

Managing the Colorado potato beetle; the need for resistance breeding

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Received: 2 April 2015 / Accepted: 9 May 2015 / Published online: 23 May 2015
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Abstract The Colorado potato beetle (CPB) is one of the pest insects that significantly can decrease the production of potato when no control measures are taken. The fast, flexible and diverse life cycle of the CPB, its highly destructive feeding habits, and high adaptability to a variety of environment stresses, have made the control of CPB a difficult task. This paper briefly reviews the information on all aspects of CPB management to come to an integrated pest management approach: the biology of the CPB, management practices including their limitations and drawbacks, as well as the need to incorporate host plant resistance into potato varieties. Several aspects of potato breeding for resistance to CPB are discussed. We evaluate the availability of natural variation present in potato wild relatives, the considerations in choosing a specific wild relative, and constraints in using them from biological, environmental and genetic point of

view, in which newly developed technologies play an important role. We also consider recently developed GM approaches. We conclude that varieties resistant to CPB are desperately needed by farmers and demanded by society, and that the means to develop them are available.

Keywords Insect-resistance · Glandular trichomes · Glycoalkaloids · Natural variation · Pest management · Potato wild relatives

The Colorado potato beetle problem

Already for a long time, the Colorado potato beetle (CPB) [*Leptinotarsa decemlineata* (Say)](Coleoptera, Chrysomelidae) threatens potato cultivation. The origin and history of the spread of CPB has been well documented by Alyokhin et al. (2013). It was first reported as a pest on potato in Nebraska in 1859 (Kennedy 2009). Later, it became the main insect pest of potato plants in the central and north-eastern United States (Radcliffe et al. 1993) and Canada (Boiteau and Le Blanc 1992), as well as in many European and some Asian Countries (Cassagrande 1990; Jolivet 1991; Liu et al. 2012). Currently, the CPB is considered as the most important insect defoliator of potatoes (Radcliffe and Lagnaoui 2007; Vreugdenhil et al. 2007). Both adult and larvae cause damage to the plant without discriminating among leaf tissue. Once the foliage is gone, beetles start to feed on stems and

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exposed tuber (Weber and Ferro 1993; Alyokhin 2009).

Defoliation of potato plants by the CPB can significantly decrease tuber production (Kennedy 2009; Alyokhin et al. 2013). Several important potato producing countries, such as Russia, Ukraine, Poland and others in Eastern Europe have reported high yield losses due to the CPB invasion (Radcliffe 1982; Heikkilä and Peltola 2004). Without the use of insecticides, CPB can cause 40–80 % yield losses in potato crops and it is estimated that the real annual losses caused by the CPB are 2–2.5 billion USD in Russia alone (Skryabin 2010). A loss of more than 75 % of the foliage can cause a total crop loss (Hare 1980; Shields and Wyman 1984).

Management practises

The fast, flexible and diverse life cycle of the CPB, its highly destructive feeding habits, and high adaptability to a variety of environment stresses, have made the control of CPB a difficult task. The CPB management and control practices include chemical treatment, biological control and cultural practices.

The main past and current control strategies of the CPB rely on the use of pesticides (Zabel et al. 2002; Grafius and Douches 2008). Despite the fact that the use of insecticides resulted in a drastic reduction of CPB populations, resistance development against the active substances has been observed. The CPB, through genetic adaptation, has been able to develop resistance to most of the registered insecticides (Grafius 1997; Stanković et al. 2004; Alyokhin et al. 2008; Sladan et al. 2012; Szendrei et al. 2012). Increasing the dosage provides only short-term relief, and greatly increases the rate of resistance development. It is expected that the CPB will develop resistance to all new insecticides deployed. Besides that, large scale application of chemical pesticides can lead to serious health and environmental problems (Wustman and Carnegie 2000; Alyokhin 2009). As a result, there is an increasing public demand for reduction of pesticide use and withdrawal of certain chemical compounds because of their harmful effects on growers, consumers, and the environment (Dik et al. 2000). Recent concern about the effect of chemical pesticides on the environment has encouraged

scientists to consider alternative, safer and more effective control agents (Alyokhin et al. 2015).

