dehne, 2004). Importantly, climate change is expected to have a profound impact on global agriculture in the next decades. Apart from changes in water availability, temperature, and soil degradation, it is expected that climate change will also have indirect consequences such as more frequent outbreaks of some plant diseases and/or pests (Evans *et al.*, 2008), partially due to changes in the plant's defensive capacity (Wang *et al.*, 2009). In addition to the selection of resistant crop varieties and crop rotation, the use of pesticides represents an effective strategy against these threats. However, pesticide use is increasingly regarded as problematical for two key reasons: the potential impacts of pesticide application on health (Bassil *et al.*, 2007) and the environment (Stanley *et al.*, 2015), and the ongoing evolution of pesticide resistance. Furthermore, strict European regulation is leading to a reduction in the number and diversity of pesticides available to farmers (Hillocks, 2012). Thus, the situation arises where production must increase without relying heavily on the use of pesticides. Therefore, the sustainable maintenance of agricultural productivity requires new strategies for crop protection.

Priming of defence: a potential IPM strategy

Plants, unlike animals, do not have specialised mobile immune cells. However, the plant's innate immune system is well equipped to fight forcefully against the majority of harmful microbes and insects by producing defensive compounds that are toxic to the attacker. To make their immune system even more fascinating, plants have evolved the ability to adapt to hostile conditions by sensitizing their immune system in response to stress signals. This is known as priming, a phenomenon that is defined by psychologists as the implicit memory effect in which exposure to a stimulus influences the response to a subsequent stimulus (Gulan&Valerjev, 2010). In compar-

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ison with the animal immune system, priming of defence is often described as plant vaccination. Priming provides an effective enhanced basal resistance, which is controlled by a multitude of genes; therefore, priming of basal resistance is effective against a broad range of biological threats (Ahmad *et al*., 2010;Conrath *et al*., 2015). Furthermore, many groups have studied the durability of priming and concluded that it can be maintained long after the initial stimulus (Pastor *et al*., 2013;Luna *et al*., 2014a) and can also be transmitted to following generations (Luna *et al*., 2012;Rasmann *et al*., 2012;Slaughter *et al*., 2012). This long-lasting maintenance of the primed state demonstrates a form of plant immunological memory that could provide a potential source for future IPM strategies.

Biological and chemical priming stimuli

Defence priming is triggered by stimuli that precede a subsequent attack by pests or pathogens. For example, volatile organic compounds (VOCs) are produced by plants upon herbivore infestation and systemically prime the hormone jasmonic acid (JA)-dependent defences in the plant and neighbouring plants (Heil&Ton, 2008). Also, systemic acquired resistance (SAR) is triggered by localized pathogen attack and is marked by priming of salicylic acid (SA)-dependent defence mechanisms (Kohler *et al*., 2002)2002, which result in an enhanced resistance to biotrophic pathogens. Furthermore, plants can establish symbiotic relationships with other organisms. Some non-pathogenic beneficial micro-organisms, such as rhizobacteria and mycorrhizal fungi, have also been shown to trigger priming of defence in a response known as induced systemic resistance (ISR; Van Wees *et al*., 2008). In addition to biological stimuli, some chemicals can induce a similar priming response. These chemicals commonly deliver a robust response (Figure 1), and for this reason they are commonly used for molecular and genetic studies. For example, endogenous SA (Kauss&Jeblick, 1995), JA (Frost *et al*., 2008), pipecolic acid (Návarová *et al*., 2012), and azelaic acid (Jung *et al*., 2009) are synthesised in response to biotic stress signals, and therefore, treatments with these chemicals prime plants to respond faster and more strongly to a subsequent attack. Moreover, chemical-induced priming has been shown to be possible after treatments with plant xenobiotic compounds such as β-aminobutyric acid (BABA) (Figure 1). This is probably one of the best characterised priming chemicals because treatments result in an impressively broad spectrum resistance (Jakab *et al*., 2001). In recent decades, major advances have been made to understand how this chemical provides robust enhanced defence in a wide range of plant species. Studies in *Arabidopsis* unravelled that BABA primes multiple defence pathways that ultimately confer resistance to many biological threats (Zimmerli *et al*., 2000;Ton *et al*., 2005). Importantly, it was demonstrated that in *Arabidopsis*, BABA is perceived by an aspartyl-tRNA synthetase (Asp-RS – Luna *et al*., 2014b), an enzyme involved in the first stages of protein synthesis, but the molecular mechanisms behind priming by this enzyme still remain to be elucidated (Schwarzenbacher *et al*., 2014).

