IDENTIFICATION OF ZEBRA CHIP TOLERANT DIPLOID AND TETRAPLOID POTATO GENOTYPES WITH GOOD PROCESSING QUALITY

A Thesis

by

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ABSTRACT

Zebra chip (ZC) disease, caused by the bacteria '*Candidatus* Liberibacter solanacearum' (Lso), and vectored by the potato psyllid (*Bactericera cockerelli* Šulc.) causes significant yield and quality losses in potatoes. Potatoes infected with the Lso bacteria make chips with zebra-like patterns that are unacceptable for consumers. Currently, insecticides are applied to minimize plant contact with the potato psyllids. The use of tolerant potato cultivars is being considered as an important part of an integrated approach to manage the disease and reduce insecticide use. Comprehensive screening of commercial and breeding clones over multiple years indicated that very little resistance was available in chipping clones. The objective was to screen additional tetraploid clones containing introgressions from crop wild relatives and also a collection of diploid clones derived from recurrent selection to identify tolerance to Lso that could be incorporated in potato breeding programs. Artificial infestation with Lso-infected psyllids was conducted in greenhouse controlled and field experiments isolated from natural insect presence. Tubers were chipped and evaluated for chip quality and ZC score. Insect mortality and egg numbers were counted to characterize insect response. Among diploids with good chipping quality and low ZC score, one highly tolerant diploid clone (DD853-02) and two tolerant clones (CC831-03 and DD812-02) were identified. Among tetraploid potatoes with good chipping quality and low ZC score, some members of the A07781 and TX12484 families showed promising tolerance in the

field and greenhouse. The findings indicate that genetic tolerance to ZC is available in potatoes with high chip quality and could be used for future breeding work.

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CHAPTER I

INTRODUCTION AND LITERATURE REVIEW

1.1 Introduction

The cultivated potato (*Solanum tuberosum* L.) is the third most important food crop for human consumption after rice and wheat. Potatoes are cultivated in more than 150 countries world-wide, representing diverse climatic zones. In 2016, the total global production was 376.8 10^6 t. Potato yield (production per unit of land) is very high (195,790 $hgha^{-1}$) (FAOSTAT, 2018). Its versatility for food is indicated by the distinct market classes including chip processing, French fry processing, dehydrated, yellows, round whites, reds with white flesh, other pigmented, and fresh market russets (Hirsch et al., 2013; International Potato Center, 2018)

In 2017, the U.S. produced 20 10^6 t of potatoes on 407.8 10^3 ha of land with average yield of 490.2 10^3 $hgha^3$ (FAOSTAT, 2018) and Texas produced 385 10^3 t or 2% of the total national production of potatoes. This production (in the USA) was consumed as 35.6% frozen fries, 25.7% fresh potatoes, 13.7% potato chips and shoestrings, 10.9% dehydrated, and the remaining 14.1% in other uses (National Potato Council, 2018).

Sustaining and increasing potato production around the world is essential to food security, especially since its projected growth rate of production in developing countries (2.7% per year compared to maize the second highest at 1.9%) (CGIAR and Scott, 2000). Per 100 g, a potato with skin contains high amounts of energy in the form of starch (17.3 g) and high-quality protein (2.5 g) with a total of 93 kcal. It is high in

vitamin C (9.6 mg), fiber (2.2 g), and potassium (535 mg). Some other nutrients include, B6 (0.6 mg), thiamine (60 mcg), folate (28 mcg), phosphorus (70 mg), calcium (15 mg), magnesium (28 mg), iron (1.1 mg), zinc (0.4 mg), and antioxidants. Although potato is not considered a good protein source, lysine is higher compared with cereal proteins (Camire et al., 2009). However, only soybean produced more protein on a per hectare basis (Kaldy, 1972). Potato can be produced in many diverse soils and climate regions, has very high yield per unit area, a low cost of production, and can be produced in stress or short cropping conditions. This role of the potato in the world as a key food source is very important (CGIAR and Scott, 2000; Lisinska and Leszczynski, 1989).

1.2 Potato Genetics and Breeding

From its origins in the Andes Highlands of Peru and Bolivia and the lowlands of Southern Chile, potato has spread around the world (Jansky and Spooner, 2017). The species was domesticated over 8,000 years ago in Bolivia and was transported to Mexico and Central America (Bradshaw and Mackay, 1994b). From there, it was taken to Europe in 1570 and later introduced in North America, Africa, and Asia. Cultivated potatoes consist of eight cultivar groups of *S. tuberosum* (Huamán and Spooner, 2002). Due to autopolyploidy, wild species introgression, and other reasons potato has the highest genetic diversity of all crops that have been currently sequenced (Hardigan et al., 2017)

Potatoes and their wild relatives are classified as a subset of Solanum in the section Petota. This group contains a large wealth of genetic resources available to breeders with relative ease of introgression into cultivars. Potato is clonally and

sometimes sexually propagated, highly heterozygous, and can be diploid (2n = 2x = 24), triploid (3x), tetraploid (4x), and pentaploid (5x). Triploids and pentaploids are sterile and can only be vegetatively propagated. Potatoes can sometimes be propagated from true potato seed (TPS) although almost 100% of commercial production today starts from tubers. Some research efforts to use TPS are ongoing in tropical climates where tuber vigor is low and long-term storage of tubers is difficult (Jansky and Spooner, 2017).

Most of the commercial varieties found in production are tetraploids; however, some diploids which equal about 75% of the total number of potato species can produce equivalent yield. *S. tuberosum* which makes up the majority of cultivated potato was formed from a hybrid of S. *stenotomum and S. sparsipilum* (Hawkes, 1990; Jansky and Spooner, 2017) A significant portion of the genetic background in *S. tuberosum* commercial cultivars was from the coastal Chile long-day adapted *S. tuberosum* subgroup, Chilotanum (Hardigan et al., 2017).

Yield, tuber quality, pest and disease resistance, maturity, and adaptation are important in the breeding selection process. Since the end use of the specific market class of potato determines the type of quality characteristics required by the market, appearance and starch composition are also very important. Cultivated potato has a narrow genetic base relative to the diversity of traits in South American cultivars and wild species (Bradshaw and Mackay, 1994a). However, extensive potato germplasm resources are available from genebanks (Jansky et al., 2013).

The first potato breeders in the Andes developed landraces that were selected for specific environments and uses (Jansky and Spooner, 2017). After the potato was introduced in Europe and North America, serious breeding efforts in the modern sense started in England in 1907 and began to flourish by the 2nd half of the 19th century. By 1900, U.S. private breeders had released over 350 cultivars. Potato breeding became a public endeavor in the 1910 when the USDA began to work on virus resistance and was expanded after 1929 when the U.S. established a National Potato Breeding Program. The International Potato Center (CIP) was founded in 1971 and began working on broadening the genetic base of potato which had up to this point remained mostly derived from similar germplasm. Today, germplasm banks around the world comprise the Association for Potato Intergenebank Collaboration which contains more than 7,000 accessions of 188 potato taxa (Bradshaw et al., 2006).

Conventional potato breeding generally starts by crossing tetraploid parents with complementary traits of interest. The genotype used as female is emasculated and pollen from the other parent (male) is used to pollinate. The fruit produced is a berry and contains true potato seed (TPS) that correspond to full-sib families. Then tubers produced from the TPS of these crosses are planted in the field for evaluation. Typically, breeding programs test 50,000-200,000 seedling tubers each year. A subset of these (1 – 2%) will be evaluated for desirable traits the following year, with a few of those continuing on to larger field plots in subsequent years until a cultivar is released (Jansky and Spooner, 2017). In this recurrent selection breeding scheme, replicated trials and

detailed phenotyping begin several years after the initial cross was made and new parents are selected to continue the cycle.

In order to cross with tetraploids, the wild diploid species can be doubled using somatic or sexual polyploidization or can be crossed with haploids of tetraploids. The breeding scheme used to integrate alleles from wild species involves reducing the ploidy by generating dihaploids, hybridizing them with exotic diploids, and finally polyploidization to tetraploids by either somatic doubling of diploids or by sexual polyploidization using 2n gametes. Breeding at the diploid level can also be done using an inbred-line based strategy to create high yielding diploid hybrids using breeding techniques currently used in other diploid crops (Jansky et al., 2016). Diploid breeding using inbred lines has been recently emphasized as the new potato breeding method of the future because its' use of modern genetic tools that are utilized in crops like corn. It is seen as an important breeding strategy for its advantage of being able to select desirable combinations of alleles and discard deleterious ones (Jansky and Spooner, 2017). In addition, higher variance occurring in diploid populations should result in higher gains when selecting at the extremes.

Potato breeding clones with introgressions from germplasm derived from wild Solanum are important for breeders as a source of resistance to many insect and disease pests. Two-hundred and nineteen wild potato tuber bearing species are recognized (Bradshaw et al., 2006) but only a small proportion has been used in breeding programs. This wild germplasm is typically used to bring in a specific gene to provide host plant resistance (Jansky and Spooner, 2017) for a specific disease or pest. Notable successes

from introgression of wild relatives has been resistance to late blight, viruses, and nematodes (Bradshaw et al., 2006).

Crossing between different ploidy levels and linkage drag are among the difficulties in using wild relatives as sources of useful genes. Interspecific crosses usually have to have the same endosperm balance number (EBN) so that there is a 2:1 ratio of maternal to paternal endosperm. For tetraploids, EBN is not a concern because tetraploids will cross with other tetraploids. For diploids, there are both 1 EBN and 2 EBN types. For 2 EBN, the chromosome can be artificially doubled to cross with tetraploids or fusion can be used to create somatic hybrids. For 1 EBN, they can sometimes be crossed with a bridge species or via somatic hybrids. Many crossing attempts may be needed to achieve a single success (Ortiz and Ehlenfeldt, 1992). Embryo rescue techniques are another way to enable the breeding of potato species that do not naturally cross (Simko et al., 2007).

Linkage drag of inferior alleles is a major difficulty during introgression with wild species. Many backcrosses are needed and still the desired result may not be realized. Molecular marker assisted selection is a tool to confirm the successful introgression of pest-resistance genes from wild species and reduce the number of backcrosses necessary to achieve successful introgression of the desired trait (Barone, 2004). Transformation using cisgenes (genes from the same species) in place of crossing has the potential to make wild species more accessible in potato breeding programs (Jacobsen and Schouten, 2007)

Because vegetative reproduction by cloning spreads diseases, including viruses and bacteria, limited-generation certification programs in potato are important to start with disease-free tissue culture materials. Agencies that certify potato seed require extensive documentation, isolation, variety purity, monitoring of disease levels, assessment of tuber physical quality, visual inspection, and post-harvest tests. In North America, all certified potatoes start from disease-free stocks in the lab, followed by seedling tuber production. The limited generation procedure usually limits certification to five years of field increase of clonal selection seed depeding on the State. Only approved varieties recognized by breeding programs, experiment stations, or other recognized institutions can be certified. Tubers from disease-free stocks are planted in the field to produce the generation 1 stocks which will be used to produce generation 2 stocks and so on to a maximum of generation 5 after which only commerical production for consumption in allowed. When marketed, seeds must be labeled for lot identification, variety, quality of tubers, class of seed, country, and certification authority (Gutbrod and Mosley, 2001).

1.3 Potato Pests and Diseases

Potato succumbs to a wide variety of pests and diseases as well as abiotic physiological disorders such as internal heat necrosis. Successful production requires management on all levels to achieve profitability. Variety selection, fertility management, chemical application, irrigation, timing of the crop are some of the many tools used to maximize production and minimize losses from pests. Breeding has been an integral part of management for controlling several serious diseases of potato. Crop

wild relatives have provided resistance to ring rot, potato cyst nematode, root knot nematode, potato virus X, potato virus Y, Colorado potato beetle, green peach aphid, potato tuber worm, late blight, Verticillium wilt, silver scurf, thrips, tobacco etch virus, soft rot, and others. There is diversity both within wild species and within individual accessions. *S. berthaultii*, *S. chacoense*, *S. sparsipilum*, *S. tarijense* are wild species that are especially abundant sources of resistance (Hiller et al., 1985; Rich, 2013; Simko et al., 2007; Wale et al., 2008).

1.4 Zebra Chip

'*Candidatus* Liberibacter solanacearum' (Lso) is a bacterial organism responsible for a disease in potato known as zebra chip (ZC). This term indicates the symptoms (dark and light pattern) caused by this organism which is especially damaging to potato chip products. ZC was first reported in Saltillo, Mexico with sporadic outbreaks in Mexico from 1994 – 2004. ZC was first detected in south Texas in 2000 and has since spread to the western U.S., Central America, and New Zealand (Munyaneza, 2015; Nelson et al., 2012; Secor and Rivera-Varas, 2004). ZC disease was reported extensively in the U.S. starting in 2004 when millions of dollars of losses started to occur (Munyaneza, 2012; Secor et al., 2006). In 2008, this disease was first reported outside the Americas in New Zealand and by 2011, ZC had spread to Oregon, Washington, and Idaho causing severe losses in this major world potato growing region (Liefting et al., 2008; Lin and Gudmestad, 2013). Greater than 50% loss is possible from this disease (Buchman et al., 2012; Munyaneza et al., 2007). Estimates of yield loss in 2011 ranged from 0.5 to 75% with an average of 18% (Guenthner et al., 2012). The complex nature

of ZC comes from its transmission by the insect vector potato psyllid (*Bactericera cockerelli*), (Munyaneza et al., 2007; Munyaneza, 2012) which feeds on potato in the same areas where ZC is a significant disease.

Lso was first identified to be the specific causal agent of ZC disease in potato in 2008 (Hansen et al., 2008). Although this disease had been reported in Mexico as early as 1994 and in the U.S. (Texas) in 2000 (Munyaneza et al., 2007), the specific pathogen causing the disease was not identified until 2008. This plant pathogen has been determined to be a nonculturable, gram-negative, phloem-limited, bacterium in the Alphaproteobacteria group that is spread from infected to healthy plants by psyllid vectors (Munyaneza, 2012). It is closely related to ('*Candidatus* Liberibacter asiaticus') that is associated with citrus greening (Huanglongbing, HLB). Lso, via the potato psyllid vector, infects tomato, pepper, eggplant, tomatillo, tamarillo, and several solanaceous weeds including silverleaf nightshade, bittersweet nightshade, and *Lycium spp*., which can serve as the primary inoculum for transmission via psyllids to a potato field (Munyaneza, 2012; Swisher et al., 2013; Thinakaran et al., 2017; Thinakaran et al., 2015). In Europe, Africa, and the Middle East Lso infects multiple crops such as carrot, celery, parsley, and parsnips via the psyllid *Trioza apicalis and Bactericera trigonica,* (Munyaneza, 2012; Munyaneza, 2015). Lso haplotypes that are present in the insects or plants are characterized based on SNPs and categorized based on haplotype analysis using SSR markers (Lin et al., 2011).Haplotypes A and B are associated with the disease in solanaceous plants, haplotype C with carrots and the vector *Trioza apicalis*, and haplotypes D and E also with carrots and the vector *Bactericera trigonica* (Munyaneza,

2015). Recently, haplotype U vectored by *Trioza urticae* was identified to affect stinging nettle (Haapalainen et al., 2018) Only one infected psyllid is needed to transmit the disease to the potato (Buchman et al., 2012; Buchman et al., 2011), but plants with multiple vectors have higher inoculation rate (85.2%) compared to a single vector (46.0%) (Rashed et al., 2012).