Biological control is often considered as the most environmentally friendly way to control CPB. Main factor in biological control is the use of natural enemies. The CPB has relatively few natural enemies, which potentially can be used in biological control programs against the CPB. Alvarez et al. (2013) reported the potential of the predatory ground beetle [*Pterostichus melanarius* (Carabidae)] in CPB management. Sablon et al. (2013) found that CPB immature stages can be controlled using the predator *Chrysoperla carnea*. Beside predatory insects, also some isolates of *Bacillus* species may be useful in CPB control as laboratory experiments showed insecticidal activity, including *B. pumilus*, *B. cereus* and *B. megaterium* (Ertürk et al. 2008). Strains of *Bacillus turingiensis* (*Bt*) have been used as foliar spray to combat CPB (Walker et al. 2003; Whalon and Wingerd 2003). Beside *Bt* sprays, also *Beauveria bassiana* sprays resulted in significant reduction of the CPB population in the field (Wraight and Ramos 2015). Despite all these promising observations, the use of such biological control agents to suppress the CPB in the field is still limited. In fact, farmers cannot rely on natural population of these agents in their potato fields, as the populations are generally very small. Mass release of biological control agents to manage peak populations has potential, although until now there are very few natural enemies that can be mass reared (Cloutier et al. 2002). In addition, population development of the natural enemy is often slower than that of the target insect, or they may require different conditions for optimal growth (Cloutier et al. 1995). The use of *Bt* sprays provides only limited protection as the toxins are photosensitive and degrade quickly compared to most other chemical insecticides (Whalon and Wingerd 2003). Also, the use of *Bt* sprays for pest control raises concerns about the potential for accelerated resistance development in the pest population to *Bt* (Sexson et al. 2005; Christou et al. 2006).

CPB populations can be reduced through the use of relatively common cultural practices, with crop rotation being the most effective and easily implemented one (Sexson et al. 2005; Alyokhin 2009). Overall yield and economic returns were significantly larger in rotated plots (Speese Iii and Sterrett 1998). However, the distance to previous potato fields could also

influence adult beetle infestation in the spring, and thus is an important factor in reducing colonization (Sexson and Wyman 2005; Huseth et al. 2012). Physical measures can be taken to control CPB population development, such as physical barriers [e.g. the use of plastic-lined trenches (Boiteau and Vernon 2001), straw mulch (Stoner et al. 1996; Stoner 1997), trap cropping (Hunt and Whitfield 1996; Hoy et al. 2000; Martel et al. 2005b)], thermal control (Laguë 1999; Rifai et al. 2004; Derafshi 2006), electromagnetic control (microwaves radiation) (Colpitts et al. 1992), pneumatic control (the use of moving air to eliminate the CPB from potato plants using machines (Rifai et al. 2004; Derafshi 2006) e.g. Beetle Eater[®], Bio-Collector[®], Bug-Buster[®]). However, the limitations and constraints in using of these tools are still high (Derafshi 2006); (Alyokhin 2009), pneumatic and thermal control techniques are non-selective, they kill beneficial insects as well (Vincent and Boiteau 2001).

The fact that the problem has not yet been solved in a satisfactory way indicates that the management of CPB is very difficult. Casagrande (1987) described the long history of the CPB control as ‘125 years of mismanagement’ and alternatives are urgently needed.

Biology of the Colorado potato beetle

The host range of the CPB is relatively narrow and largely confined to some 20 species within the *Solanaceae* family (Hsiao 1988; Kennedy 2009). Compared to eggplant, tomato or pepper, the cultivated potato is the more suitable host (Hitchner et al. 2008; Li et al. 2013).

The life cycle of the CPB consists of an egg stage, four larval stages, pupal stages, and an adult stage (Fig. 1). It starts with adult CPB overwintering in the soil for a period that can be as short as 30 days (Capinera 2001). After emerging in the spring adults disperse by walking and flying to their host (Boiteau et al. 2003). The CPB is a polygamous species, with both males and females performing multiple copulations with different partners (Alyokhin et al. 2013). After 5–10 days, females begin depositing masses of 20–60 eggs, yellow–orange in color, on the lower surfaces of host-plant foliage (Hare 1990). A mated female can lay up to 800 eggs in her lifetime and produce up to three generations per year depending on

the climatic conditions (Walgenbach and Wyman 1984; Ferro et al. 1985). Depending on the temperature, eggs will hatch 4–12 days after oviposition (Tauber et al. 1988). All eggs within a mass hatch simultaneously, and the larvae begin feeding immediately. Fully fed fourth-instar larvae stop feeding and pupate in the soil. Its life-cycle comprises a quiescent pre-pupal stage before pupation (Hare 1990). Adult emerge from pupation, after 5–7 days (Tauber et al. 1988; Boiteau and LeBlanc 1992). Depending on temperature, photoperiod, and host plant condition, adults may mate, migrate, cease feeding or enter diapause (Voss and Ferro 1990).