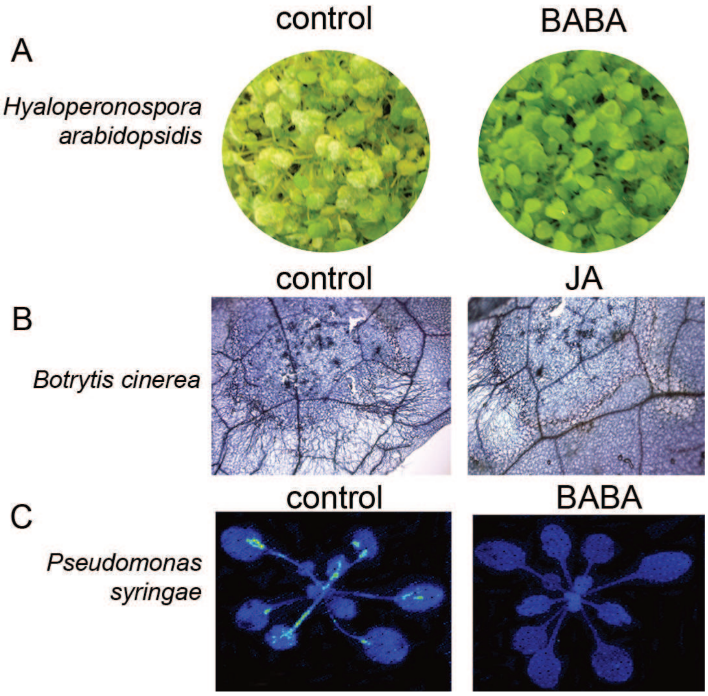

Figure 1. Chemically-induced resistance (IR) in *Arabidopsis*. A) β-amino butyric acid (BABA)-IR against *H. arabidopsidis*. B) *JA-IR against B. cinerea.* Pictures represent trypan blue-stained leaves infected with *B. cinerea* by drop inoculation. C) BABA-IR against *P. syringae*. Green spots illustrate the presence of a bioluminescent strain of *P. syringae*.

The costs of plant *vaccination*

The plant's energy resources are shared between two key processes: development and protection against threats. The activation of resistance triggers a rapid energy re-allocation from development to defence. Therefore, mounting a resistance response is costly and potentially impacts plant fitness. Priming is a relatively non-costly defence mechanism in terms of such trade-offs due to the fact that primed plants do not mount a full immune response until needed. However, there are scenarios where priming has been shown to incur costs for the plants. For example, the initial stimuli used to prime plants can trigger the direct activation of defence mechanisms. A very good example of this occurs after treatments with high concentrations of the SA analogue benzothiadiazole BTH (Azami-Sardooei *et al*., 2013). Similarly, treatments with a high concentration of BABA trigger the direct activation of defence mechanisms that mainly manifests as a reduction in growth (Figure 2). Interestingly, consistent with the issue of energy allocation, Van Hulten *et al*. (2006) reported that in environments with low disease pressure, priming results in a slight reduction in plant fitness (Van Hulten *et al*., 2006). Another aspect to take into consideration is the costs that can occur due to cross-talk between different hormone-dependent defence signalling pathways. For instance, using the best characterised hormonal cross-talk between SA and JA, plants that are primed to activate SA-dependent *Pathogenesis Related* (*PR*) genes (and therefore would be more resistant to biotrophic pathogens) would be compromised in their defence capacity against necrotrophic pathogens (Koornneef & Pieterse, 2008). Therefore, the costs associated with hormonal cross-talk could potentially result from the down