From the site of infection, Lso seems to follow a source to sink movement of carbohydrates in the phloem (Levy et al., 2011). Like HLB, infection causes blocking of sieve tubes and disruption of flow from source to sink. This apparently benefits the bacteria and signals starvation to the plant causing starch accumulation in the leaf tissue (Kim et al., 2009; Nwugo et al., 2017). The pathogen can translocate from an infected leaf to a tuber tissue in four to seven days (Rush et al., 2015). The timing and rate of symptom development is variable, but the first symptoms, which include purpling or yellow leaves, were observed at three to four weeks after infestation for susceptible cultivars such as Atlantic. At this time following infection, qPCR can be first used to detect the presence of the bacteria.

After infection of the potato plant with Lso by the potato psyllid, the above-ground symptoms may show yellow or purplish discoloration, upward rolling and cupping of the leaves, stunting, chlorosis, swollen nodes, shortened internodes, proliferation of auxiliary buds, aerial tubers, browning of vascular system, leaf scorching, and early plant death (Munyaneza, 2012).

The progression of ZC disease from infection of the above ground plant until the darkening symptoms in the tubers can happen as rapidly as two weeks (Rashed et al.,

2014). Tubers that have been infected usually will not produce sprouts because the disease dissociates the mobilization of carbohydrate and protein reserves (Munyaneza et al., 2008). Those that do sprout have very low vigor and will likely die after a few weeks (Rashed et al., 2015). The infected tuber symptoms include enlarged lenticels, collapsed stolons, browning of the vascular tissue, striping, necrotic flecking, and streaking of medullary ray tissue. When freshly cut, rapid browning from ZC occurs in tubers exposed to the air from enzymatic oxidation of phenolic compounds. Frying intensifies the internal streaking and blotches to very dark brown consequently leading to large losses for the potato chip industry (Munyaneza, 2012).

Tuber biochemical changes also occur, including increased free amino acids, phenolic compounds, salicylic acid, ion leakage, and changes in mineral and reducing sugar content (sucrose, glucose, and fructose). Thirteen free amino acids were higher with some of the highest increases in proline, tyrosine, histidine, tryptophan, isoleucine, and leucine. (Rashed et al., 2013; Rubio-Covarrubias et al., 2017; Wallis et al., 2012). A reduction in protein was caused by protein catabolism possibly caused by a loss of protease inhibitors (Kumar et al., 2015). Phenolic compounds increased in the tubers include the precursors of lignin and tannins which are part of the plants defense pathways (Wallis et al., 2015b). Other enzymes and compounds were increased that indicated high oxidative stress in diseased tubers causing Lso infected tubers to consume more metabolic energy. These changes included enhanced dehydrogenase, changes in cellular redox, and two - four times increased respiration. Higher glutathione reductase,

ascorbate free radical reductase, and a sustained increase in oxidase (NOX) were among many enzymes that were increased indicated high stress.

An analysis of gene expression, showed that there was a net increase but a downregulation of photosynthesis related genes suggesting that Lso reduced resource efficiency. Protease inhibitors which are known to inhibit microbe proteases were upregulated in the leaves and downregulated in the roots indicated apparent weakness in the root system to overcome the infection. In addition, K is greatly increased in diseased leaf and root tissues. Other minerals also changed when infested, with ZC, Ca and Mg decrease in the leaf and increase in the root. Fe, Mn, Zn, and Cu were increased in the root, but only Fe was increased in the leaf. The increase in K likely corresponds with an increase of starch since accumulated K results in a co-regulated expression of starch synthase from Lso (Nwugo et al., 2017). Another study identified that ZC caused cell death in tubers resulting in many small irregularly shaped lesions in the tuber with compounds such as lignin surrounding the lesions. This suggests that ZC induces a hypersensitive response leading to programmed cell death (Miles et al., 2010).

Transcriptomic sequencing has identified genes that Lso caused to be differentially expressed, supporting the hypothesis that Lso reduces metabolism, signaling, and plant defenses. Photosynthesis and phytohormone regulation genes were downregulated and metabolic pathways related to cell wall synthesis, metabolism, and phenolic compounds were altered. Two similar chip varieties, Atlantic and Waneta showed significant differences in differentially expressed genes. Some of the reduced

degree of susceptibility on Waneta may be the reason for these differences (Levy et al., 2017).

The control of this disease with insecticides (Butler et al., 2011) is essential to the potato chipping industry. It is successfully controlled with early detection and careful timing of products such as Admire (imidacloprid) and Movento (spirotetramat) to control the potato psyllid. (Goolsby et al., 2007; Levy et al., 2011). The cost to the grower is high, with one grower study in 2009 – 2011 documenting an average cost in Texas of $740 per hectare and an average of 7.9 applications of insecticide (Guenthner et al., 2012). It is estimated that production costs would increase by 17% in Idaho if ZC were to become a problem in that area (Guenthner et al., 2012). Since even one psyllid can infect the plant these methods are costly, with variable effectiveness, and rely on application of toxic chemistries. Recently, resistance to neonicotinoid-based insecticides such as imidacloprid has been found in Texas psyllids leaving the future control of psyllids by current insecticides in doubt (Hawkes, 2016; Prager et al., 2013). Development of new cultivars that contain resistance or tolerance to ZC would be a substantial contribution to the potato industry.

In the last decade, as ZC disease has become more widespread, efforts have been increased to select for resistance or tolerance to either the psyllid or the bacteria. What has confounded the results to date is that tolerance/resistance mechanisms may be to the insect, the pathogen, or a combination of them. Selected cultivated varieties for ZC yield loss were tested and it was found that while there was some degree of variability in susceptibility to ZC, all varieties tested had yield losses ranging from 49.9% to 87.2%.

(Munyaneza et al., 2011). It was determined that there is an urgent need to develop varieties with resistance/tolerance to this disease. Based on results of several years of research, it was suggested that Lso tolerance and possible resistance exists in wild species (Wallis et al., 2015a). This research found five tolerant clones out of 283 clones and advanced selections tested, and indicated that these five had some wild species material in their parentage. Data from the Toluca Valley, Mexico (Rubio-Covarrubias, 2016) indicated a significant reduction in the percentage of tubers with ZC symptoms, progression of the disease curve, and the severity of the internal tuber discoloration in some selected clones that were tested. Results by (Lévy et al., 2015) showed differences in susceptibility to Lso among clones. This indicates that some level of tolerance to the pathogen can occur and selection for tolerance/resistance to ZC could provide beneficial breeding clones for the potato industry. Researchers have looked at psyllid development from eggs on no-choice feeding assays and found that some potato genotypes produced significantly fewer psyllids from the eggs from a strong antibiotic effect (Diaz-Montano et al., 2013). However, it should be noted that infection by Lso happens very soon after contact with the first psyllids, so these genotypes still have infection by the pathogen regardless of eventual psyllid development from hatched eggs.

Not finding good resistance in commercial varieties tested in field trials, work has been continued to screen wild species for potential resistance. While the number continues to be updated, there are at least 219 species of wild potatoes. With such a vast pool of potential genetic resources, it is a largely unknown and untapped genetic reservoir. In the limited wild material that has been screened (Cooper and Bamberg,

2014; Cooper and Bamberg, 2016) found that some *S. verrucosum* and *S. bulbocastanum* accessions in the US potato germplasm bank were resistant to the psyllid. Tri-species potato material derived from *S. tuberosum*, *S. etuberosum*, and *S. berthaultii* had significantly reduced feeding by psyllids in feeding tests (Novy et al., 2010b). *S. raphanifolium, S. tarijense*, and *S. chacoense* were used in ARS breeding clones that were bred for resistance to cold induced sweetening and were indicated to have ZC tolerance (Wallis et al., 2015a). The US Potato Genebank mini-core collection was screened for resistance to the psyllid as well as tolerance to ZC indicated by lowest yield reductions on infested plants compared to the control. PI 310927 *S. berthaultii* and PI 558050 *S. commersonii* were found to be tolerant to ZC as indicated by tuber production level and resistant to the psyllid. PI 458425 *S. jamesii* and PI 592422 *S. jamesii* were found to have high insect mortality and low oviposition (Levy et al., 2018).

Evaluation of commercial potato chip varieties has shown susceptibility to ZC (Anderson et al., 2012; Lévy et al., 2015; Munyaneza et al., 2011). Although the degree of susceptibility varies, existing studies have shown susceptibility across a broad range of commercial cultivars in all market classes. Low discoloration in some experimental tolerant lines associated with low phenolic content indicates that tolerance can occur without the extra production of phenolic compounds (Rubio-Covarrubias et al., 2017). Breeding clones A07781-3lb, A07781-4lb and A07781-10lb are full sibs derived from *S. chacoense* had lower Lso titer and tuber symptom expression. *S. chacoense, S. etuberosum*, and *S. berthaultii* are likely to have the highest potential to find reduced susceptibility to ZC (Rashidi et al., 2017),

1.5 Potato Psyllid

Potato psyllid *Bactericera cockerelli* (Sulc), has been known as a destructive pest of potato even when it does not contain '*Candidatus* Liberibacter solanacearum'. Outbreaks of psyllid yellows disease (caused by the feeding behavior of the psyllid) were described in 1927 and 1938 (Butler and Trumble, 2012). Although it remains a serious economic pest of solanaceous crops, the insect is controlled by insecticides such as Admire (imidacloprid) and Movento (spirotetramat) which are the most commonly used. Its role as the vector of Lso makes understanding its movement, abundance, and control methods very important to limiting the spread of ZC disease. For this reason, monitoring psyllids using yellow sticky cards is an important management portion of a ZC integrated pest management (IPM) program, (Goolsby et al., 2007; Goolsby et al., 2012). However, since even one psyllid can destructively infect the plant, a low-input IPM method is likely not practical for chipping or French fry processing potatoes because of ZC (Trumble et al., 2016)

The optimum temperature for development of the psyllid is at 27 °C and they will not survive above 35 °C (Munyaneza et al., 2012). If climate conditions are ideal, three to seven generations of psyllids are likely completed in one year. When the temperatures increase in late spring, the potato psyllid migrates from the Southwest U.S. and Mexico northward into the Western Rocky Mountain states and Canadian provinces. In cooler regions of Mexico and Central America, psyllids are able to reproduce and develop throughout the year without migration (Munyaneza, 2012).

Lso concentrations in the plant tissue (titer) is related to the initial inoculum injected into the plant by the psyllid (Rashed et al., 2016). Additionally, variation in psyllid feeding and numbers of psyllids may result in different levels and rates of symptom development. These variations are compounded by the environment and potato variety which makes analysis of Lso symptoms very challenging. This is confounded by the fact that climate factors also affect vectoring efficacy, disease progression, and tuber development (Wallis et al., 2015a).

1.6 Chip Quality

Chip processing potatoes are likely to be later maturing potato varieties with high starch content (Lisinska and Leszczynski, 1989). To be desirable for processing, potato tubers must be mature, low in reducing sugars, high yielding, high in dry matter, high in specific gravity, and uniform in size and shape. The producer controls these qualities by optimizing genetic, cultural, and environmental factors. Frying duration, oil temperature, oil type, pre-treatment of the potato, and tuber itself all effect the final quality of the chip (Santis et al., 2007). Potato tubers are tested for quality and visual appearance before and after chipping and chip color is evaluated by the consumer which prefers a light colored chip without dark imperfections (Pedreschi et al., 2016). When fried, the potato chip has specific marketing requirements which include a reducing sugar content of $< 2.5 – 3$ mg/gram and a glucose level less than 0.35 mg/g for chips and less than 1.2 mg/g for French fries to prevent browning during the frying process (Buchman et al., 2012; Lisinska and Leszczynski, 1989). Starch content based on specific gravity is also

important. Most processed potato products need a specific gravity of 1,080 or higher for ideal absorption of the oil used in preparation (Wallis et al., 2012).

Potatoes used for chips are stored at a minimum of 10 °C and above 90% relative humidity because cooler temperatures can cause the starch to be converted to sucrose reducing sugars (Marwaha, 1997). This conversion of starch in cold storage is known as cold induced sweetening, which is also enhanced by the length of storage and the free amino acid content in the tuber. When cold induced sweetening occurs it results in browning of potato chips during frying (Blenkinsop et al., 2004).

Conditions in the field may also affect potato chip quality. Internal brown spot, heart necrosis, corky ringspot, and canker internal rust spot are all disorders that result in browning in chips. These are physiological disorders caused by photoperiod response along with genetic, fluctuating temperature, fluctuating moisture, and nutrition factors (Wolcott and Ellis, 1959).

The biochemical processes of browning in the potato chips are also associated with ZC and have been analyzed and likely caused by a combination of reducing sugars, polymeric polyphenolic compounds, and cell death (Miles et al., 2010). The analysis of tubers has also shown that ZC positive tubers have higher phenolic content (Navarre et al., 2009) causing enzymatic oxidation and higher reducing sugars which combine with free amino acids in the Maillard reaction (non-enzymatic browning). This reaction is determined by the reducing sugar content based on the reaction between amine groups and free amino acids and the reducing sugars (Miles et al., 2010). These symptoms are most visible after frying causing the burnt and striping pattern (Wallis et al., 2012). Lso

infected tubers had specific gravity values lower than the minimum 1,080 four weeks after psyllid infestation. Chips infested with ZC also contain higher than ideal levels of glucose, which also contributes to poor chip quality (Buchman et al., 2012).

Lso titer increases during the storage process of the tuber and tubers previously determined to be Lso negative can begin to show symptoms not shown at harvest. The pathogen can translocate from an infected leaf to a tuber tissue in four to seven days. This means that it is necessary to monitor and control late-season psyllid infestation until four days before harvest because of the potential of symptom development in storage even though there were no symptoms detected at harvest (Rashed et al., 2018; Rashed et al., 2015).

1.7 DNA Extraction and PCR

Detection of Lso in the plant is performed by polymerase chain reaction (using conventional polymerase chain reaction (cPCR) and quantitative polymerase chain reaction (qPCR) using primers from a region between the 16S and 23S rDNA and/or adenylate kinase (adk) genes. Primers sets Lso TX 16/23 F/R and Lso adk F/R (Ravindran et al., 2011) and Lso-931F/LsoLSS (Fujiwara and Fujikawa, 2016) have been developed from this region in the pathogen and selected from a group of possible primers tested for reliable diagnosis at different levels of Lso infection. Leaf, stem, and tuber tissue can all be used to extract DNA for cPCR and qPCR. Using qPCR is more useful than cPCR because detection of Lso is higher with qPCR. Up to 47% and 53% detection was found in symptomatic tubers for two types of cPCR used, 88% with TaqMan qPCR, and 94% with SYBR Green qPCR (Beard et al., 2012). SYBR Green

qPCR was specific, accurate, and cost effective method for detection. It was found that unacceptable browning can occur at titers below the limit of cPCR detection assays and also Lso may be detected in tubers that do not show any symptoms when fried (Beard et al., 2012). Pathogen detection using qPCR is detectable starting in the 2nd week using qPCR on the upper and middle-tier leaves, and through the rest of the plant by week eight. Several studies indicated that cPCR is unreliable for indicating presence on the bacteria (Beard et al., 2012; Levy et al., 2011; Li et al., 2009).

1.8 Tolerance and Resistance

Resistance is used to refer to the plant's ability to reduce infection level and tolerance means the extent a plant can maintain low ZC symptom expression (Agrios, 1988; Rashidi et al., 2017). It is important to specifically define tolerance and resistance because these terms are sometimes defined differently by different researchers. In ZC, a decrease of infection is measured by quantifying the bacteria titer of Lso in the plant. Since this was not done it cannot be specifically stated that resistance has been found based on this definition. The definition of tolerance is relative based on the degree of symptoms on the check clones that were used. If fewer symptoms (in fried chips) of ZC disease were observed in a clone compared to the untreated tubers of that clone and to both Atlantic and Waneta checks these were declared as tolerant and also suggested that resistance may exist and would need to be confirmed using qPCR to detect the level of bacteria present.

