Potato Zebra Chip: An Overview of the Disease, Control Strategies, and Prospects

Victoria Mora1, Manikandan Ramasamy1, Mona B. Damaj1, Sonia Irigoyen1, Veronica Ancona2, Freddy Ibanez1,3, Carlos A. Avila1,4 and Kranthi K. Mandadi1,5*

1 Texas A&M AgriLife Research and Extension Center, Weslaco, TX, United States, 2 Department of Agriculture, Agribusiness, and Environmental Sciences, Citrus Center, Texas A&M University-Kingsville, Weslaco, TX, United States, 3 Department of Entomology, Minnie Bell Heep Center, Texas A&M University, College Station, TX, United States, 4 Department of Horticultural Sciences, Texas A&M University, College Station, TX, United States, 5 Department of Plant Pathology and Microbiology, Texas A&M University, College Station, TX, United States

*Correspondence:
Kranthi K. Mandadi
kkmandadi@tamu.edu

INTRODUCTION

Potatoes (Solanum tuberosum L.) constitute a centuries-old world dietary staple, with total world production estimated at 368.2 million tons in 2018 (Faostat, 2020). The United States is the fifth largest potato producer, after China, India, Russia, and Ukraine (Faostat, 2020), with an industry valued at $3.5 billion (USDA, 2019; Faostat, 2020). About one-third of United States grown potatoes are for processing, of which 63–83% are for frying, chipping and other packaged products, and the rest for fresh market, fodder, or used as seed (USDA, 2019). Potato domestication resulted in cultivars with reduced glycoalkaloid tuber content, making them more palatable and leading to increased tuber size and improved carbon fixation and transport (Spooner et al., 2014; Machida-Hirano, 2015). Few hardy wild potatoes were also crossed with their cultivated relatives to improve disease resistance, yield and quality for almost a century (Jansky et al., 2013). This yielded highly marketable improvements, like enhanced processing quality for chipping and frying, and resistance to some viruses and nematodes (Douches et al., 1996; Hirsch et al., 2013; Bethke et al., 2017). However, their low genetic diversity led to vulnerability to pests and diseases, and acute inbreeding depression.
EARLY REPORTS OF ZEBRA CHIP DISEASE

Zebra chip (ZC) disease was first reported in 1994 in Saltillo, Mexico, and later in South Texas, United States in 2000 (Munyaneza et al., 2007, 2009). The fastidious phloem-limited bacterium, Candidatus Liberibacter solanacearum (CLso), was identified as a putative causal agent. CLso is transmitted to plants by the potato-tomato psyllid Bactericera cockerellii Sulc (Munyaneza et al., 2007; Hansen et al., 2008; Liefting et al., 2009). Vegetative symptoms of ZC disease on plants include leaf chlorosis, discoloration, curling or upward rolling, aerial tubers, axillary bud proliferation, stunted growth, and eventually premature plant death (Figure 1). CLso-infected potato tubers are often deformed and of poor quality, exhibiting collapsed stolons, vascular ring browning and brown flecks. When fried for chips, the brown discoloration becomes darker, making chips bitter to taste, and unmarketable (Figure 1D).

CLso-infected potato tubers are often deformed and of poor quality, exhibiting collapsed stolons, vascular ring browning and brown flecks. When fried for chips, the brown discoloration becomes darker, making chips bitter to taste, and unmarketable (Figure 1D).

Despite the relatively recent origins of ZC, potato psyllid infestation was first documented in peppers in Colorado, United States and was described as a potential pest in 1909 by Sulc (1909). The detrimental effects of psyllids were not fully noticed until 1927, when vast outbreaks of what was then described as small citrus circulative phylloxerid (Richards and Blood, 1933; Carter, 1939; Arslan et al., 2013). Although initially PY was thought to be associated with toxins released by psyllid feeding, so far, no other pathogens or toxins have been associated with PY. Hence it led to a hypothesis that PY could be a mild case of ZC, wherein CLso was present at low, undetectable levels in the affected plants (Richards and Blood, 1933; Carter, 1939; Arslan et al., 1985; Munyaneza et al., 2011; Monger and Jeffries, 2018).

Nevertheless today, the potato psyllid is considered an A1 quarantine pest by the EPPO (European and Mediterranean Plant Protection Organization), and as a primary vector for CLso, together cause significant economic losses (PM, 2017).