Important factors affecting host plant location by the CPB are vegetation diversity, plant size, plant visual and olfactory cues (Fernandez and Hilker 2007). Most reports focus on visual (e.g. colour (Szentesi et al. 2002; Döring and Skorupski 2007)) and olfactory (plant volatiles) cues. Host plant identification by the adult CPB is influenced by volatile chemical compounds produced by *Solanum* species. Several compounds, including *trans*-2-hexen-1-ol, 1-hexanol, *cis*-3-hexen-1-ol, *trans*-2-hexenal and linalool, methyl salicylate, and (*Z*)-3-hexenyl acetate have been suggested to play a role in this interaction (Visser et al. 1979; Dickens 2000; 2002; Martel et al. 2005a). Damaged leaves may increase the attraction of the host plant to CBP adults (Bolter et al. 1997; Schütz et al. 1997), as damage may trigger the release the volatile compound(s).

Feeding behaviour of the CPB is strongly affected by stimulants released by potato leaves. The sterol fraction (cholesterol, β -sitosterol and stigmasterol) acts as a stimulant to CBP larvae feeding (Szafranek et al. 2008). There are also compounds that act as feeding deterrents present in potato leaves. Extract of leaves of *S. berthaultii* that were rinsed with methylene chloride and acetone deterred CBP adults from feeding (Yencho et al. 1994). Extracts of *S. tarijense* leaves also have a deterrent effect on the CPB (Pelletier and Dutheil 2006). Morphological characters may also play a role in deterring CPB feeding. The CPB displays a unique behaviour when it comes into contact with *S. tarijense* leaves, which are abundantly populated by trichomes, as it abandons the plant by letting itself fall to the ground after a few minutes. However, feeding of CPB is also limited after trichome removal, suggesting that there are also other compounds in leaves or the leaf structure itself, apart from the glandular trichomes, that deter CPB feeding

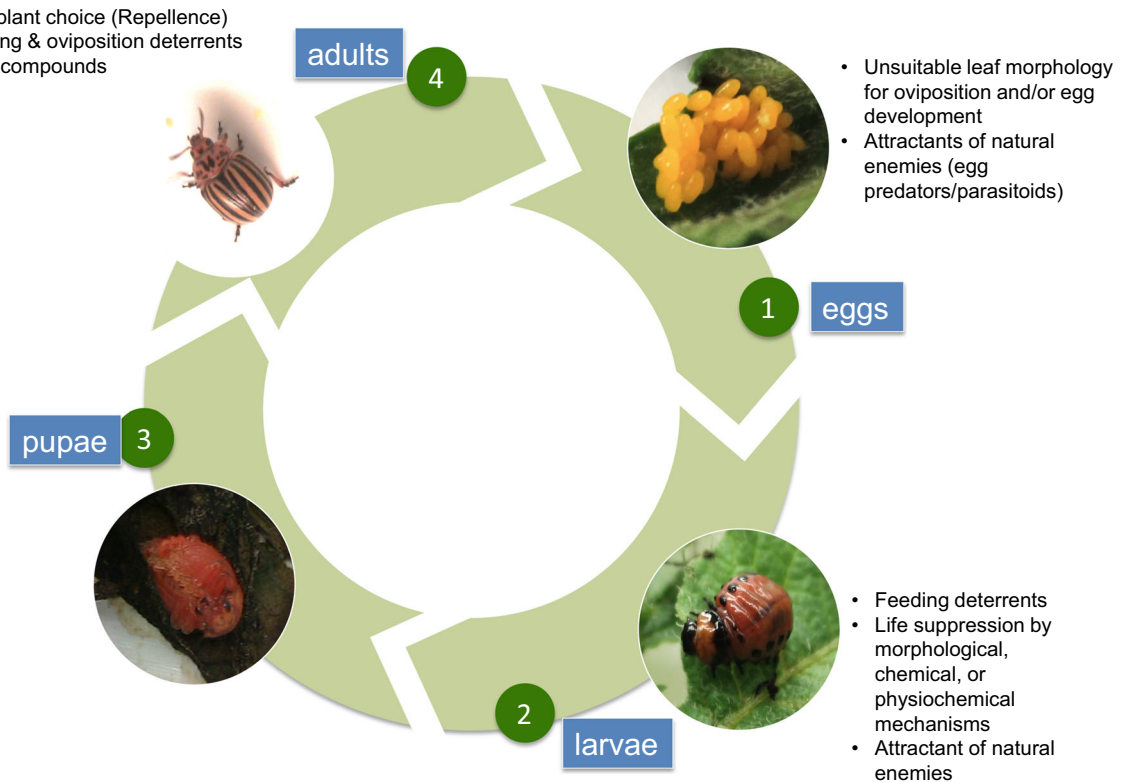


Fig. 1 Life-cycle of Colorado potato beetle (CPB) and resistance components that may affect these stages. The pupal stages is not likely to be affected by any plant resistance factor since pupation takes place in the soil. Feeding and oviposition behavior of the CPB is strongly affected by stimulants or deterrents released by potato leaves. The volatiles released by

the leaves will also strongly affect the host plant choice of the adult CPB. The presence of toxic compounds will strongly affect life history parameters (adult/larvae survival, number of eggs deposited, and development rate of adult/larvae) during the feeding stage

(Pelletier and Dutheil 2006). In *S. berthaultii* the presence of type A trichomes is a fundamental prerequisite for resistance to the CPB, while the presence of type B droplets containing sucrose esters increase the level of resistance in the presence of trichome type A (Neal et al. 1989). Trichomes of tomato also acts as feeding deterrent to CPB (Tian et al. 2012). As potato is one of the most important crops worldwide, many potato breeding programs have as an objective to develop potato cultivars that are resistant to insect pests.