1.9 Project Objectives

More comprehensive screening is needed to determine if tolerance is available and the potential of this tolerance to be used in future breeding. The most efficient and reliable way to do this must be found, so that breeding programs can readily assess the clones in their breeding program. Phenotypic traits needed to indicate ZC tolerance, quality level of each clone, and the standards best able to describe. The objectives of this project were:

- To identify potato clones (tetraploid and diploid) with both high processing quality and tolerance to ZC disease.
- To compare greenhouse and field ZC screening methods to assess advantages and disadvantages of each.
- To evaluate the tuber and yield characteristics of ZC tolerant germplasm.
- To validate a final set of ZC tolerant and susceptible clones in a controlled field study to check for consistency.

CHAPTER II

MATERIALS AND METHODS

2.1 Germplasm Used in Greenhouse and Field

- Twelve tetraploid clones that had shown reduced susceptibility to ZC in previous screening tests (average ZC score lower than four on a 0 – 5 scale) conduction by the Texas breeding program.
- Three tetraploid clones from the (NCPT) 2017 National Chip Processing Trial (only in greenhouse experiment).
- Nine tetraploid clones with introgressions from crop wild relatives with known pest and disease resistance in their pedigrees from USDA ARS in Aberdeen, Idaho.
- Twenty-one diploid clones from a recurrent selection program of *S. tuberosum* Grp. Phureja, *S. microdontum,* and *S. berthaultii, S. chacoense* from Michigan State University.
- Four diploid accessions from the potato mini-core collection (only in greenhouse experiment) (Levy et al., 2018).
- Four check varieties Atlantic and Waneta chippers; Russet Norkotah and Reveille Russet fresh market russets. (All four were included in the greenhouse. Atlantic and Waneta were included in the field.)

2.2 Germplasm Used in Validation Study

- Five tetraploids from the Texas breeding program
- Three tetraploids with introgressions from crop wild relatives
- One tetraploid from the NCPT trial
- Three diploids from the recurrent selection clones
- Three of the most susceptible clones from the greenhouse screening
- Atlantic and Waneta as checks

Tetraploid clones with reduced susceptibility to ZC disease were identified from four (2013 – 2016) years of screening by the Texas Potato Breeding program under field conditions. During this period, if a clone had a ZC chip score of 4 or 5 it was dropped, but if not it was kept to screen again the next year. Twelve clones had average ZC chip scores below 4 and were included in our study.

Tetraploid clones were selected from the 2017 NCPT field study that had good chip quality and had 0% ZC infestation in the field. Since, they likely missed infection in the field they were included in the greenhouse screening.

Tetraploid clones from the USDA breeding program in Aberdeen, ID obtained from Richard Novy were included in the field and greenhouse because these all contained introgressions from wild potato species in their pedigrees. Since some of these wild potato species may have tolerance to ZC, it was thought that it would be useful to test advanced tetraploid clones from crop wild relatives that had already been developed and would be closer to the production pipeline than materials collected directly from the wild.

Diploid potato selections provided by David Douches at Michigan State University to screen for ZC tolerance were generated by crossing five diploid species (*S. tuberosum* Grp. Tuberosum, *S. tuberosum* Grp. Phureja, *S. microdontum*, and *S. berthaultii*, *S. chacoense* as source of self-compatibility for the germplasm pool) in a recurrent selection (RS) breeding method (Douches, D., Personal Communication).

PI 310927, PI 558050, PI 592422, and PI 458425 were obtained from John Bamberg (USDA-ARS, United States Potato Genebank, Sturgeon Bay, WI). These four accessions were identified out of a greenhouse screen of a mini-core collection of 80 accessions. Individual clones of accessions PI 310927 and PI 558050 were included because they were identified as having the strongest insect resistance and low yield reduction in infected plants compared to control plants. PI 592422 and PI 458425 were included because they had high insect mortality and low oviposition (Levy et al., 2018).

Atlantic, Waneta, Russet Norkotah, and Reveille Russet were included as checks. Atlantic is the standard for chipping and has been thoroughly studied and found to be susceptible to ZC. Waneta is also a commercial chipping variety and has shown a reduction in susceptibility compared to Atlantic (Levy et al., 2017). Russet Norkotah was included to represent the russet market class of potato. Reveille Russet (also a fresh market russet) was included because it was selected in Texas during years with high psyllid populations.

2.3 Insect Vector

Potato psyllids from an Lso infected colony were used as the inoculation source for the greenhouse and field experiments. Potato psyllids were raised in the

Tamborindeguy laboratory in the Department of Entomology at Texas A&M University. The psyllids were Northwestern haplotype. An Lso-uninfected colony was obtained from Dr. Henne, AgriLife Wesalco, TX. Infected psyllids were obtained by rearing insects on Lso-infected plants (Yao et al., 2016). The Lso-infected psyllid colonies, maintained on tomato plants in the Tamborindeguy lab, have been tested with diagnostic PCR for Lso infection, and have an average 80 – 100% infection rate with Lso. (Huot et al., 2018; Lévy et al., 2013).

2.4 Field Screening

The field trial screening plots were planted near Springlake, TX (34°11N, 102°30W, altitude of 1,115 m) in April 2017. The plots were on center pivot irrigation with Tivoli fine sand soil type. N-P-K fertilizer (121.1-28-28 kg/ha) was applied to the plots. No seed treatment was applied to the potato tubers. Chemicals applied during the growing season included Movento, Minecto Pro, Transform WG, and Sivanto insecticides; Scala, Luna Tranquility, and NUCOP fungicides; and Roundup, Dual Magnum, Matrix, Stealth, Makaze, Brawl, Gly Star Original, and Metribuzin 75 CA herbicides. These trials experienced above average precipitation in the last week of June, first and last week of July, and second week of August. Temperatures were recorded by Easy Log USD (Lascar Electronics, Whiteparish, UK) sensors from May 14 – Aug 21, 2017 both inside and outside the cage. Inside cage temperatures (Figure 1) averaged 24.3 °C, minimum of 7.2 °C, and maximum of 47.2 °C. Outside cage temperature averaged 24.5 °C, minimum of 4.5 °C, and maximum of 45 °C.

The field trial was planted on 4 April 2017 for all clones except MRS 127-2, MSV 313-2, MSW 044-1, MSW 075-2, MSZ 219-1, and MSZ 219-14 planted on 11 April 2017. Seventy total clones included 21 diploid clones from the Michigan State University Potato Breeding and Genetics Program, 9 tetraploid clones with wild introgressions from USDA Potato Germplasm Research Aberdeen, ID, 12 tetraploid chipping clones from Texas A&M Potato Breeding Program, 26 tetraploid chipping clones selected by National Chip Processing Trial (NCPT) breeding programs, and Atlantic and Waneta tetraploid chipping clones for the standard check. 1.83 m width x 7.32 m length x 0.91 m height enclosed cages covered with white LS Econet 4045 (AB Ludvig Svensson, Kinna, Sweden) mesh insect screen (0.40 x 0.45 mm) over 2.54 cm diameter PVC poles were used as enclosures to keep out all flying insects from the field trial (Figure 2). Cages were designated as infested and non-infested to ensure 100% isolation from potential psyllid escapes. The non-infested cages were planted with two plants per clone and the treatment cages were planted with four plants per clone. These were spaced at 22.86 cm between plants and 30.48 cm between clones at a depth of 15.2 cm.

Insects were placed on the plant at the time when tubers where beginning to develop, but still had six more weeks to develop symptoms after infection, (Rashed et al., 2013). Approximately 70 days after planting psyllids were placed on the plants on June 6th. Three psyllids were placed into a plastic Eppendorf (Eppendorf, Hauppauge, NY) tube that was placed into an organza mesh bag and tied onto a leaf and removed on

June 12th (Figure 3). Tubers were harvested on Aug. 21st, stored at 18.3°C until chipped on Aug. 24th 2017.

2.5 Greenhouse Screening

The greenhouse screening experiment was planted on September 5th, 2017 in Snook, TX (30°31'N 96°26'W, altitude of 67 m) about 10 miles from College Station, TX. Temperatures were recorded by Easy Log USD (Lascar Electronics, Whiteparish, UK) sensors in both non-infested and infested greenhouses. The infested greenhouse temperature averaged 20.2°C, minimum of 13.9 °C, and maximum of 31.1°C (Figure 4). The non-infested greenhouse temperature averaged 23.2 °C, minimum of 16.7 °C, maximum of 33.9 °C (Figure 5).

Fifty-two total clones included 21 diploid clones from Michigan State University Potato Breeding and Genetics Program, nine tetraploid clones with wild introgressions from USDA Potato Germplasm Research Aberdeen, ID, ten tetraploid chipping clones from Texas A&M Potato Breeding Program, three tetraploid chipping clones from the National Chip Processing Trial (NCPT) breeding programs, four of the most tolerant to Lso wild diploid accessions from the potato mini-core collection from a previous greenhouse screen completed at Texas A&M (Levy et al., 2018), Russet Norkotah and Reveille Russet tetraploid russet clones for the standard check for russets, and Atlantic and Waneta tetraploid for chipping clones. One tuber was planted 5.1 cm deep in 3.79 liter plastic nursery pots filled with Sunshine Mix #1 (Sungro, Agawam, MA) with starter fertilizer Osmocote (Scotts Miracle-Gro, Marysville, OH) on steel benches in a climate controlled polycarbonate greenhouse with natural lighting (Figure 6). Two non-

infested pots and four infested pots were planted per clone. Non-infested pots were placed in a separate greenhouse of the same type and the infested pots to ensure 100% isolation from possible psyllid escapes during infestation. The pots were initially placed 0.3 m apart and later moved to 0.6 m apart when the plants became over 0.3 m tall. A bamboo stake was placed into each pot and the plant was tied to the stake to keep it from falling over. Plants were fertilized with 4.93 mL Peters (J.R. Peters, Allentown PA) 20-10-20 N-P-K fertilizer per 3.79 L of water approximately every other week starting in mid-October.

Approximately six weeks after planting, psyllids were placed on the plants on Oct. 27th. This was at the time when tubers where beginning to develop, but still had six more weeks to develop symptoms after infection, (Rashed et al., 2013). Three psyllids were placed into a plastic Eppendorf (Eppendorf, Hauppauge, NY) tube that was placed into an organza mesh bag and tied onto a leaf and removed Nov. 3rd (Figure 3). Four clones had plants that died shortly after the insects were removed and ZC score and chip quality was not reported for these clones. Tubers were harvested on Dec. 15th and chipped on Dec 20th.

2.6 Data Collected

The number of live and number of dead psyllids were counted and expressed in percentage. Leaves were inspected for psyllid eggs and designated as a number code for no eggs (0), few eggs approximately less than 15 (1), and many eggs approximately more than 15 (2). Insect mortality and egg presence were recorded 6 days after placing

them on the plants. Data was taken on total tuber weight and total tubers per plant. Average tuber weight (yield) per plant was also calculated.

All tubers were chipped three days after harvest. Eight chips per plant (unless a fewer number of tubers were available) were sliced using an industrial meat slicer (Figure 7) at 1.3 mm thickness and fried for 1 minute 25 seconds in vegetable oil at 182.2 °C (Figure 8). The chips were rated for ZC score (0 – 5) with 5 the highest level of ZC browning (Figure 9), the number of chips showing ZC symptoms expressed as percentage (percent ZC), chip quality rating (1 – 5) with 5 the lowest chip quality (based on browning) (Figure 10), number of good chips (absence of any defects), and number of bad chips not suitable for the chipping industry. Good and bad chips were expressed in percentage of total chips for each plant since the total number of fried chips was not equal for each plant. Least square means and standard errors were calculated for each clone using JMP statistical software.

2.7 Designation of Tolerance and High Tolerance of Clones

Tolerance with high chip quality was declared if average ZC score per clone < 2.5 and average chip quality score was < 3.0 because chip quality above 3.0 is not acceptable for chips (Snack Food Association, 1995). The difference between average chip quality ratings of infested and non-infested < 1 to indicate minimal change due to ZC tuber symptoms based on the average for the clone.

High tolerance was declared if no incidence of ZC symptoms was observed on the chips or the average ZC score was very low (< 1.5).

2.8 Statistical Analysis

All statistical analyses were performed using JMP Pro 13 edition (SAS Institute Inc., Cary, NC). The traits analyzed were ZC chip score, percent good chips, percent ZC, chip color, percent insects alive, insect eggs, total tuber weight per plant, tuber number, and average weight per tuber. Since the traits were not normally distributed (Shapiro-Wilk test for normality) mixed models that do not require normality were used. For statistical calculations, each plant was considered to be a replication within a split plot design (infested and non-infested sub-plots), non-randomized experimental design. For traits comparing infested and non-infested, a nested model was used to separate clones into infested and non-infested groups. Clones and test (non-infested and infested) were considered as fixed effects, whereas reps and the interactions involving reps were considered random. Comparison of infested and non-infested was performed using Student's t-test for each trait. Least square means were used to approximate the means because the data set had missing data. JMP was used to generate least square (LS) means. LS means were compared using Student's t test. The effect tests in the analysis of variance model were used to determine if there were significant differences between clones and between tests (non-infested and infested). Multivariate methods analysis using pairwise correlations in JMP were used to calculate correlations for each trait separately for infested and non-infested and for comparing greenhouse and field. A correlation estimate ≥ 0.65 was considered strong, and 0.50 and 0.64 was considered moderately strong, and < 0.49 was considered weak. The level of significance used in all comparisons was $\alpha = 0.05$.

2.9 Field Validation Study

Eighteen potato accessions were planted by hand near Bushland, TX (35°12'N 101°54'W, altitude of 1132 m) on May 16th 2018. FL 1867 was planted as a positive and negative check. They were covered with cages (4 tubers of the same cultivar/cage) before emergence in two replications which were setup in a randomized complete-block design spaced 30 inches apart. Plants in the cages were infested at flowering with psyllids carrying '*Candidatus* Liberibacter solanacearum' (Lso). Six psyllids from an Lso infected colony of the Central haplotype were placed at the base (leaned against the base) of each plant in a 50-ml tube on June 20, 2018. Individual psyllids carried both Lso A and B haplotypes. The psyllids were left to feed for a week after which they were sprayed with pesticides. Plants were harvested on August 7, 2018. Immediately after harvest, the tubers were taken to the laboratory where three tubers/plant (whenever possible) were randomly selected, sliced at proximal end, and evaluated for ZC severity on 0 (healthy) to 3 (severe browning or necrosis) scale (Figure 12) (Rashed et al., 2013) and sampled for qPCR analysis to determine Lso titer level of the tuber. A protocol from (DNeasy® Plant Mini Kit (Qiagen, Valencia, CA, USA) was modified and used for DNA extraction (Rashed et al., 2015).