CLso-HAPLOTYPES AND DIVERSITY

Twelve different CLso haplotypes have been reported so far [A, B, C, D, F, G, H (Con), U, Cras1 and Cras2] (Wen et al., 2009; Munyaneza et al., 2010; Nelson et al., 2011, 2013; Teresani et al., 2014; Haapalainen et al., 2018, 2020; Mauck et al., 2019; Contreras-Rendón et al., 2014; Haapalainen et al., 2018, 2020; Sumner-Kalkun et al., 2020). In addition to B. cockerelli, other relatives in the Triozidae family (Hemiptera) transmit certain CLso haplotypes. For example, haplotype F found in carrots is vectored by Triozia apicalis Förster (Munyaneza et al., 2010). Haplotypes D and E are transmitted by the carrot psyllid vector, Bactericera trigonica Hodkinson (Nelson et al., 2011; Swisher et al., 2014; Borges et al., 2017; Charkowski et al., 2020). While, CLso haplotype U identified in northern Europe, is associated to Triozia urticae psyllid (Haapalainen et al., 2018). In the Americas, ZC disease is primarily associated with the haplotypes A, B, and F. CLso A and B are transmitted by B. cockerelli, while the vector of haplotype F is still unknown.
Currently, a primary approach to manage ZC is by controlling the psyllid vector populations. Components of integrated pest management (IPM) such as chemical, cultural, and biocontrol strategies have been implemented worldwide (Vereijssen et al., 2018). Extensive monitoring and detection of psyllid population densities (Goolsby et al., 2007). While, other studies have found sticky traps to be useful for monitoring psyllid populations, even at low densities (Goolsby et al., 2007).

For psyllid control, pesticide use has been the main course of action in several regions. Typical pest management guidelines for potato psyllids include the application of neonicotinoids like imidacloprid and thiamethoxam at planting as a seed treatment, with a subsequent foliar application to control adults and nymphs (Prager et al., 2013; Vereijssen et al., 2015; Núñez et al., 2019). Unfortunately, excessive use of pesticides led to incidences of neonicotinoid resistance in Southwestern United States, South Texas, and Northern Mexico (Prager et al., 2013; Chávez et al., 2015; Szczepaniec et al., 2019). As such pesticide reliance is both economically and environmentally unsustainable.

Some cultural methods for the control of psyllids have also been tested. Such as by using certified clean seed, and planting non-host plants in crop rotations to maintain disease free planting areas (Vereijssen et al., 2018). In warmer climates such as in Southern United States, planting dates could be altered to delay exposure to potato psyllids (Guenthner et al., 2012). Few organic farmers have also found some success using physical barriers such as mesh covers to lower psyllid infestations (Merfield et al., 2015).

Lastly, biocontrol strategies have also been employed. Natural enemies of the psyllid, such as ectoparasitoids, coccinellids, and entomopathogenic fungi have shown promising effects against psyllids, by parasitizing them at multiple life stages, in greenhouse and laboratory studies (Al-Jabr, 1999; MacDonald et al., 2010; Lacey et al., 2011; Walker et al., 2011; Mauchline and Stannard, 2013; Rojas et al., 2015). Deployment of such natural enemies as biocontrol agents in greenhouse production systems (e.g., tomato) or in the field-scale (e.g., potato) could allow growing an earlier crop and reduce reliance on insecticides.

**HOST PLANT RESISTANCE AND BREEDING STRATEGIES FOR ZC RESISTANCE**

Efforts were made to study host plant resistance toward developing ZC resistant potato cultivars. Plants employ different mechanisms to protect themselves against pathogens and insects. Some host-plant resistance mechanisms are constitutive, such as physical or pre-formed structural barriers and release of chemicals that disrupt pathogen transmission, insect feeding, and oviposition. Other plant defenses, such as volatile compounds emission or upregulation of resistance genes can also be triggered.
in response to a pest or pathogen (Dicke and Van Poecke, 2002; War et al., 2012). The host resistance mechanisms to pests can also be categorized as antixenosis and antibiosis. Generally, antixenosis refers to a deterring effect that plants can have on insect behavior, where antibiosis affects their lifecycle and reproduction (Painter, 1951; Kogan and Ortman, 1978; Smith, 2005).