Resistance breeding using natural variation

The limitations of biological control and culture practices explained above have led to a strong dependence of farmers on insecticides as the main

way of controlling CPB outbreaks. As an alternative, integrated pest management (IPM) approaches have been implemented in potato cultivation (VanderZaag 2010; Alyokhin et al. 2015). IPM includes the combination of biological control, crop management practices, and chemical control. However, despite much talk about its benefits, IPM is still far from being universally adopted by commercial potato growers (Alyokhin 2009). There are no commercial cultivars on the market that show a strong level of resistance towards the CPB, although some level of avoidance is seen on the cultivar Dakota Diamond (Thompson et al. 2008). It may be that also in other cultivars a low level of CPB resistance is present. However, it is likely that it remained unnoticed, as farmers will not tolerate the presence of any beetle in their potato field. Incorporation of host plant resistance into potato varieties may be an effective tool in the management of CPB. It is

likely to be a valuable addition to the IPM system (Fig. 2).

Wild relatives are already well known as good and reliable sources of resistance traits for plant genetic improvement in potato (Rudolf 1958) including resistance to insect pests (Hajjar and Hodgkin 2007; Broekgaarden et al. 2011; Pelletier et al. 2011). Specifically for the CPB, a number of resistance factors have been identified in wild relatives of potato which may be exploited in breeding programs (Table 1). Resistance may be based on antixenosis, e.g. affecting host plant choice, or antibiosis, e.g. affecting life history traits of the CPB, but these different mechanisms are not always easy to separate.

The glandular trichomes of *S. berthaultii*, *S. tarijense*, and *S. neocardenasii* have been linked to CPB resistance (Dimock et al. 1986; Neal et al. 1989; Yencho and Tingey 1994; Jansky et al. 1999; Pelletier et al. 1999; Pelletier and Dutheil 2006). Next to potato, glandular trichome based CPB resistance has also been found in tomato (Kennedy and Sorenson 1985;

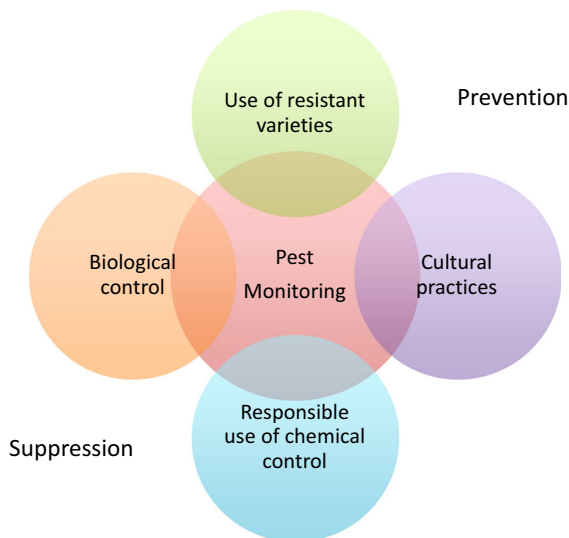


Fig. 2 The position of resistant varieties in an integrated pest management (IPM) program. In general IPM includes the combination of biological control, crop management practices, and (limited) chemical control. Incorporation of resistant varieties may be a valuable addition to the IPM system. Resistant varieties can be used together with cultural practices (e.g. field sanitary and crop-rotation measures) to prevent infestation. Resistant varieties may also increase the suppression of the pest development in combination with biological control. An effective pest monitoring is essential to minimize the use of chemical control

Carter et al. 1989). The glandular trichomes based resistance may be mediated by a physiochemical mechanism. When a beetle lands on a leaf and touches the type B trichomes (which are trichomes with an ovoid gland at its tip which continuously secretes a clear viscous exudate) the type B trichomes will coat the beetle with the sticky exudate and agitate the beetle. Next the beetle will disrupt the heads of the type A trichomes (which are short trichomes with a four-lobed membrane-bound gland at their apex), which will result in insect immobilisation, cessation of feeding and death (Gregory et al. 1986).