Lso was quantified using a ViiA7 Real-Time PCR System (Applied Biosystems, Carlsbad, CA.) and comparative Ct method (ΔΔCt) with Eukaryotic 18S rRNA (VIC/MGB probe, primer limited, Applied Biosystems) for an endogenous control (Rashed et al., 2015) TaqMan Universal Master Mix (Applied Biosystems), 0.3 µM forward primer LsoF (Li et al., 2009) 0.3 µM reverse primer HLBr (Li et al., 2006) and

0.25 µM HLBp TaqMan probe (Li et al., 2006)) was used for the reaction mix. Relative quantity (RQ) of Lso in each sample was normalized to the control and calculated based on 6,250 genome copies per RQ value (Rashed et al., 2015). RQ of uninfected tubers is zero (Paetzold, L., Personal Communication, 2018). Tubers were shipped to College Station and six tubers were evaluated for ZC symptoms as fresh and chipped (Figure 11). The tubers were sliced at 1.3 mm thickness and fried for 1 minute 25 seconds in vegetable oil. Before frying, the fresh chips were rated for ZC symptoms of the fresh tubers on a 0 – 3 scale (Figure 12). After frying, the chips were rated for ZC score (0 – 5) with 5 the highest discoloration of ZC, the number of chips showing ZC symptoms expressed as percentage, chip quality rating (1 – 5) with 5 the lowest chip quality (based on browning). Least square means and standard errors were calculated for each clone using JMP statistical software.

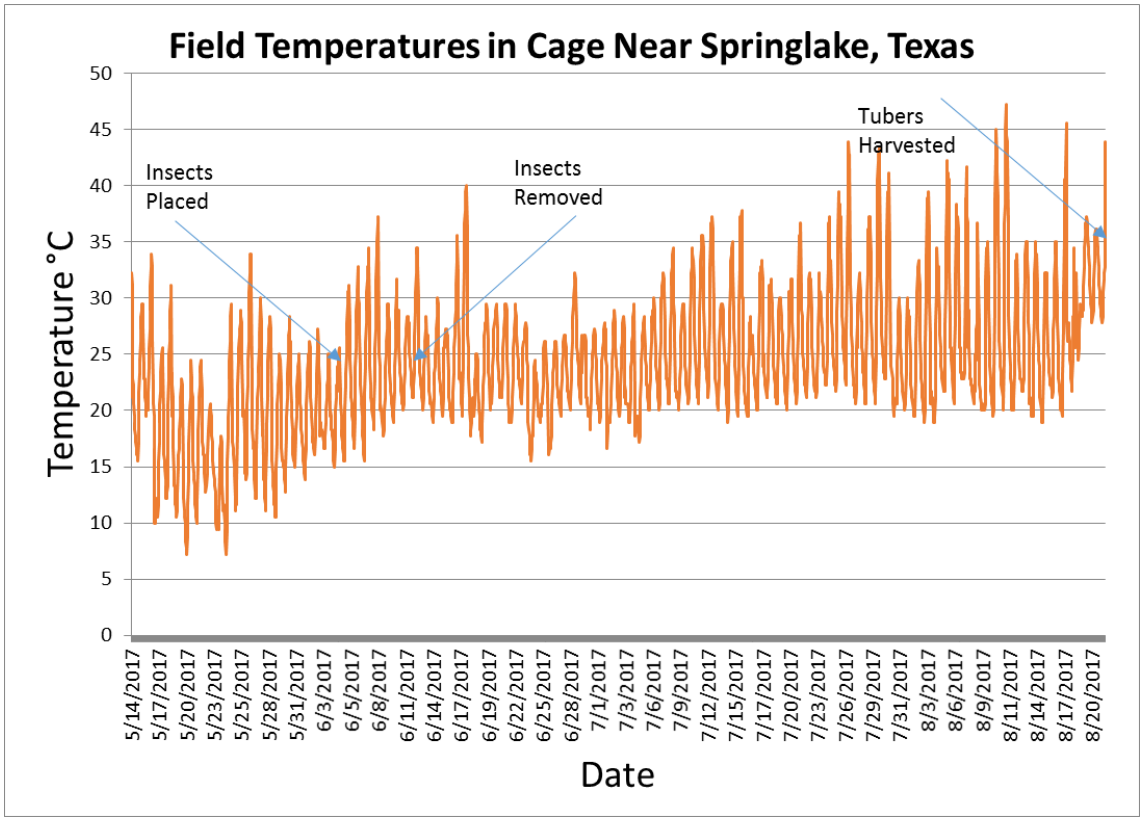

Figure 1. Temperatures in Celsius recorded inside the cage in the field near Springlake, TX during the growing season.

Figure 2. Field cages near Springlake, TX during the growing season

Figure 3. Tube with psyllid insects placed onto the potato plant leaf

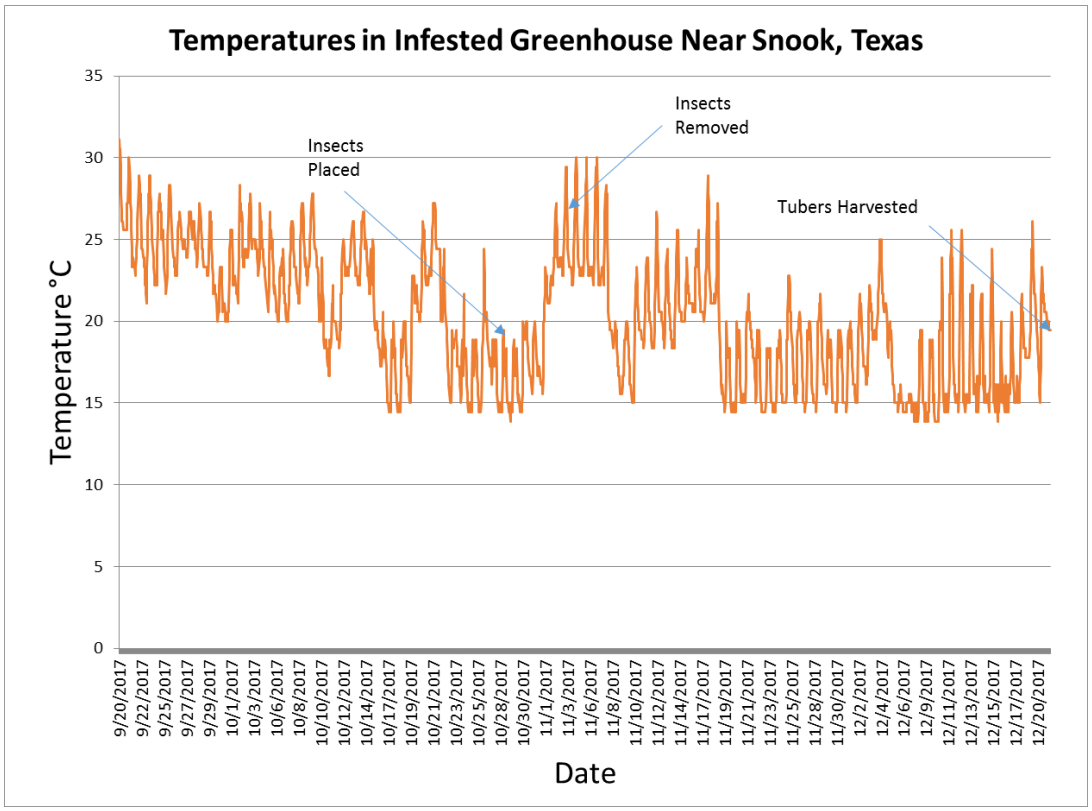

Figure 4. Temperatures in Celsius recorded in the infested greenhouse near Snook, TX.

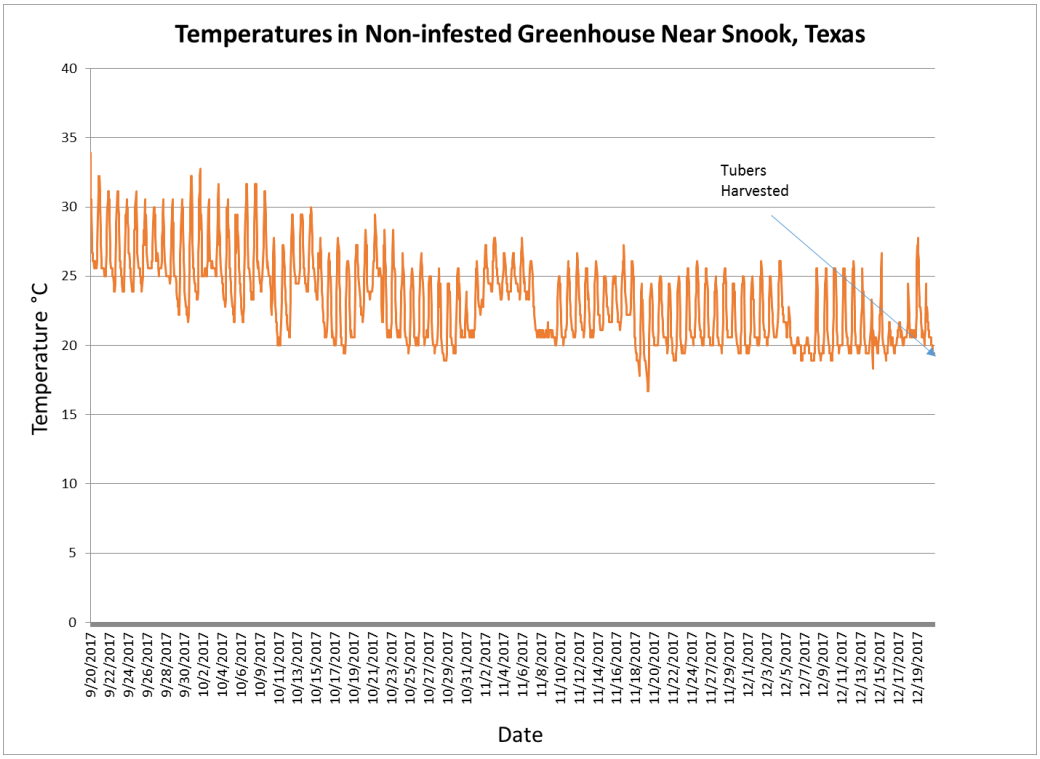

Figure 5. Temperatures in Celsius recorded in the non-infested greenhouse near Snook, TX.

Figure 6. Potato plants in the greenhouse

Figure 7. Industrial slicer used to precisely cut tubers to 1.3 mm thickness.

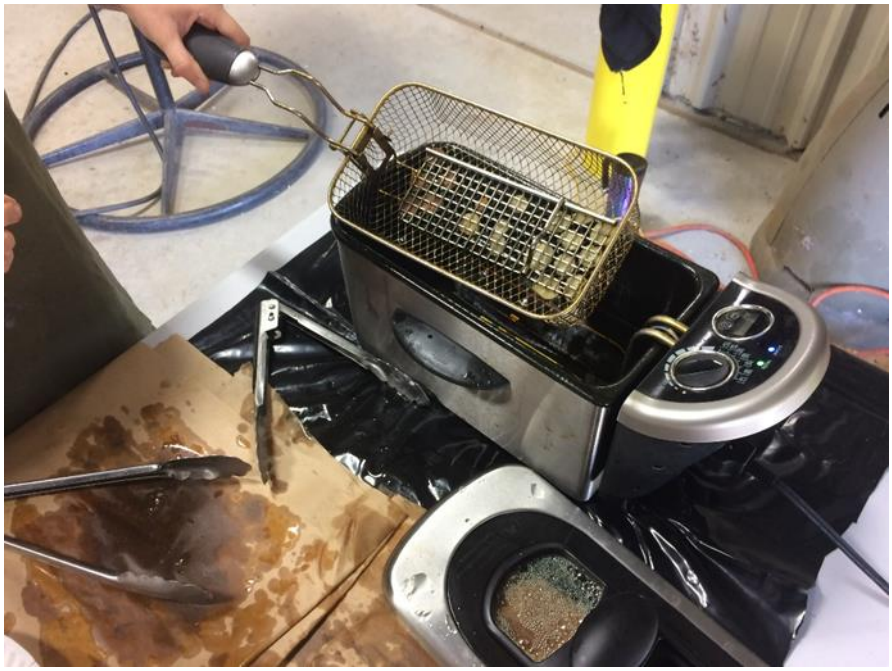

Figure 8. Chip fryer used to test fry potato chips for analysis.

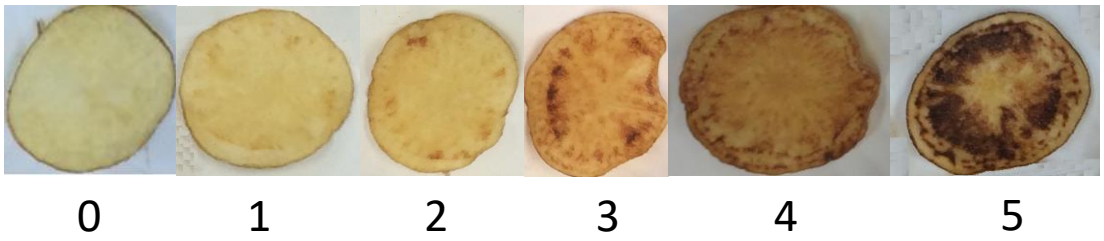

Figure 9. Zebra chip score (0 – 5) scale left to right used to indicate severity of symptoms on potato chips.

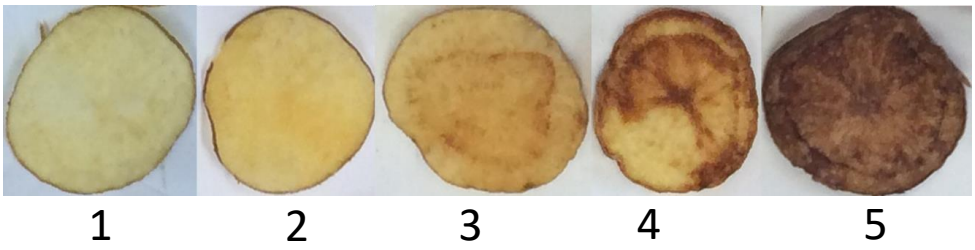

Figure 10. Chip quality score (1 – 5) scale left to right used to indicate the level of chip browning.

Figure 11. Zebra chip symptoms in fresh compared to chipped tubers

Figure 12. ZC symptoms in fresh tubers from (‘FL 1867’), with 0 representing no disease and 3 representing severe ZC symptoms

CHAPTER III

RESULTS

3.1 Greenhouse Results

3.1.1 Tetraploid

Twenty-six tetraploid clones were screened in the greenhouse. Waneta and three other tetraploid clones died and this data was excluded from chip quality and ZC score analysis, but were included for all the other traits since tubers were produced. Chip quality on these twenty-two clones (including Atlantic, Reveille Russet, and Russet Norkotah as checks) averaged 2.6, ranging from 1.1 to 4.3 for infested clones and averaged 1.3, ranging from 1.0 to 2.8 for the non-infested clones (Table 1, Figure 23). Five of the infested clones (TX12484-2W, AOR07781-2, A07781-10lb, MSV 358-3, TX05249-10W) had infested chip quality scores <2.0 indicating these as the best overall for chip quality. Ten clones had a difference in chip quality (infested – non-infested) of ≤ 1.0 (Figure 23). The clones ranked from most to least tolerant were TX12484-2W, AOR07781-2, A07781-10lb, MSV 358-3, TX05249-10W, A05379-211, Atlantic, A10667-3, POR06V12-3, and TX14710-7W. Out of these tolerant clones AOR07781-2, A07781-10lb, and A05379-211 had percentage of good chips higher than 80% and POR06V12-3 and TX14710-7W had the lowest percentage of good chips (Figure 23).

The ZC chip score was evaluated for fried tubers for 22 tetraploid clones screened in the greenhouse. The average ZC chip score for each clone was 2.2, ranging from 0.3 to 3.8 (Table 2 and Figure 24). Eleven clones (AOR07781-2, TX12484-2W,

MSV 385-3, A07781-10lb, TX14710-7W, TX05249-10W, Atlantic, A07781-4lb, A05379-211, A10667-3, POR06V12-3) had ZC scores <2.5 which is potentially tolerant. These 22 clones had average percent ZC symptoms of 32.4% on fried chips, ranging from 8.3% to 64.6% (Table 2 and Figure 24). The 11 potentially tolerant clones ranged from 8.3% to 37.5% ZC on chips (Figure 24).