In the case of ZC, several varieties of potato and potato hybrids were identified to possess some degree of tolerance to ZC disease. In some varieties, tolerance was attributed to the antixenotic effects of glandular trichomes (Butler et al., 2011; Diaz-Montano et al., 2014; Rubio-Covarrubias et al., 2017). While few varieties appear to have a genetic basis for tolerance to CLs0 in addition to having effects on the psyllid behavior (Rashidi et al., 2017; Fife et al., 2020). Recently, few wild-relatives of tomato, S. pennelli, and S. corneliomulleri were identified to possess resistance to B. cockerelli (Avila et al., 2019), with several quantitative trait loci (QTL) associated with insect mortality and lower fecundity in S. habrochaites. Such QTL in wild species could be a valuable source for breeding resistance to cultivars, however, their complex inheritance, modes of action, and pathogen-vector-host interactions require further characterization.

**FUTURE PROSPECTS AND STRATEGIES FOR ZC RESISTANCE**

In the past, lack of advanced genomic tools, combined with the cost effectiveness of chemical control strategies led to heavy reliance on pesticides, rather than prioritizing the development of new resistance varieties to pests/pathogens (Rowe, 1992; Spooner and Bamberg, 1994). However, recent advances in genomics and genetics resources (Varshney et al., 2005; Broekgaarden et al., 2011) including those for potato1, should help in identifying desirable traits, alleles, and marker development to develop new ZC resistance cultivars. For instance, the availability of the potato reference genome sequence, the discovery of SNPs in elite North American potato germplasm and the development of the Infinium 8,303 potato array have helped in identification of genes linked to improved agronomic traits (Hamilton et al., 2011; Massa et al., 2011; Felcher et al., 2012). The resources also enabled marker-assisted selection (MAS), which helps identify markers tightly linked to a target locus, instead of relying on phenotypic selection alone in making selections for crosses. Thus, MAS can be used to accelerate introgression of desirable ZC tolerance traits from various potato breeding clones or wild species into cultivar development. Several studies showed the potential of improving potato traits by increasing heterozygosity and genetic diversity of parental clones (Mendoza and Haynes, 1974; Bradshaw and Ramsay, 2005; Janksy and Peloquin, 2006). Thus, more focus will need to be given for identification and introgression of alleles from a diverse pool of genetic resources, including wild species, landraces, and cultivated potatoes (Bethke et al., 2019).

Introgression of desirable traits from related or distant species to cultivated potatoes using genetic engineering (GE) can be a viable alternative to speed cultivar development and reduce introgression of undesirable genetic material or traits (Halterman et al., 2016). Few example, GE potatoes that received United States regulatory approval include the “NewLeaf” Bt potatoes for resistance against Colorado beetle (Leptinotarsa decemlineata), “InnateTM” potatoes with resistance to fungal disease (late blight) and acrylamide formation2 (Halterman et al., 2016). Despite the significant advantages of GE crops, the costs associated with R&D and regulatory approval is tremendous and necessitates private sector investments, or public-private partnership. Furthermore, the GE products face marketing hurdles due to public skepticism (Halterman et al., 2016).

Selected traits can also be modified/introduced by genome editing technologies such as TALEN or CRISPR-Cas9 without introducing new foreign DNA (Wolt et al., 2016; Hameed et al., 2018). Derived plant products potentially face less regulatory scrutiny and approval burden. For instance, the United States regulatory body (USDA APHIS) determined that several transgene-free, genome-edited potato plants with disease resistance and other superior agronomic traits, would not be considered regulated under 7 CFR part 340 (Wolt et al., 2016). Although this does not preclude regulation by other agencies world-wide, it is nevertheless a significant advantage when it comes to commercialization.

**CONCLUSION**

Since its first report in 1994, ZC disease is now established in several potato producing regions worldwide. The putative causal agent, CLs0, can also infect other economically significant Solanaceae crops, thus posing an even more threat to the agricultural industry. IPM strategies (chemical, cultural, and biological control) have been implemented to manage psyllid vector population and limit ZC disease. However, we still need long-term solutions. Recent developments in potato genetic resources and crop improvement technologies could be further leveraged for developing new potato cultivars with genetic resistance to the psyllid and/or CLs0. In combination with IPM practices, the ZC resistant or tolerant cultivars could be deployed in the future to effectively manage ZC disease.