Another well-known resistance factor present in wild relatives of potato are the glycoalkaloids. Glycoalkaloids have also been reported in relation to insect pest resistance, including CPB (Wierenga and Hollingworth 1992; Sanford et al. 1996; Kowalski et al. 1999b; Rangarajan et al. 2000; Pariera Dinkins et al. 2008). *Solanum chacoense* produces an abundant level of steroidal glycoalkaloid compounds, leptines and leptinines (Mweetwa et al. 2012). Leptines and leptinines can inhibit the development of CPB (Kowalski et al. 1999a; Lorenzen et al. 2001) and significantly affect oviposition preference of adult beetles (Lyytinen et al. 2007). Tomatine and aglycone solanidine, two other glycoalkaloid, have also been reported for their role in resistance to CPB (Barbour and Kennedy 1991; Kowalski et al. 2000). Tomatine is present in many *Solanum* species (Gelder et al. 1988), including tuber-bearing wild relatives of potato such as *S. okadae* (Pelletier et al. 2001) and *S. neocardenasii* (Dimock et al. 1986).

Also other compounds present in wild relatives of potato have also been linked to CPB resistance, methylene chloride in *S. berthaultii* (Yencho et al. 1994), unknown volatiles compound of *S. tarijense* (Pelletier and Dutheil 2006), and unknown toxic compounds in *S. tridum* (Sikinyi et al. 1997).

Considerations in choosing specific wild relatives as donor of resistance

From the information presented above it can be concluded that wild relatives are a rich source for CPB resistance traits. However, there are still some important issues to consider before using (some of) the crop wild relatives in a breeding program aimed at obtaining CPB resistant potato varieties.

Table 1 Wild relative species of potato (*Solanum*) resistant to Colorado potato beetle

No	Species	Ploidy and (Endosperm balance number(EBN)) ^a	Mechanism of resistance to Colorado potato beetle	Resistance factor	References for resistance
1	<i>S. chacoense</i>	2X(2EBN)	Antibiosis	Leptines, lepitins, leptinine	(Sanford et al. 1996; Yenchó et al. 2000; Hutvágner et al. 2001; Sagredo et al. 2009; Mweetwa et al. 2012)
2	<i>S. berthaultii</i>	2X(2EBN)	Antixenosis/antibiosis	Glandular trichomes Methylene chloride	(Pelletier et al. 1999; 2001) (Yenchó et al. 1994)
3	<i>S. trifidum</i>	2X(1EBN)	Antibiosis/antixenosis	Toxic compounds	(Sikinyi et al. 1997; Pelletier et al. 1999; 2001)
4	<i>S. tarijense</i>	2X(2EBN)	Antibiosis/antixenosis	Trichomes, volatiles compounds on trichomes	(Pelletier et al. 1999; 2001; Pelletier and Dutheil 2006; Fréchet et al. 2010)
5	<i>S. pinnatisectum</i>	2X(2EBN)	Antixenosis		(Pelletier et al. 1999; 2001; Chen et al. 2003; Hai et al. 2006)
6	<i>S. okadae</i>	2X	Antibiosis	Tomatines	(Pelletier et al. 2001)
7	<i>S. acroglossum</i>	2X(2EBN)			(Pelletier et al. 2001; Pelletier 2007)
8	<i>S. chomatophilum</i>				(Pelletier et al. 2001; Pelletier 2007)
9	<i>S. paucisectum</i>	2X(2EBN)			(Pelletier et al., 2001; Pelletier 2007)
10	<i>S. piurae</i>	2X(2EBN)			(Pelletier et al., 2001; Pelletier 2007)
11	<i>S. tarnii</i>	2X			(Pelletier et al. 2001; Pelletier 2007)
12	<i>S. oplocense</i>	2X(2EBN), 4X(4EBN), 6X(4EBN)			(Pelletier et al. 2001)
13	<i>S. capsibaccatum</i>		Antixenosis		(Pelletier et al. 1999; 2001)
14	<i>S. jamesii</i>	2X(1EBN)	Antixenosis/antibiosis		(Pelletier et al. 1999; 2001)
15	<i>S. polyadenium</i>	2X	Antibiosis		(Pelletier et al. 1999; 2001; Fréchet et al. 2010)
16	<i>S. neocardenasii</i>	2X	Antibiosis	Tomatines, glandular trichomes	(Dimock et al. 1986)

^a According to Spooner and Hijmans (2001)

Relying on a high content of glycoalkaloids should be done with care as glycoalkaloids are hazardous to human health (Dinkins and Peterson 2008). In 1990 it was suggested that the maximum tolerable level of total glycoalkaloids per kg raw potato is 200 mg. However, because the safety margin is small efforts should be made to reduce the levels of glycoalkaloids in new potato varieties to no more than 100 mg total glycoalkaloids per kg potato (Andersson 1999). Therefore low levels of glycoalkaloids in the tubers

are a prerequisite. The expression of glycoalkaloids may differ between leaves and tuber of a potato plant, as was reported by Gelder et al. (1988) and Friedman (2006), which may open possibilities for breeding varieties with high levels of glycoalkaloids in the leaves and low levels in the tubers.