The mean percent live insects at seven days after placing on the plants was 34.0% and ranged from 8.3% to 66.7% on all clones (Table 2 and Figure 25). A07781-10lb had the highest percentage of live insects. Four clones had no insect eggs at the end of seven days (Figure 25).

Average tuber number per plant averaged 9.4, ranging from 3.8 to 23.8 in the infested and averaged 10.5, ranging from 3.0 to 25.0 in the non-infested (Table 1, Figure 26). There were no significant differences between infested and non-infested clones for tuber number per plant. Average weight per tuber for each clone was 9.7 g, ranging from 2.2 g to 25.9 g in the infested and was 21.3 g, ranging from 3.2 g to 57.5 g in the non-infested (Table 1, Figure 26). The non-infested tetraploid clones had significantly higher average tuber weights than the infested ones. Average yield was 76.1 g, ranging from 12.5 g to 197.5 g per plant for the infested and was 155.4 g, ranging from 80.0 g to 220.0 g for the non-infested plants (Table 1, Figure 26).

3.1.2 Diploid

Twenty-five diploid clones were screened in the greenhouse. Two diploid clones were excluded because they did not produce tubers that could be chipped. Atlantic, Reveille Russet, and Russet Norkotah were included as checks. Waneta was planting as an additional check but this clone died and this data was excluded from chip quality and ZC score analysis, but were included for all the other traits since tubers were produced. Chip quality scores of the 23 diploid clones averaged 2.8, ranging from 1.0 to 4.5 in the infested clones and a mean of 1.6, ranging from 1.0 to 4.0 in the non-infested clones (Table 1 and Figure 27). Six of the infested diploid clones (DD853-02, DD851-07, CC831-03, DD847-06, and PI 558050 *S. commersonii*) had chip quality scores ≤ 2.0 and these were indicated as the best overall chipping quality, (Figure 27). Eighteen non-infested diploid clones had chip quality scores ≤ 2.0 indicating that many of the diploids tested were potentially suitable for chipping. Eleven diploid clones had a difference in chip quality (infested – non-infested) of ≤ 1.0 (Figure 27) indicating low effect from ZC infestation. These clones ranked from most to least tolerant were DD805-05, DD853-02, PI 558050 *S. commersonii*, DD851-07, CC806-02, PI 310927 *S. berthaultii*, CC831-03, DD847-06, DD812-02, CC805-01, and DD849-08. Out of these tolerant clones DD853-02, DD851-07, PI 558050 *S. commersonii*, and CC807-01 had percentage of good chips for infested at 80% or higher and PI 310927 *S. berthaultii* and DD805-05 had very low percentage of good chips (Figure 27).

ZC chip score was evaluated for fried tubers of the 23 diploid clones screened in the greenhouse. The mean ZC chip score was 2.1 and ranged from 0.0 – 4.5 (Table 2 and

Figure 28). Twelve clones (DD851-07, CC831-03, DD847-06, DD812-02, CC806-02, CC809-02, Atlantic, PI 558050 *S. commersonii*, CC811-03, DD805-08, CC807-01, DD805-05, and CC805-01) had ZC chip score <2.5 but >0 and these were designated as potentially tolerant, (Figure 28). Two clones (DD853-02 and PI 310927 *S. berthaultii*) had ZC chip scores = 0 and these were considered to have very high tolerance. These 23 clones had an average percent ZC symptoms of 37.5% ranging from 0% to 92.7%. The 12 potentially tolerant clones ranged from 8.3% to 37.5% ZC discolored chips (Figure 28).

Mean percent insects alive at seven days after placing the insects was 38% and ranged from 0.0% to 66.7% on all clones. Three clones had no insect eggs at the end of seven days (Table 2 and Figure 29).

Average tuber number per plant was 19.1, ranging from 3.8 to 50.0 in the infested and a mean of 20.5, ranging from 3.0 to 74.5 in the non-infested (Table 1 and Figure 30). There were no significant differences between infested and non-infested clones for tuber number per plant. Average weight per tuber for each clone was 7.3 g, ranging from 1.4 g to 18.2 g in the infested and was 9.6 g, ranging from 1.4 g to 57.5 g in the non-infested. The non-infested diploid clones had significantly higher average tuber weights than the infested ones. Average yield was 116.6 g, ranging from 20.0 g to 232.5 g per plant for the infested and was 146.0 g, ranging from 20.0 g to 300.0 g for the non-infested plants (Figure 30)

3.1.3 Greenhouse Summary

Among tetraploids, clones TX12484-2W (Figure 15), MSV 385-3, (Figure 18) A07781-10lb, TX05249-10W, and AOR07781-2 (Figure 14) had the best characteristics combining both ZC chip score < 2.5, chip quality score < 2.5, chip difference (infested – non-infested < 1), and better chip quality score than the best check variety which was Atlantic. The mean ZC score for the experiment was 2.2 and the mean percentage of ZC was 32.4% for all the clones. (Table 2).

Among diploids, clones DD853-02, DD851-07, CC831-03 (Figure 18), DD847-06, PI 558050 *S. commersonii* (Figure 21), DD812-02 (Figure 19), and CC806-02 had the best characteristics combining both ZC chip score < 2.5, chip quality score < 2.5, chip difference (infested – non-infested < 1), and better chip quality score than the best check variety which was Atlantic. The mean ZC score for the experiment was 2.1 and the mean percentage of ZC was 37.5% for all the clones (Table 2).

Overall incidence of ZC (percentage of tubers with ZC in the whole experiment) was 32.9% (diploids 38.7% and tetraploids 28.0%). Mixed model comparisons for infested and non-infested traits indicated significant differences in good chips percentage, chip quality, average yield g, and average weight per tuber. No significant differences were observed between infested and non-infested for tuber number (Table 1).

3.2 Field Results

3.2.1 Tetraploid

Twenty-three tetraploid clones were screened in the field including Atlantic and Waneta as checks. Nine of the tetraploid clones screened in the field did not show any ZC symptoms in fresh or chipped tubers. Since other field and greenhouse screens with these same clones did show symptoms, these clones were considered not infected with ZC even though the insects were placed on the plant. Chip quality scores of 23 tetraploid clones (including Atlantic and Waneta as checks) screened in the field averaged 2.5, ranging from 1.9 to 4.6 for the infested clones and averaged 1.9, ranging from 1.0 to 4.8 for the non-infested clones (Table 3 and Figure 31). Two of the infested clones (A07781-10lb and TX12484-3W) had both infested and non-infested chip quality scores <2.5 indicating them as the best overall for chip quality. Clone TX12484-2W had a chip quality score of 2.5 for the infested which was the same as the Waneta check. Seven clones had a difference in chip quality (infested – non-infested) of ≤ 1.0 (Figure 31). The clones ranked from most to least tolerant were A10667-3, A05379-211, A07781-10lb, PALB03035-7, TX12484-3W, A10667-2, and Atlantic. Of these most tolerant clones, none of them had good chip percentage above 80%. The lowest percentage good chips were A10667-2 with 0% good chips and A10667-3 with < 12.5% good chips (Table 3 and Figure 31).

The ZC chip score was evaluated for fried tubers for the 23 tetraploid clones. The mean rating for these clones was 0.9 (Table 4 and Figure 32). Nine clones had a ZC score of 0 and these were considered non-infested. The remaining 14 clones had a ZC

chip score range from 0.3 to 2.5 (Figure 32). Seven clones (A07781-10lb, A10667-2, A10667-3, AOR07781-2, PALB03035-7, TX12484-3W, A07781-3lb, and TX14710-7W) had ZC scores <2.0 which is potentially tolerant (Figure 32). Atlantic, TX12484-2W, and Waneta had ZC chip scores of 2.0 which is really close to tolerant. The percentage of ZC averaged 12.2%, ranging from 0% to 40% (Table 4). The 14 clones with greater than 0% had percent ZC symptoms on individual fried chips that ranged from 2.1% to 40%. The potential tolerant clones ranged from 2.1% to 23.3% ZC discolored chips (Figure 32).

Mean percent insects alive at seven days after placing on the plants was 18.7% and the range was 0.0% to 88.3% on all clones (Table 4 and Figure 33). Ten clones had no alive insects at the end of seven days. Fifteen clones had no insect eggs at the end of seven days (Figure 33).

Average tuber number per plant was 10.2, ranging from 1.0 to 21.5 in the infested and was 12.0, ranging from 7.5 to 28.0 in the non-infested (Table 3 and Figure 34). There were no significant differences between infested and non-infested clones for tuber number per plant. Average weight per tuber for each clone was 53.4 g, ranging from 35.3 g to 81.2 g in the infested and was 55.7 g, ranging from 18.1 g to 99.8 g in the non-infested (Figure 34). The non-infested tetraploid clones did not have significantly higher average tuber weights than the infested ones. Average yield was 532.4 g, ranging from 45.4 g to 982.0 g per plant for the infested and was 669.4 g, ranging from 36.3 g to 1782.6 g for the non-infested plants (Figure 34).

3.2.2 Diploid

Twenty-one diploid clones were screened in the field including Atlantic and Waneta as checks. One of the diploid clones did not produce tubers so it was excluded from the data. Six of the diploid clones screened in the field did not show any ZC symptoms in fresh or chipped tubers. Since the greenhouse screen with these same clones did show symptoms, it is considered that these clones were not infected with ZC even though the insects were placed on the plant. Chip quality scores of 20 diploid clones screened in the field averaged 2.8, ranging from 1.1 to 4.7 for the infested clones and averaged 2.4, ranging from 1.0 to 5.0 for the non-infested clones (Table 3 and Figure 35). Seven of the infested clones (DD853-02, CC804-01, CC813-02, CC811-05, DD812-02, CC805-01, CC831-03) had both infested and non-infested chip quality scores <2.5 indicating them as the best overall for chip quality, (Figure 35). Eleven clones had a difference in chip quality (infested – non-infested) of ≤ 1.0 (Figure 35). The clones ranked from most to least tolerant were DD812-02, DD805-08, CC805-01, CC804-01, DD853-02, CC831-03, DD805-05, CC807-01, CC813-02, Atlantic, and CC811-05. Of the tolerant clones, DD853-02, CC813-02, and DD812-02 had higher than 80% good chips. DD805-08 had very low percentage of good chips at 24.4% (Table 3 and Figure 35).

The ZC chip score was evaluated for fried tubers for the 20 diploid clones. The average percentage of ZC infected tubers was 28.0%. These had an average rating of 0.8 (Table 4). Six clones had a ZC score of 0 and these were considered non-infested. The remaining 16 clones had a ZC chip scores that ranged from 0.3 to 2.5. Ten clones

CC804-01, DD853-02, DD812-02, DD805-05, CC813-02, CC805-01, CC831-03, CC811-05, CC811-03, CC807-01, and DD851-07 had ZC chip scores <2.0 which is potentially tolerant. The lower incidence of ZC in this experiment required us to be stricter in the criteria used to declare tolerance. Atlantic and Waneta had ZC chip scores of 2.0. However, Atlantic was used as a susceptible check, thus in order to declare a clone as tolerant, the ZC chip scores had to be lower than Atlantic. These 16 clones had percent ZC symptoms on individual fried chips with a mean of 13.1 %, ranging from 1.7% to 43.3%. The potential tolerant clones ranged from 1.7% to 43.3% ZC discolored chips (Table 4 and Figure 36).

Average percent insects alive at seven days after placing on the plants was 9.0% and a range from 0.0% to 52.8% on all clones (Table 4 and Figure 37). Nine clones had no alive insects. Seventeen out of twenty-two clones had no insect eggs at the end of seven days (Figure 37).

Average tuber number per plant was 24.5, ranging from 4.5 to 57.0 in the infested and was 30.2, ranging from 8.0 to 67.0 in the non-infested (Table 3 and Figure 38). There were significant differences between infested and non-infested clones for tuber number per plant. Average weight per tuber for each clone was 20.1 g, ranging from 9.7 g to 95.0 g in the infested and was 22.8 g, ranging from 11.1 g to 99.8 g in the non-infested (Figure 38). The non-infested diploid clones did not have significantly higher average tuber weights than the infested ones. Average yield was 402.9 g, ranging from 220.7 g to 898.1 g per plant for the infested and was 581.1 g, ranging from 344.7 g to 857.9 g for the non-infested plants (Figure 38).

3.2.3 NCPT (National Chip Processing Trial)

Eleven of the NCPT clones screened in the field did not show any ZC symptoms in fresh or chipped. It is considered that these clones were not infected with ZC even though the insects were placed on the plant. Chip quality scores of 11 clones screened in the field that showed ZC symptoms ranged from 1.6 to 3.5 for the infested clones and 1.0 to 2.5 for the non-infested clones (Figure 39). Five of the infested clones (AC01151-5W, MSV030-4, NY 121, W 8822-1, AF 4157-6) had both infested and non-infested chip quality scores <2.5 indicating them as the best overall for chip quality, (Figure 39). Five clones had a difference in chip quality (infested – non-infested) of ≤ 1.0 (Figure 39). The clones ranked from most to least tolerant were AC01151-5W, MSV030-4, NY 121, W 8822-1, and NY 152. Of the most tolerant only AC01151-5W had percentage of good chips above 80% and NY 152 had the lowest percentage of good chips at 40.9% (Figure 39).

The ZC chip score was evaluated for fried tubers for the 22 clones and the mean was 0.8 (Table 4). Eleven clones had a ZC score of 0 and these were considered non-infected. The remaining eleven clones ranged from 0.3 to 3.8 ZC chip score. Ten clones NY 121, AF 4157-6, AC01151-5W, W 8822-1, NDTX081648CB-13W, and Snowden had ZC chip scores <2.0 which is potentially tolerant. These twenty-two clones had average percent ZC symptoms on individual fried chips with a mean of 8.9% and a range from 1.7% to 40%. The potential tolerant clones ranged from 1.7% to 20% ZC discolored chips (Table 4 and Figure 40).

Average percent insects alive at seven days after placing on the plants was 15.7 with a range from 0.0% to 41.7% on all clones (Table 4). Eight clones had no alive insects. Nineteen out of 21 clones had no insect eggs at the end of seven days (Figure 41).

Average tuber number per plant was 11.0, ranging from 3.3 to 26.8 in the infested and was 9.0, ranging from 1.0 to 24.5 in the non-infested (Table 3 and Figure 42). There were no significant differences between infested and non-infested clones for tuber number per plant. Average weight per tuber for each clone was 69.4 g, ranging from 32.7 g to 141.3 g in the infested and was 59.3 g, ranging 30.2 g to 133.1 g in the non-infested (Figure 42). The non-infested tetraploid clones had significantly lower average tuber weights than the infested ones. Average yield was 697.3 g, ranging from 232.8 g to 1342.6 g per plant for the infested and was 528.8 g ranging 54.4 g to 1519.5 g for the non-infested plants (Figure 42).

3.2.4 Field Summary

Among tetraploids, clones A07781-10lb (Figure 13) and TX12484-3W (Figure 16) had the best characteristics combining both ZC chip score < 2.0, chip quality score < 2.5, chip difference (infested – non-infested < 1), and better chip quality score than the best check variety which was Waneta. Clone TX12484-2W (Figure 15) had similar chip quality score, ZC chip score, and chip difference as the Waneta check. The mean ZC score for the experiment was 0.9 and the mean percentage of ZC was 12.2% for all the clones (Table 4).