**AUTHOR CONTRIBUTIONS**

KM supervised the study. All others contributed to the preparation and editing of the review.

**FUNDING**

This study was supported by funds from Texas A&M AgriLife Research Insect-Vectored Disease Seed Grant (124190-96210), USDA-NIFA-AFRI (2018-70016-28198; HATCH 1023984), and Foundation for Food and Agricultural Research New Innovator Award (534299) to KM.

---

1http://solcap.msu.edu/; https://www.polyploids.org/

2https://apnews.com/article/1d5c790ad18f4e825898c44ec047bf
Massa, A. N., Childs, K. L., Lin, H., Bryan, G. J., Giuliano, G., and Buell, C. R. (2015). Diversity of potato genetic resources. Bred. Sci. 100, 191ñ196. doi: 10.1093/bioclee/24.2.175

Henriquez, A., Kalischuk, M., Lynn, J., Meers, S., Johnson, D., and Kawchuk, H., Tamborindeguy, C., Scheuring, D. C., Herrera, A. M., Silva, A., Hernández-Deheza, M. G., Rojas-Martínez, R. I., Rivera-Peña, A., Zavaleta-Mejía, M. T., and Painter, R. H. (2015). Tuber transmission of ‘Candidatus Liberibacter solanacearum’ and its haplotypes in historical seed from collections of carrot and related Apiaceae species. Eur. J. Plant Pathol. 141, 213ñ225. doi: 10.1007/s10658-013-9986-7

Murphy, A. F., Rondon, S. I., and Jensen, A. S. (2013). First report of potato psyllids, Bactericera cockerelli (Hemiptera: Cicadellidae), infecting eggplant in the southwestern United States and Mexico. Plant Dis. 97, 1654ñ1654. doi: 10.1094/pdis-06-13-0641-pdn

Nelson, W. R., Sengoda, V. G., Alfaro-Fernandez, A. O., Font, M. I., Crosslin, J. M., and Munyaneza, J. E. (2013). A new haplotype of ‘Candidatus Liberibacter solanacearum’ identified in the Mediterranean region. Eur. J. Plant Pathol. 135, 633ñ639. doi: 10.1007/s10658-012-1021-3

Mauchline, N., and Stannard, K. (2013). Evaluation of selected entomopathogenic fungi and bioinsecticides against Bactericera cockerelli (Hemiptera). N. Z. Plant Prot. 66, 324ñ324. doi: 10.3843/npzp.2013.66.5707

Moura et al. Zebra Chip Disease of Potato

Mauck, K. E., Sun, P., Meduri, V. R., and Hansen, A. K. (2019). New Ca. Liberibacter psyllaurous haplotype resurrected from a 49-year-old specimen of ‘Solanum umbelliferum’: a native host of the psyllid vector. Sci. Rep. 9, 1ñ13.
Bactericera cockerelli

PM. (2017). 9/25 (1) Bactericera cockerelli and 'Candidatus Liberibacter solanacearum'. EPPO Bull. 47, 513–523. doi: 10.1111/epb.12442

Prager, S. M., Vindiola, B., Kund, G. S., Byrne, F. J., and Trumble, J. T. (2013). Considerations for the use of neonicotinoid pesticides in management of Bactericera cockerelli (Hemiptera: Triozidae). J. Crop Prot. 54, 84–91. doi: 10.1016/j.cropro.2013.08.001

Rashidi, M., Novy, R. G., Wallis, C. M., and Rashed, A. (2017). Characterization of host plant resistance to zebra chip disease from species-derived potato genotypes and the identification of new sources of zebra chip resistance. PLoS One 12:e0183283. doi: 10.1371/journal.pone.0183283

Richards, B. (1928). A new and destructive disease of the potato in Utah and its economic impacts. J. Agric. Res.

Richards, B., and Blood, H. (1933). Psyllid yellows of the potato. J. Agric. Res.

Rojas, P., Rodríguez-Leyva, E., Lomeli-Flores, J. R., and Liu, T.-X. (2015). Biology and life history of Tamarixia triozae, a parasitoid of the potato psyllid Bactericera cockerelli. Biol. Control 60, 27–35. doi: 10.1016/j.biocontrol.2014.06.014

Rosson, P., Niemeyer, M., Palma, M., and Ribera, L. (2006). Economic Impacts of Zebra Chips on the Texas Potato Industry center for North American Studies.