When breeding for resistance to insects it would be desirable when the resistance mechanism (or combination of mechanisms) is effective against other insects as well, as this may reduce insecticide use

even further. However, often there is only limited information on this. Tomatine has been reported in relation to leafhopper (*Empoasca fabae*) resistance in potato (Dahlman and Hibbs 1967). Some other glycoalkaloids were not associated with resistance to any insect pest of potato (Tingey and Sinden 1982; Flanders et al. 1992). The glandular trichomes have been linked to resistance against several important potato pests. They were associated with resistance to green peach aphid (*Myzus persicae*) (Avé et al. 1987; Flanders et al. 1992; Alvarez et al. 2006), potato flea beetle (*Epitrix cucumeris*), and *E. fabae* (Tingey and Sinden 1982; Flanders et al. 1992). They also negatively affect the oviposition, larval growth and establishment of *Phthorimaea operculella* in a potato crop (Malakar and Tingey 2000; Horgan et al. 2007). Therefore, in terms of the range of protection against insect pest, glandular trichomes may target most insect species. In tomato, this glandular trichome based resistance may not be liked by growers because of the stickiness of the foliage. For potato this looks less of a problem and glandular trichomes may be an effective way to control the CPB. However, the presence of glandular trichomes might also negatively affect the performance of the natural enemies as reported in *Datura wrightii* (Gassmann and Hare 2005) and *Medicago sativa* (Lovinger et al. 2000). Riddick and Simmons (2014) reviewed current knowledge on this issue and concluded that trichomes of tomato and potato can be harmful to economically important predators. They suggest further research on the effects of glandular trichomes on natural enemies and that strategies to ensure their survival are being developed. However, it may be that glandular trichomes, perhaps supplemented with glycoalkaloids, already provide full protection to the potato crop.

Constraints in using wild relatives for breeding

There are still some general constraints in the use of wild relatives for breeding i.e. biological constraints such as hybrid sterility and low cross-ability, retention of undesirable agronomic traits (Hajjar and Hodgkin 2007). Crossing difficulties may be one of the main reasons for the underutilization of wild relatives of potato in breeding. The fact that most cultivated potatoes are tetraploid, whereas most wild relatives are diploid makes it difficult to transfer desirable traits

from the wild to the cultivated (Chavez et al. 1988). Furthermore, interspecific hybridization is limited to species with the same endosperm balance number (EBN) (Johnston et al. 1980). Ploidy level and EBN number of wild *Solanum* species are provided by Spooner and Hijmans (2001). Another potentially biological constraint that breeders have to deal with is the lack of flowering and different photoperiodic reactions of wild relatives of potato (Rudorf 1958; Almekinders et al. 2009).

Introgression of genes from wild relatives into *S. tuberosum* often also results in the transfer of undesirable growth and tuber traits (linkage drag) typical for the wild species (Tingey and Yencho 1994; Grafius and Douches 2008). Wild relatives generally have poor agronomic performance, e.g. low productivity and crop quality. Efforts to reduce linkage drag in breeding with wild relatives through backcrossing are costly and time-consuming, and will no doubt effect the speed with which new cultivars are released (Hajjar and Hodgkin 2007). However, the use of molecular markers may reduce the problems and speed up breeding. In this regard it is also very helpful that the potato genome sequence is available now (Potato Genome Sequencing Consortium 2011). This sequence will greatly facilitate the development and selection of molecular markers to be used for introgression breeding.

Confirmation of the previously described resistances is essential as variation within accessions may exist and because the pest insect may adapt to the species. Some wild relatives previously reported for their resistance to CPB have lost their effectiveness. It has been reported that performance of the CPB on *S. berthaultii* is now comparable to that on the susceptible *S. tuberosum* (Alyokhin 2009). Using Quantitative Trait Loci (QTL) analysis, the lack of colocalization between the CPB resistance QTL and QTL for leptine, as well as the identification of highly resistant individuals that have very low leptine content (Sagredo et al. 2009) suggests that resistance to CPB from *S. chacoense* is qualitatively different from previous findings suggesting that leptines are highly correlated with resistance to CPB. A similar situation was found in *S. berthaultii*. Previously, QTL for glandular trichomes were detected on chromosome 1, 2, 4, 5 and 9 (Bonierbale et al. 1994). However, further analysis suggested that the trichomes may not account for all of the resistance against CPB since the major and consistent QTL for resistance that was

detected on chromosome 1 was not associated with any trichome QTL (Yencho et al. 1996). More resistance screenings using other wild relatives and more detailed QTL analysis should be conducted to enlarge the number of putative sources of resistance that can be used in breeding program. Resistances may have different levels of genetic complexity as was shown recently for whitefly resistance in tomato, by comparing the resistance originating from *S. pennellii* with the resistance from *S. galapagense* (Firdaus et al. 2013). Similar situations may exist in potato as well. Also it may be possible to identify similar resistance genes in species from which it is easier to introgress, as was shown in the case of late blight resistance (Wang et al. 2008).