Among diploids, clones CC804-01, CC805-01, CC813-02, CC831-03 (Figure 18), DD812-02 (Figure 19), DD853-02 (Figure 20) had the best characteristics combining both ZC chip score < 2.0, chip quality score < 2.5, chip difference (infested – non-infested < 1), and better chip quality score than the best check variety which was Waneta. The mean ZC score for the experiment was 0.8 and the mean percentage of ZC was 13.1% for all the clones. (Table 4).

In the NCPT, three clones AC01151-5W, NY 121, and W 8822-1 had the best characteristics combining both ZC chip score < 2.0, chip quality score < 2.5, chip difference (infested – non-infested < 1). The mean ZC score for the experiment was 0.8 and the mean percentage of ZC was 8.9% for all the clones (Table 4).

Incidence of ZC (percentage of tubers with ZC in the whole experiment) was 18.3% (diploids 19.9%, tetraploids 21.5%, and NCPT 14.0%). Mixed model comparisons for infested and non-infested traits indicated significant differences in good chips percentage and chip quality. No significant differences were observed between infested and non-infested for average yield g average weight per tuber, or tuber number (Table 3).

3.3 Clones Tolerant in Both the Greenhouse and Field

Fourteen of the tolerant clones in the greenhouse were also tested under field conditions with 71% of those clones tolerant in both field and greenhouse.

Diploid clones: CC831-03 (Figure 18), DD812-02 (Figure 19), DD853-02 (Figure 20) were identified as tolerant in both the greenhouse and field. Diploid clone DD853-02 was identified as highly tolerant because no incidence of ZC symptoms were

observed on the plant or chip in the greenhouse, and chip quality for the infested tubers was close to 1.0 in both the greenhouse and field. Four additional diploid clones (DD851-07, DD847-06, PI 558050 *S. commersonii*, and CC806-02) were identified as tolerant with low ZC score and with good chip quality in the greenhouse. However these clones did not have good chipping quality in the field. Tetraploid clones: A07781-10lb (Figure 13) was the only clone identified as tolerant in both the field and greenhouse. Clone TX12484-2W (Figure 15) was tolerant in the greenhouse and had a similar ZC quality score, ZC chip score, and chip difference as Waneta in the field.

3.4 Correlation of Traits

In the greenhouse, there were strong positive correlations between percentage of ZC symptoms with ZC chip score; and chip quality with ZC chip score, and percent ZC. There was a strong negative correlation between percent ZC and percent good chips and between chip quality and percent good chips. There was a moderately strong negative correlation between percent good chips and ZC chip score. There was a weak correlation between tuber number and average yield; average weight per tuber and average yield; and between insect eggs and percent alive insects. There was a weak negative correlation between average weight per tuber and tuber number (Table 5).

In the field, there were strong positive correlations between percent ZC with ZC chip score. There was strong negative correlation between chip quality and percent good chips. There was moderately strong correlation between chip quality and ZC chip score and percent ZC. There was moderately strong negative correlation between average weight per tuber and tuber number. There was weak correlation between average weight

per tuber and average yield per plant. There was weak negative correlation between percent good chips and ZC chip score and also with percent ZC and percent good chips (Table 6).

Comparing the field and greenhouse, there was a moderately strong correlation between tuber number in the field and greenhouse. There were no other correlations between the field and greenhouse traits for the clones (Table 7).

3.5 Field Validation Study

Chip quality scores of three diploid clones and 13 tetraploids clones including Atlantic and Waneta as checks in the field validation study averaged 3.81 and ranged from 2.31 to 5.0 for all clones. No clones had chip quality scores < 2.0. TX12484-3W had a chip quality score < 2.5 which is considered acceptable chip quality. ZC chip score averaged 3.5, ranging from 1.9 to 5.0. TX12484-3W, CC825-06, and DD853-02 had ZC chip scores < 2.5 which is potentially tolerant (Figure 43). The ZC symptoms on fried tubers were more noticeable than in fresh tubers (Figure 11). These 16 clones had percent ZC on fried tubers with a mean of 87.3% and a range of 50% to 100%. On fresh tubers the percent ZC averaged 51.9% with a range of 0% to 97.9% (Figure 44). RQ values indicating Lso titer ranged from 0.4 to 257.4 in the infested tubers and were 0.0 in the non-infested tubers. DD853-02, A07781-4lb, and TX14710-7W had RQ values much lower than the Atlantic and Waneta checks which may indicated very high tolerance to ZC (Figure 45). In summary, only TX12484-3W (Figure 16) had both acceptable chip quality and a tolerant ZC chip score.

Table 1. Least square means comparisons of chip and yield traits evaluated in infested (psyllids from an Lso infected colony) and non-infested clones (tetraploid and diploid) under greenhouse conditions near Snook, TX in 2017.

	Chip Quality (1-5)	Good Chips (%)	Tubers (no/plant)	Tuber weight (g/tuber)	Yield (g/plant)
Tetraploid					
Infested	2.6	66.3	9.4[z]	9.7	76.1
Non-infested	1.3	88.1	10.5[z]	21.3	155.4
Diploid					
Infested	2.8	56.7	19.1[z]	7.3	116.6
Non-infested	1.6	78.0	20.5[z]	9.6	146.0
All Clones					
Infested	*2.7*	*61.8*	*14.0*[z]	*8.6*	*95.5*
Non-infested	*1.4*	*83.4*	*15.3*[z]	*15.7*	*150.9*

[z]Means (within font color) were not significantly different at $P \leq 0.05$. All other traits were significantly different between infested and non-infested clones.

Table 2. Summary statistics of ZC and insect related traits evaluated in ZC infested tetraploid potato clones and diploid clones screened under greenhouse conditions near Snook, TX in 2017.

Tetraploids	ZC (%)	ZC score (0-5)	Insects alive (%)	Eggs (0-2)
Mean	32.4	2.2	34.0	0.5
St. error	3.3	0.2	3.1	0.1
Min	8.3	0.3	8.3	0.0
Max	64.6	3.8	66.7	1.5
Count	22	22	26	26

Diploids	ZC (%)	ZC score (0-5)	Insects alive (%)	Eggs (0-2)
Mean	37.5	2.1	38.0	0.8
St. error	5.1	0.3	4.2	0.1
Min	0.0	0.0	0.0	0.0
Max	92.7	4.5	66.7	2.0
Count	23	23	24	24

Table 3. Least square means comparisons of chip and yield traits evaluated infested (psyllids from an Lso infected colony) and non-infested clones (tetraploid, diploid and from the National Chip Processing Trails – NCPT) under field conditions near Springlake, TX in 2017.

	Chip Quality (1-5)	Good Chips (%)	Tubers (no/plant)	Tuber Weight (g/tuber)	Yield (g/plant)
Tetraploid					
Infested	2.5	48.2	10.2[z]	53.4[z]	532.4[z]
Non-infested	1.9	76.2	12.0[z]	55.7[z]	669.4[z]
Diploid					
Infested	2.8	48.1	24.5	20.1[z]	402.9
Non-infested	2.4	69.4	30.2	22.8[z]	581.1
NCPT					
Infested	2.4	56.0	11.0[z]	69.4	697.3
Non-infested	1.9	70.2	9.0[z]	59.3	528.8
All Clones					
Infested	*2.5*	*50.8*	*14.9*[z]	*48.5*[z]	*548.4*[z]
Non-infested	*2.1*	*72.0*	*16.6*[z]	*46.8*[z]	*592.5*[z]

[z]Means (within font color) were not significantly different at $P \leq 0.05$. All other traits were significantly different between infested and non-infested clones.

Table 4. Summary statistics of ZC and insect related traits evaluated in ZC infested tetraploid, diploid, and NCPT potato clones screened under field conditions near Springlake, TX in 2017.

Tetraploids	ZC (%)	ZC score (0-5)	Insects alive (%)	Eggs (0-2)
Mean	12.2	0.9	18.7	0.1
St. error	2.8	0.2	5.0	0.0
Min	0.0	0.0	0.0	0.0
Max	40.0	2.5	83.3	0.7
Count	23	23	23	23

Diploids	ZC (%)	ZC score (0-5)	Insects alive (%)	Eggs (0-2)
Mean	13.1	0.8	9.0	0.1
St. error	3.1	0.2	2.3	0.0
Min	0.0	0.0	0.0	0.0
Max	43.3	2.5	33.3	0.5
Count	20	20	20	20

NCPT	ZC (%)	ZC score (0-5)	Insects alive (%)	Eggs (0-2)
Mean	8.9	0.8	15.7	0.0
St. error	2.8	0.2	3.3	0.0
Min	0.0	0.0	0.0	0.0
Max	40.0	3.8	41.7	0.8
Count	22	22	21	21

Table 5. Pearson correlations (r) of chipping traits, insect records and yield parameters of potato clones infested with psyllids from an Lso infected colony under greenhouse conditions near Snook, Texas in 2017.

Correlations†	ZC Chip Score	Percent Good Chips	Percent ZC	Chip Color	Percent Insects Alive	Insect Eggs	Total Weight (g)	Tuber Number	Average Weight (g) Per Tuber
ZC Number of Chips	0.7188	-0.6281	0.8751	0.6984	0.1054	0.1058	0.4578	0.2682	0.1147
ZC Chip Score	---	-0.6129	0.8052	0.8948	0.0903	0.0197	0.1935	0.0065	0.1384
Percent Good Chips		---	-0.7449	-0.762	0.0149	0.0518	-0.1426	0.1095	-0.1947
Percent ZC			---	0.7604	0.0803	0.05	0.2057	0.0359	0.1088
Chip Color				---	0.0206	0.0047	0.2408	-0.0488	0.2325
Percent Insects Alive					---	0.3504	0.1302	0.1565	0.0114
Insect Eggs						---	0.0827	0.0582	-0.0076
Total Weight (g)							---	0.4663	0.4939
Tuber Number								---	-0.3718

†Underlined lines indicate weak ($0.3 < r < 0.5$), moderately strong ($0.5 < r < 0.65$), or very strong ($r > 0.65$) correlations.

Table 6. Pearson correlations (r) of chipping traits, insect records and yield traits of potato clones infested with psyllids from an Lso infected colony under field conditions near Springlake, TX in 2017.

Correlations†	ZC Chip Score	Percent Good Chips	Percent ZC	Chip Color	Percent Insects Alive	Insect Eggs	Total Weight (g)	Tuber Number	Average Weight (g) Per Tuber
ZC Number of Chips	0.8723	-0.4325	0.9244	0.6088	0.0649	0.2257	0.0637	0.0464	-0.0008
ZC Chip Score	---	-0.3945	0.8686	0.6271	0.125	0.1992	0.0588	-0.0317	0.0477
Percent Good Chips		---	-0.4724	-0.7212	-0.0956	-0.1134	0.0057	0.0319	0.0398
Percent ZC			---	0.5696	0.1081	0.2908	-0.037	-0.0514	0.0026
Chip Color				---	0.0507	0.1045	0.091	0.0779	-0.0662
Percent Insects Alive					---	0.2764	0.1873	0.0719	0.1165
Insect Eggs						---	0.0506	0.1032	-0.0822
Total Weight (g)							---	0.2962	0.4489
Tuber Number								---	-0.5052

†Underlined lines indicate weak ($0.3 < r < 0.5$), moderately strong ($0.5 < r < 0.65$), or very strong ($r > 0.65$) correlations.

Table 7. Pearson correlations (r) of field and greenhouse chipping traits, insect records and yield traits of potato clones infested with psyllids from an Lso infected colony in 2017.

Field†	Greenhouse ZC Chip Score	Percent Good Chips	Percent ZC	Chip Color	Percent Insects Alive	Insect Eggs	Total Weight (g)	Tuber Number	Average Weight (g) Per Tuber
ZC Chip Score	-0.1016	0.0873	-0.1555	-0.1109	0.0241	0.1018	-0.1081	-0.0285	-0.0793
Percent Good Chips	-0.015	0.0224	0.0451	-0.013	0.1984	0.0592	0.1857	0.1123	0.0855
Percent ZC	-0.1229	0.1416	-0.2006	-0.1379	-0.0163	0.103	-0.1201	0.0155	-0.1002
Chip Color	0.0179	-0.0975	-0.0079	0.0333	-0.0184	0.0811	-0.1645	-0.0968	-0.1043
Percent Insects Alive	0.0147	-0.0273	0.0018	0.0361	-0.179	-0.1023	-0.1328	-0.0088	-0.0794
Insect Eggs	-0.0462	-0.0545	-0.0041	-0.0447	-0.0038	0.0621	-0.1008	0.0344	-0.126
Total Weight (g)	-0.0334	0.0213	-0.0347	-0.0492	-0.0961	-0.195	-0.0181	-0.0792	0.0261
Tuber Number	0.1425	-0.1491	0.1496	0.1082	0.0888	0.0356	0.2768	0.5809	-0.2802
Average Weight (g) Per Tuber	-0.1237	0.1494	-0.1361	-0.1059	-0.225	-0.2501	-0.1446	-0.349	0.2186

†Underlined lines indicate weak ($0.3 < r < 0.5$), moderately strong ($0.5 < r < 0.65$), or very strong ($r > 0.65$) correlations.

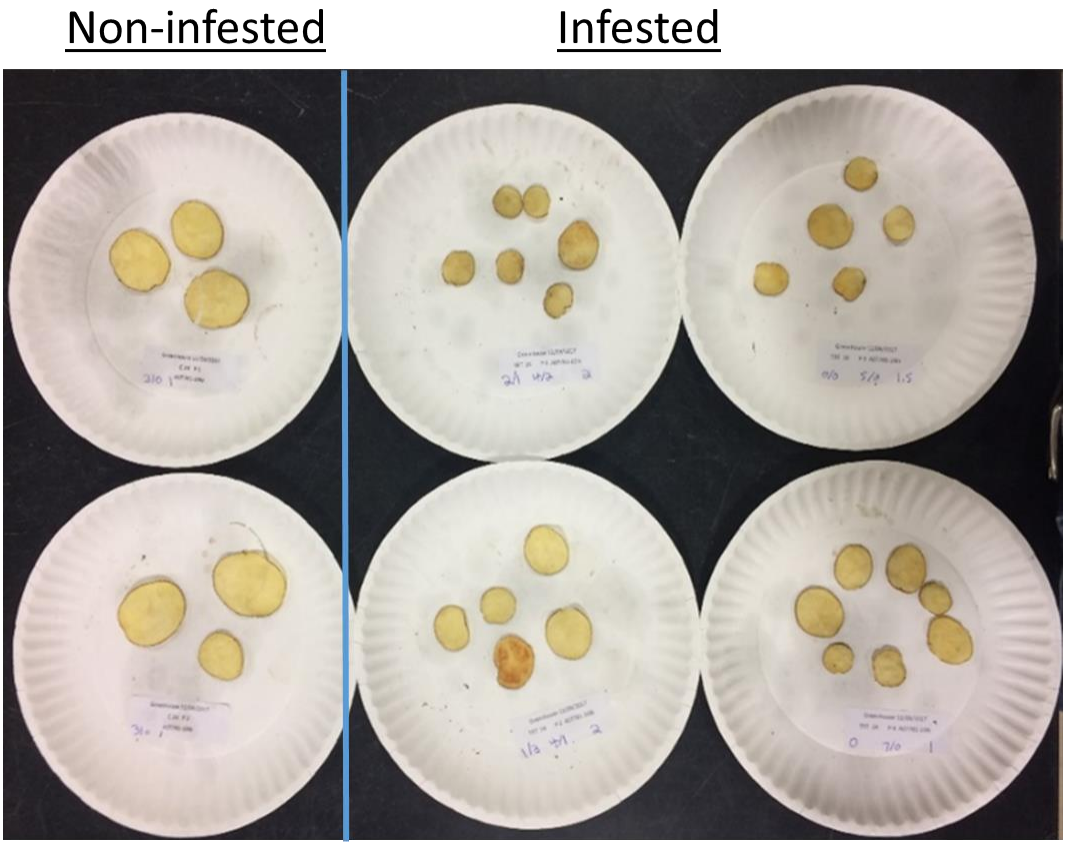

Figure 13. Potato chips of the ZC tolerant tetraploid clone A07781-10lb from non-infested and infested tests