Swisher Grimm, K., and Garczynski, S. (2019). Identification of a new haplotype of 'Candidatus Liberibacter solanacearum' in Solanum tuberosum. Plant Dis. 103, 468–474.

Szczepaniec, A., Varela, K. A., Kiani, M., Paetzold, L., and Rush, C. M. (2019). Incidence of resistance to neonicotinoid insecticides in Bactericera cockerelli across Southwest U.S. J. Crop Prot. 116, 188–195. doi: 10.1016/j.cropro.2018.11.001

Teresani, G. R., Bertolini, E., Alfaro-Fernández, A., Martínez, C., Tanaka, F. A. O., Kitajima, E. W., et al. (2014). Association of 'Candidatus Liberibacter solanacearum' with a vegetative disorder of celery in Spain and development of a real-time PCR method for its detection. Phytopathology 104, 804–811. doi: 10.1094/phyto-07-13-0182-r

Teulon, D., Workman, P., Thomas, K., and Nielsen, M. (2009). Bactericera cockerelli incursion dispersal and current distribution on vegetable crops in New Zealand. N. Z. Plant Prot. 62, 136–144. doi: 10.30843/nzpp.2009.62.4783

Thomas, J., Geering, A., and Maynard, G. (2018). Detection of 'Candidatus Liberibacter solanacearum' in tomato on Norfolk Island. Australia. Australas. Plant Dis. Notes 13:7.

USDA. N. (2019). Potatoes 2018 Summary. United States: USDA.

Varshney, R. K., Grauner, A., and Sorrells, M. E. (2005). Genomics-assisted breeding for crop improvement. Trends Plant Sci. 10, 621–630. doi: 10.1016/j.tplants.2005.10.004

Vereijssen, J., Smith, G. R., and Weintraub, P. G. (2018). Bactericera cockerelli (Hemiptera: Triozidae) and Candidatus Liberibacter solanacearum in potatoes in New Zealand: biology, transmission, and implications for management. J. Integr. Pest Manag. 9:13.

Walker, G., Macdonald, F., Larsen, N., and Wallace, A. (2011). Monitoring Bactericera cockerelli and associated insect populations in potatoes in South Auckland. N. Z. Plant Prot. 64, 269–275. doi: 10.30843/nzpp.2011.64.6009

Wallis, R. L. (1955). Ecological Studies on the Potato Psyllid as a Pest of Potatoes. Washington: D.C.

War, A. R., Paulraj, M. G., Ahmad, T., Buhroo, A. A., Hussain, B., Ignacimuthu, S., et al. (2012). Mechanisms of plant defense against insect herbivores. Plant Signal. Behav. 7, 1306–1320. doi: 10.4161/psb.21663

Wen, A., Mallik, I., Alvarado, V., Pasche, J., Wang, X., Li, W., et al. (2009). Detection, distribution, and genetic variability of 'Candidatus Liberibacter'species associated with zebra complex disease of potato in North America. Plant Dis. 93, 1102–1115. doi: 10.3684/036.093.093.004

Wolt, J. D., Wang, K., and Yang, B. (2016). The regulatory status of genome-edited crops. Plant Biotech. J. 14, 510–518. doi: 10.1111/pbi.12444

Yao, J., Saenkham, P., Levy, J., Ibáñez, F., Noroy, C., Mendoza, A., et al. (2016). Interactions ‘Candidatus Liberibacter solanacearum’—Bactericera cockerelli: haplotype effect on vector fitness and gene expression analyses. Front. Cell. Infect. Microbiol. 6:62. doi: 10.3389/fcimb.2016.00062

Conflict of Interest: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Copyright © 2021 Mora, Ramosamy, Damen, Iriyogey, Ancona, Ibáñez, Avila and Mandadi. This is an open-access article distributed under the terms of the Creative Commons Attribution License (CC BY). The use, distribution or reproduction in other forums is permitted, provided the original author(s) and the copyright owner(s) are credited and that the original publication in this journal is cited, in accordance with accepted academic practice. No use, distribution or reproduction is permitted which does not comply with these terms.