Prospects of CPB resistance breeding

Breeding for insect resistance can be carried out at the diploid or tetraploid level. However, due to the yield gap most breeding is still at the tetraploid level, but efforts to set up diploid breeding programmes have recently intensified (Hutten et al. 1995; Lindhout et al. 2011). Breeding at the diploid level using self-compatible materials has specific advantages, a.o. it is more targeted and much faster than breeding at the tetraploid level (Lindhout et al. 2011).

Several newly developed technologies can be used to solve the constraints related to the introgression of resistance traits from wild relatives of potato into tetraploid cultivated potato (Jansky 2006; Jansky et al. 2013) (Fig. 3). With the use of embryo rescue and other techniques to overcome inter-specific crossing barriers it is possible to make hybrid combinations involving different species and to transfer many new traits (Hajjar and Hodgkin 2007). By manipulation of ploidy level, with due regard to EBN, virtually any potato species can be utilized for the introgression of desirable genes into *S. tuberosum* (Ortiz 2001). Using bridge crosses, auxin treatments, and mentor pollen, breeders should be able to introgress genes from wild relatives that previously were considered to be sexually incompatible with the cultivated potato (Jansky 2006). In addition, somatic fusions can also be used as alternative to sexual hybridizations (Pandey et al. 2010).

A QTL mapping approach has been used to identify the chromosomal region involved in CPB resistance in potato with resistance originating from *S. chacoense*

(Sagredo et al. 2009) and from *S. berthaultii* (Yencho et al. 1996). Marker assisted introgression also offers the possibility of faster progress than can be achieved by traditional back-crossing in potato breeding (Bradshaw et al. 2006). Molecular markers associated with leptinine production in *S. chacoense* may be used to this purpose (Ronning et al. 1999; Hutvágner et al. 2001).

Breeding potato for resistance against CPB will benefit from the availability of reliable and informative screening methods. Although field evaluations always will be the ultimate reference as in that case plants and pests grow in their natural environment, they are often difficult as they are less controlled. Factors like multiple infestations by insects, other pathogens or changing abiotic conditions may obscure the evaluations. Infesting CPB on the field may also contaminate other field experiments as well as other crops. There are some methods, which can be used to test the CPB more easily. Laboratory-based methods, such measuring leaf consumption by adult CPB in petri dishes (Nandy et al. 2008; Cooper et al. 2009), suppression of larval survival and inhibition of larval growth on detached leaves (Lorenzen et al. 2001; Cooper et al. 2009) can be good methods for evaluation of CPB resistance in potato as long as they reflect the resistance expressed in the field. Several rearing methods for CPB have been established to support the lab-based evaluation method (Gelman et al. 2001; Thorpe and Bennett 2003).

Resistance breeding using transgenic approaches

Potato breeding in general is difficult and time consuming as most cultivated potato varieties are tetraploid, making it difficult to transfer desirable traits between cultivars and have them expressed in progeny (Grafius and Douches 2008).

This had led to the development of transgenic potato plants (Fig. 3). Transgenic potatoes were among the first successfully produced transgenic crop plants (An et al. 1986). Genetic engineering of potato has focused on insect resistance, disease resistance, nutritional enhancement, stress tolerance and vaccine delivery. Regarding the development of resistance to CPB, genes employed were *Bt* and inhibitors of insect digestive enzymes. A significant inhibitory effect of proteinase inhibitor to the CPB was found (Michaud