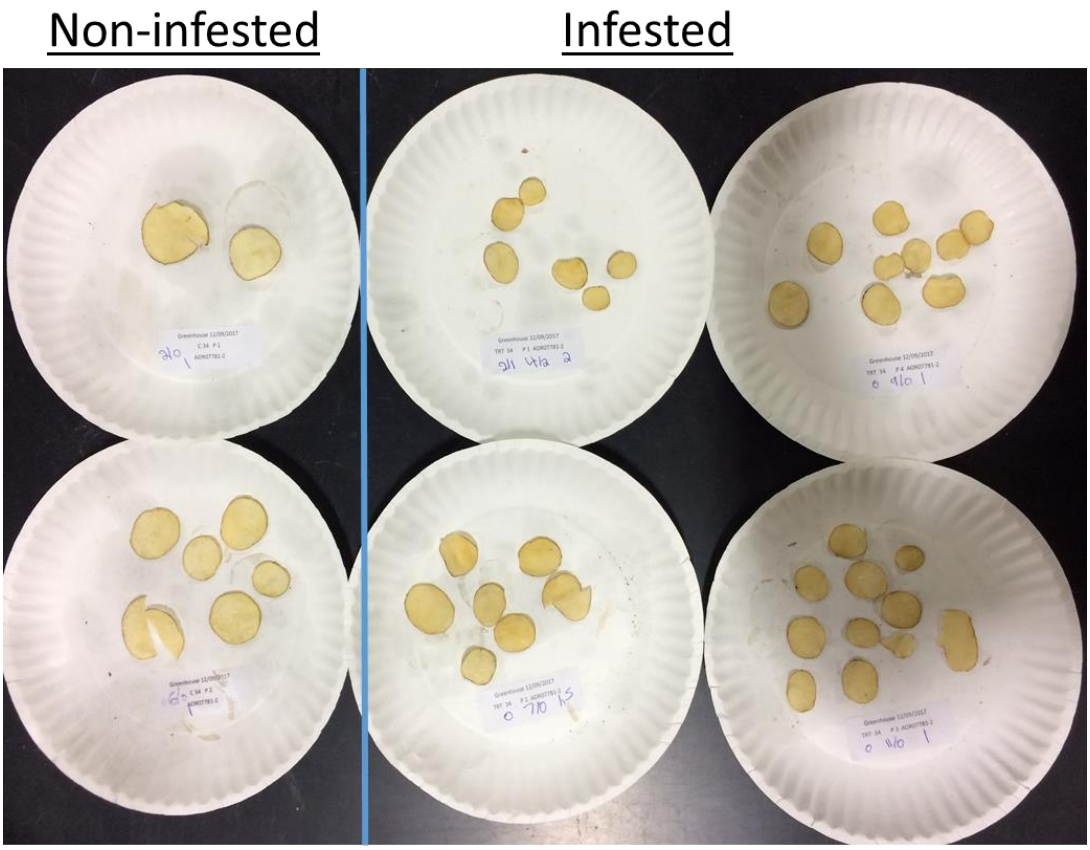

Figure 14. Potato chips of the ZC tolerant tetraploid clone AOR07781-2 from non-infested and infested tests

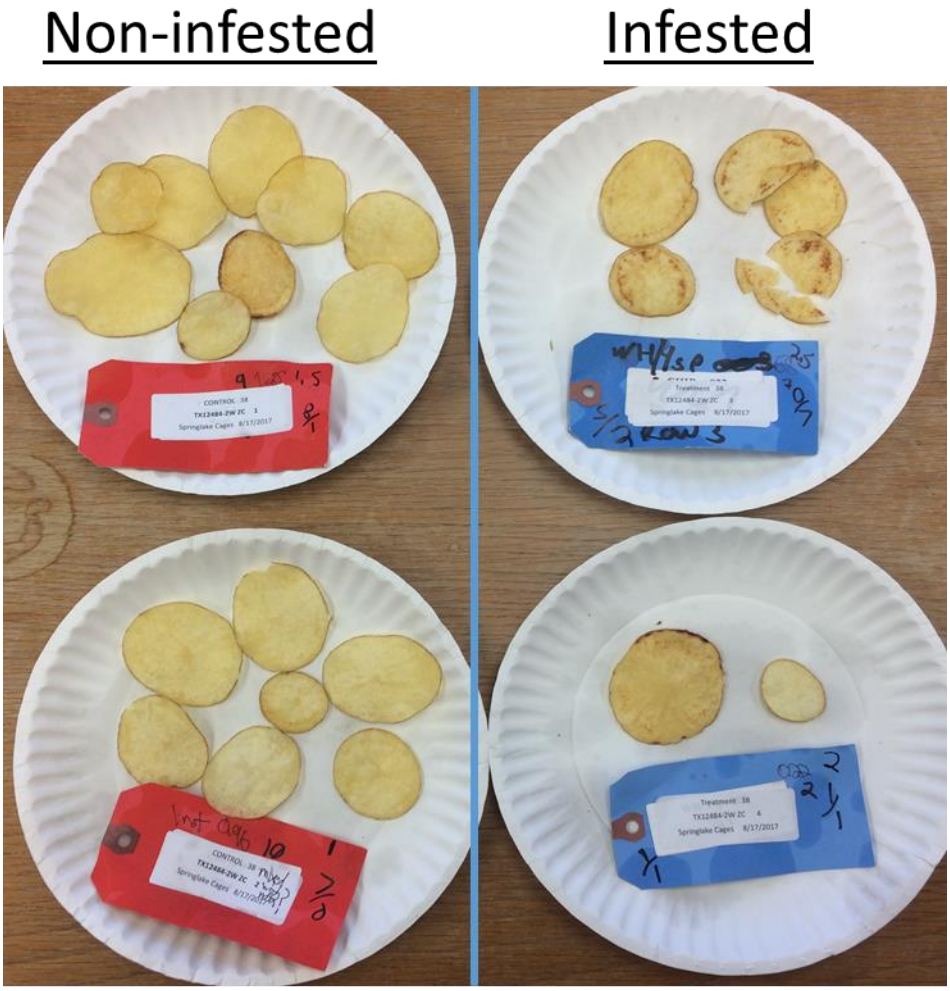

Figure 15. Potato chips of the ZC tolerant tetraploid clone TX12484-2W from non-infested and infested tests

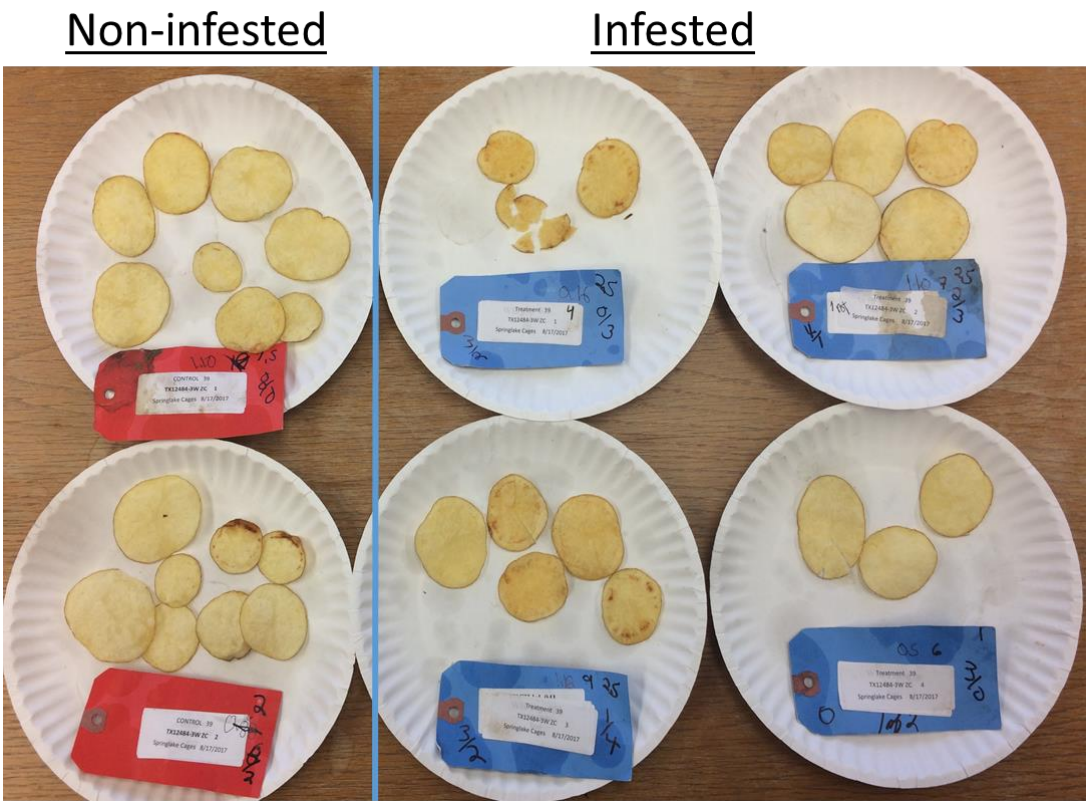

Figure 16. Potato chips of the ZC tolerant tetraploid clone TX12484-3W from non-infested and infested tests

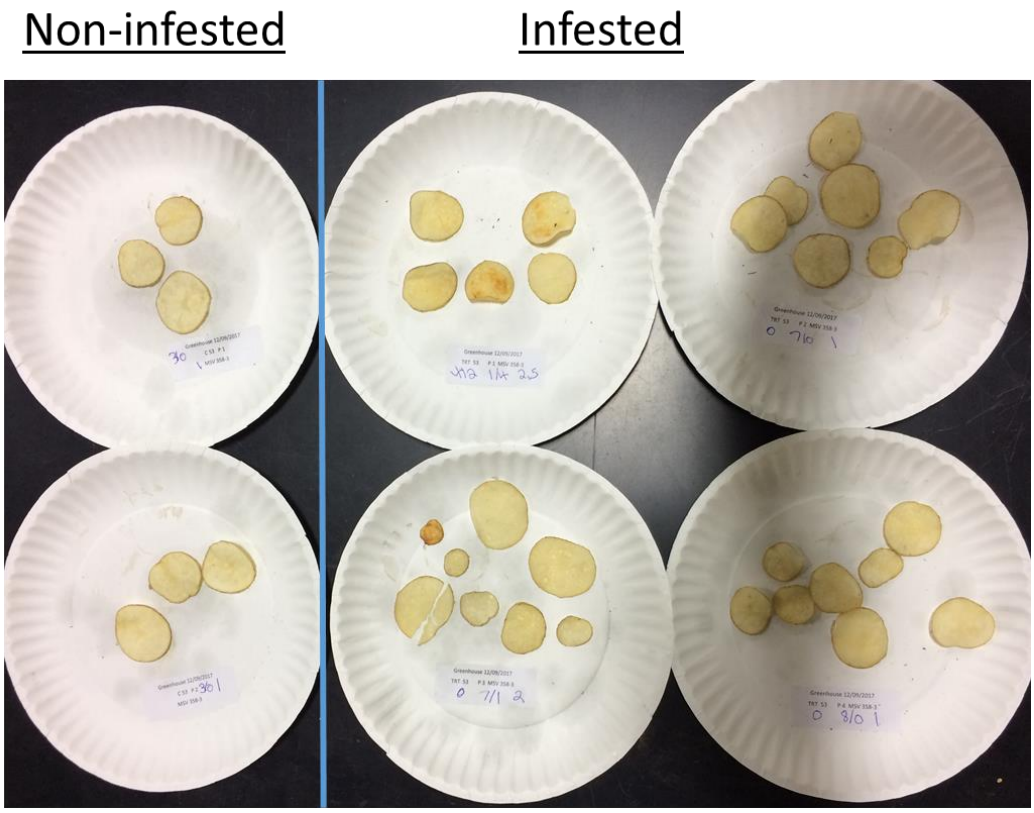

Figure 17. Potato chips of the ZC tolerant tetraploid clone MSV 385-3 from non-infested and infested tests

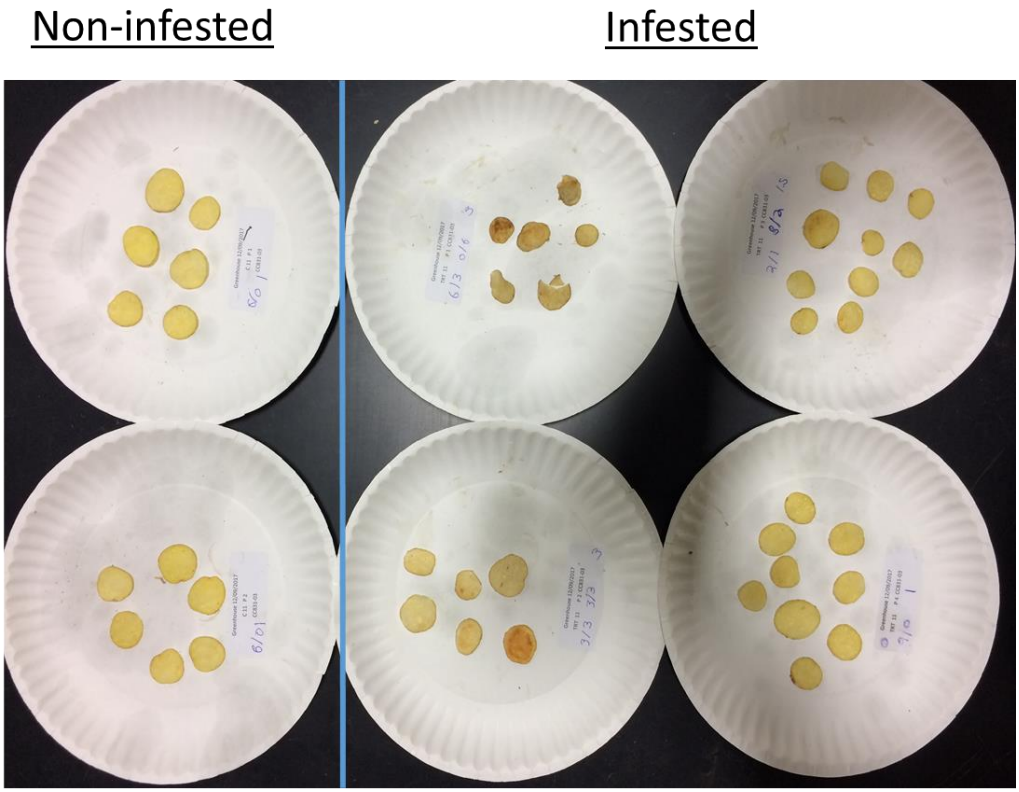

Figure 18. Potato chips of the ZC tolerant diploid clone CC831-03 from non-infested and infested tests