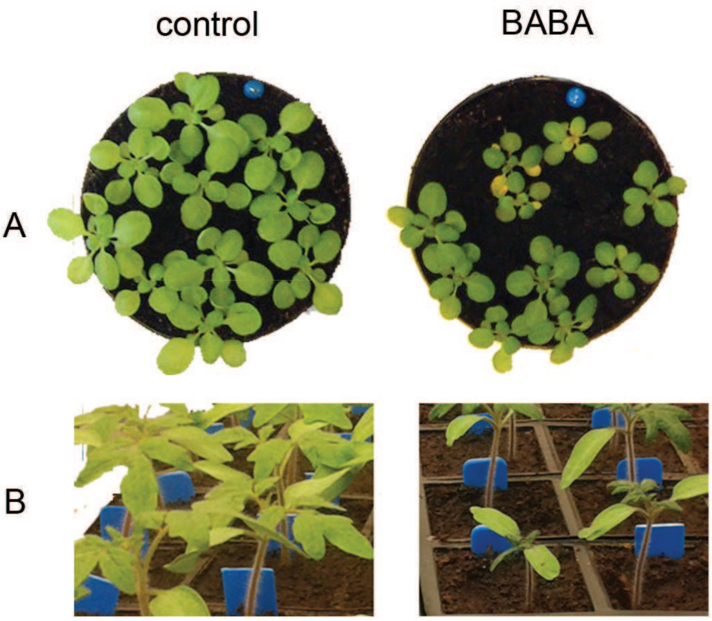

Figure 2. High concentrations of β-amino butyric acid (BABA) induce growth reduction in *Arabidopsis* (A) and tomato (B).

regulation of the defence response that would consequently leave the plant vulnerable to a specific threat. In addition, it is also possible that the plant's primed state interferes with the relationship between the plant and beneficial organisms. For example, it has been reported that priming the SA pathway compromises the interaction with mycorrhizal fungi (de Roman *et al.*, 2011) although this interaction was not affected after treatment with BABA at priming-inducing concentrations (Luna *et al.*, 2015). Finally, an inherent risk of this phenomenon is that, when priming is set, plants become more sensitive to mount a defence response and could activate this costly defence mechanism to false alarm signals that do not represent a serious threat. All in all, even if the costs associated with priming of defence are considerably lower than the ones triggered by the direct activation of resistance mechanisms, they still need to be taken into consideration when translating this research into the field.

Green *vaccination* in the field

Priming inducing stimuli have been reported to enhance the defence capacity of crops with mitigated fitness costs associated with them (Walters *et al.*, 2013). However, even if extensively underrepresented in comparison with agrochemicals, these stimuli have been reported to have effects in field experiments. For example, ISR-inducing microorganisms such as the bacterium *Pseudomonas fluorescens* has been shown to reduce *Fusarium* wilt disease (Leeman *et al.*, 1995). The agritech market has developed novel products using beneficial root-colonizing microorganisms, such as the bacterium *Bacillus subtilis* and the fungus *Trichoderma gamsii*. The use of these commercial products has been shown to enhance resistance to fungal and bacterial diseases in crops (Rana, 2013). Importantly, the development of new products has yielded agro chemicals that have been proven to enhance the defence capacity of crops in the field even when, on some occasions, the purpose of the product was to act only as a fungicide. For instance, isotianil-based fungicide products have been shown to reduce bacterial and fungal diseases by activation of SAR (Ogawa *et al.*, 2011). Also, tiadinil-based fungicide products have been shown to protect against diseases and pests by priming herbivore-induced volatiles that attract beneficial organisms in camelina fields (Maeda&Ishiwari, 2012). Extensive evidence has been gathered to show the role of VOC in priming neighbouring plants, however, this has yet to be proven under field conditions (Stenberg *et al.*, 2015). Nevertheless, a recent paper has described enhanced resistance in plants that have been exposed to other plants treated with the SA-analogue BTH. This exposure resulted in enhanced resistance to the anthracnose disease fungal pathogen by priming the expression of *PR* genes in beans (Quintana-Rodriguez *et al.*, 2015). Well characterised chemicals, such as BABA, have been demonstrated to enhance resistance by priming of defence mechanisms in the field and in some cases their action also provided a synergistic effect in combination with the use of pesticides (Cohen, 2002). Importantly, the folate precursor para-aminobenzoic acid (PABA) has been successful in inducing resistance against viruses and citrus canker disease caused by *Xanthomonas axonopodis*, and its use resulted in an increase in yield (Song *et al.*, 2013). Therefore, the scientific community is embracing the idea of investigating whether priming plants for defence could offer a new strategy for pest and disease control.