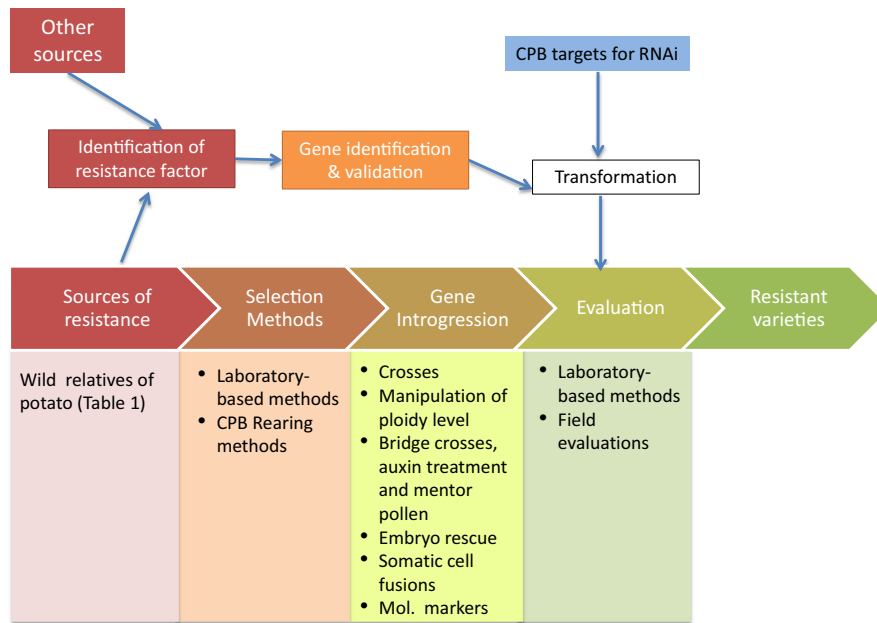


Fig. 3 Develop of Colorado potato beetle (CPB) resistant varieties. CPB-resistant potato varieties can be developed through classical breeding programs and genetic modification approaches. Wild relatives have been identified and characterized as sources of resistance to CPB in potato (Table 1). Tools and techniques to carry out the successive steps in the development of CPB resistant varieties are available (steps in wide arrows, tools in the boxes below the arrow). Several

technologies can be used to solve the constraints related to the introgression of the resistance traits into the cultivated potato, notably to solve crossing barriers and to facilitate backcrossing using markers. Apart from classical breeding techniques, resistant varieties may also be obtained through genetic modification (e.g. by using resistant genes from other sources or by RNAi approaches targeting essential genes of the CPB)

et al. 1993; Šmid et al. 2013). However, the practical application may not be so easy as it was shown that CPB easily adapted to the proteinase inhibitors (Zhu-Salzman and Zeng 2015). Genetically modified potato cultivars expressing the Cry3A toxin were first introduced in 1995 (Thomas et al. 1997). They provide a good control of the CPB and were commercially available in the USA from 1996–2000 (Grafius and Douches 2008). Also in the case of *Bt*-proteins the CPB develops resistance (Alyokhin et al. 2008). Recently, double-stranded RNA (dsRNA) targeted against the *ACT* gene was used to produce CPB resistant potato plants (Zhang et al. 2015). The *ACT* gene encodes the essential cytoskeletal protein β -actin. Using transgenic plants that produced the dsRNA in the chloroplast genome, Zhang et al. (2015) were able to show that resulting RNA interference (RNAi) caused a 100 % mortality of the CPB in 5 days. It is interesting to note that by expressing the dsRNA in the chloroplast the construct was below or near the detection level in the tuber, which may make

it more acceptable for the consumer (Zhang et al. 2015). An attractive feature of the RNAi approach is that it is highly insect species specific and that many potential target genes are available (Zhang et al. 2013), thus providing ample opportunity for fine tuning and implementing resistance management strategies. The availability of the *L. decemlineata* transcriptome (Kumar et al. 2014) will be very helpful in this respect.

Conclusion

It is clear that potato varieties resistant to the CPB are desperately needed by farmers and demanded by society. Natural variation of wild relatives of potato can be used as sources of resistance for the development of CPB-resistant potato varieties. It is desirable to combine different resistance mechanisms, preferably affecting different life stages of the insect, which will result in a more sustainable long term solution of

the insect problem in potato. From an environmental and management point of view it will be good to focus on broad working resistance mechanisms, e.g. mechanisms that affect other pest insects as well, in order to achieve the cutback in insecticide use. Several options for this seem to be present in the available wild relatives of potato. Although there are barriers to overcome, the newly developed technologies and approaches can be used to solve the problems associated with the introgression of the resistance from the wild relatives into the cultivated potato.

Apart from using resistance sources from wild relatives through classical breeding schemes, resistance may also be obtained through genetic modification. The recently developed RNAi approaches to combat pest insects, although still in their infancy, look very promising (Zhang et al. 2015). Several difficulties still need to be overcome before their full potential in insect pest control can be exploited (Burand and Hunter 2013; Katoch et al. 2013; Zhang et al. 2015). The biggest challenge being public acceptance. The use of natural variation avoids the complex public debate and regulatory issues with respect to GM crops which is present in many countries especially in Europe (Grafius and Douches 2008).

In conclusion, materials and tools to develop CPB-resistant (and more broadly insect resistant) potato varieties through classical breeding programs and GM approaches are available and should be used to make potato production more sustainable (Fig. 3).

Acknowledgments This work was financially supported by a Grant from the ministry of Economic affairs of the Netherlands (project nr. BO-26.02-003-009).

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