In search of the right formulation

Taking all of the above into consideration, in order to exploit the plant's immune system to provide IPM strategies, several obstacles need to be overcome. Firstly, one of the most important objectives is to make priming in crops more effective. Unlike resistant varieties or the use of chemical pesticides, priming hardly ever confers full protection on its own. On their own, priming stimuli could cause disappointment for farmers, normally used to the high efficacy of conventional pesticides. Secondly, the priming response needs to be made less variable. It is understood that the variability observed in field experiments might be due partly to plants being already primed by other stimuli in their growth environment. Thirdly, we need to overcome the hurdle that priming sometimes results in penalties in fitness or in interactions with other beneficial organisms. Fourthly, the application of the priming stimuli in commercial growth conditions can be difficult and non-economic. Therefore, in order to solve these potential obstacles, the right formulation requires the incorporation of a battery of measures to achieve an effective, less variable, non-detrimental and easy-to-apply priming response.

At this point, it is clear that there is an urgent need for targeted studies under commercial crop growth conditions. Several studies have endeavoured to provide IPM strategies that include priming of defence as one of the components and potentially overcome partially the obstacles listed above. For instance, it was shown that the combination of favourable genetic traits and fungicides results in a synergistic effect in the protection of *Arabidopsis* against *Hyaloperonospora arabidopsidis* (Friedrich *et al.*, 2001). More recently, in crops, a new product called TrichoPlusTM (BASF) has been developed using a *Trichoderma asperelloides* strain JM41R fertile

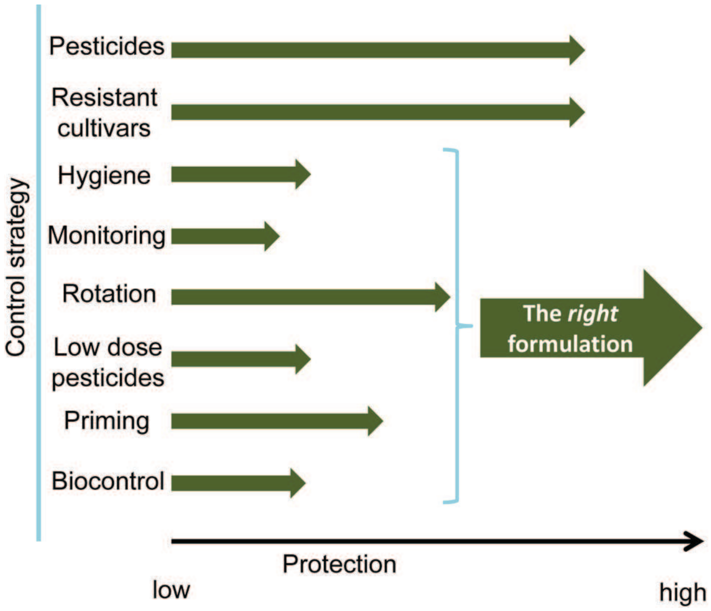

Figure 3. Schematic representation of the integration of priming into IPM strategies to obtain the right formulation for high protection.

substrate that enhances resistance to soil-borne pathogenic fungi and at the same time increases plant growth. The use of beneficial microorganisms, therefore, offers promising solutions as they enhance resistance, promote plant development (Ousley *et al.*, 1993) and can be easily applied in the field. Another study has optimised the BABA- and JA-induced resistance response in tomato against grey mould (Luna *et al.*, 2015). Here, it was shown that it is possible to incorporate treatments with priming-inducing chemicals into agronomic practice to provide easy means of application, for example, by optimising seed coats to release the chemicals into the system slowly while the seeds are germinating. Furthermore, Moya-Elizondo&Jacobsen (2016) have integrated further control measures and demonstrated in a dryland wheat field trial, a combination of fungicide, resistant varieties and the induction of SAR reduced *Fusarium* crown rot disease (caused by *Fusarium pseudograminearum*). These integrative studies show that the exploitation of the immune capacity of the plant to reduce disease represents a benefit, which greatly increases when combined with a battery of measures to deliver robust disease control (Figure 3). Therefore, green *vaccination* is a tool for the much needed second green revolution.

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Estrella Luna-Diez is a Research Fellow at the P3 Centre for translational Plant and Soil Biology at the University of Sheffield. Her research focusses on exploiting the immune capacity of economically-important crops to defend themselves against pests and diseases. During her PhD and post-doc, Estrella studied the fundamental basis of priming of defence, an evolutionary phenomenon by which plants sensitize their immune system to fight biological threats. Her current research aims to bridge the gap between fundamental knowledge and applied products, with the focus set on the tomato crop system.