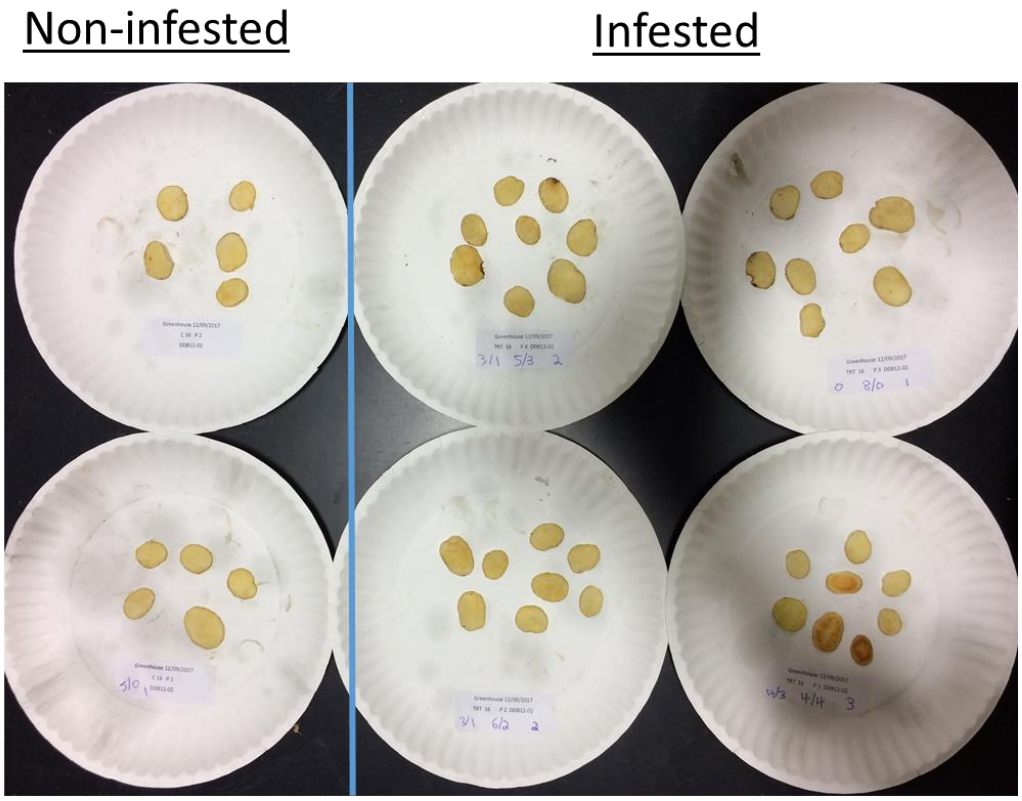

Figure 19. Potato chips of the ZC tolerant diploid clone DD812-02 from non-infested and infested tests

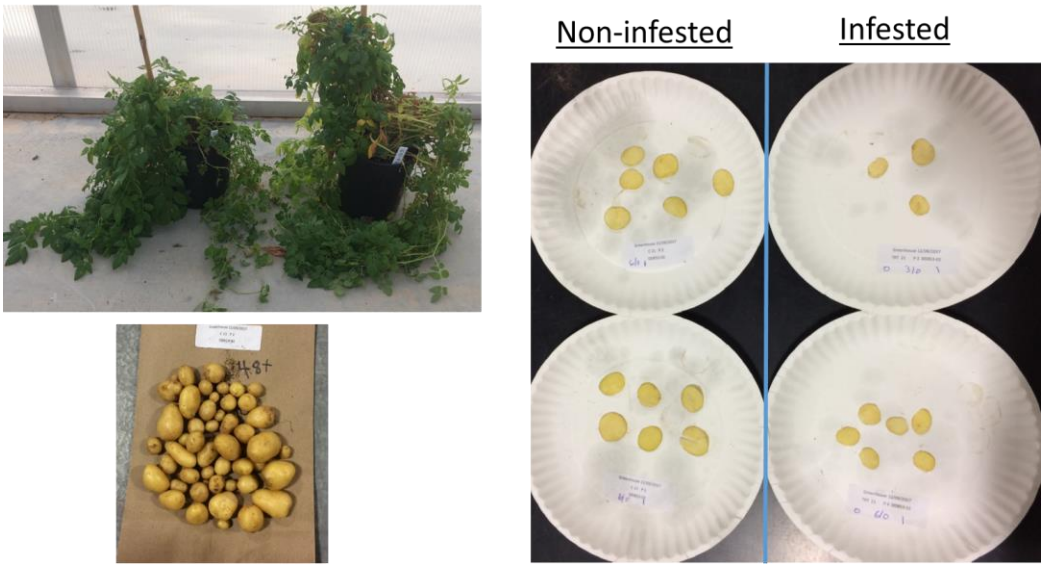

Figure 20. Plants, tubers, and potato chips from non-infested and infested tests of the ZC tolerant diploid clone DD853-02

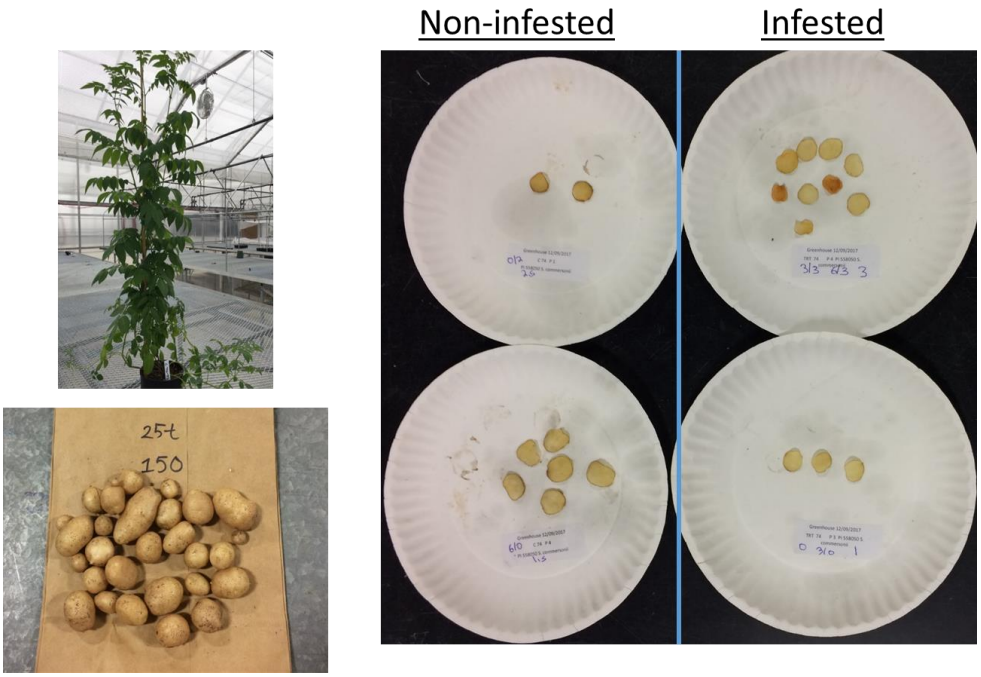

Figure 21. Plants, tubers, and potato chips from non-infested and infested tests of the ZC tolerant diploid clone *S. commersonii*

Figure 22. Plants, tubers, and potato chips from non-infested and infested tests of the ZC tolerant diploid *berthaultii*

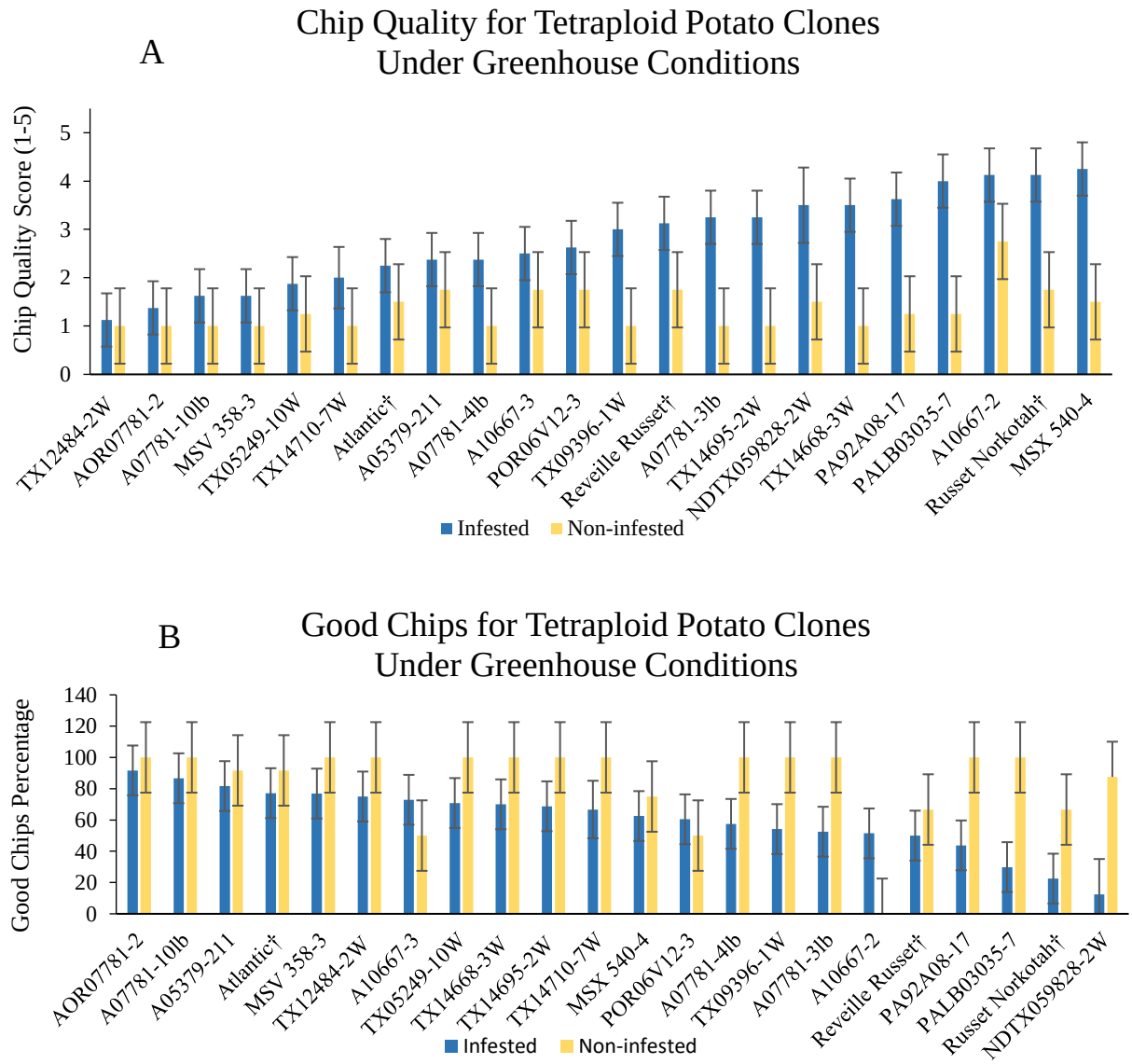

Figure 23. Quality of chips for tetraploid potato clones grown under greenhouse conditions near Snook, TX in 2017. Average chip quality scores (1 = light chip, 5 = very dark chip) (A), and percentage of good chips (no defects) (B) from infested (psyllids from an Lso infected colony) and non-infested tubers fried immediately after harvest. Values are least square means ± standard error. Clones were sorted from left to right with best chip quality (A) on the left and highest percentage of good chips (B) on the left. Atlantic† was used as the standard chipping variety check. Russet Norkotah† and Reveille Russet† were used as additional tetraploid checks.

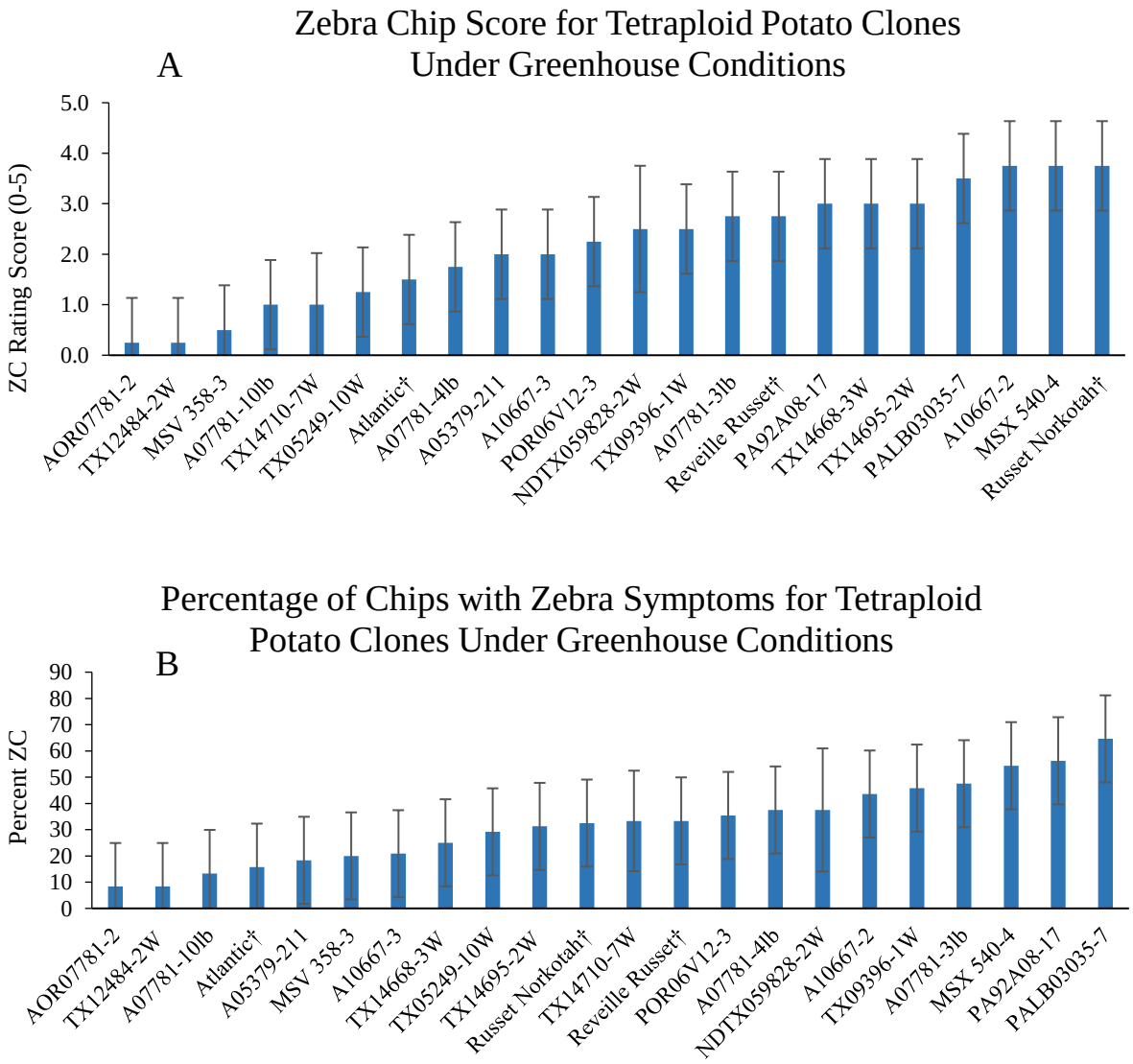

Figure 24. Level of ZC damage for tetraploid potato clones grown under greenhouse conditions near Snook, TX in 2017. Average ZC chip scores (0 = no symptoms, 5 = severe symptoms) (A) and average percentage of chips with zebra symptoms per plant (B) from infested (psyllids from an Lso infected colony) tubers fried immediately after harvest. Values are least square means ± standard error. Clones were sorted from left to right with lowest ZC score (A) on the left and lowest percent ZC (B) on the left. Atlantic† was used as the standard chipping variety check. Russet Norkotah† and Reveille Russet† were used as additional tetraploid checks.

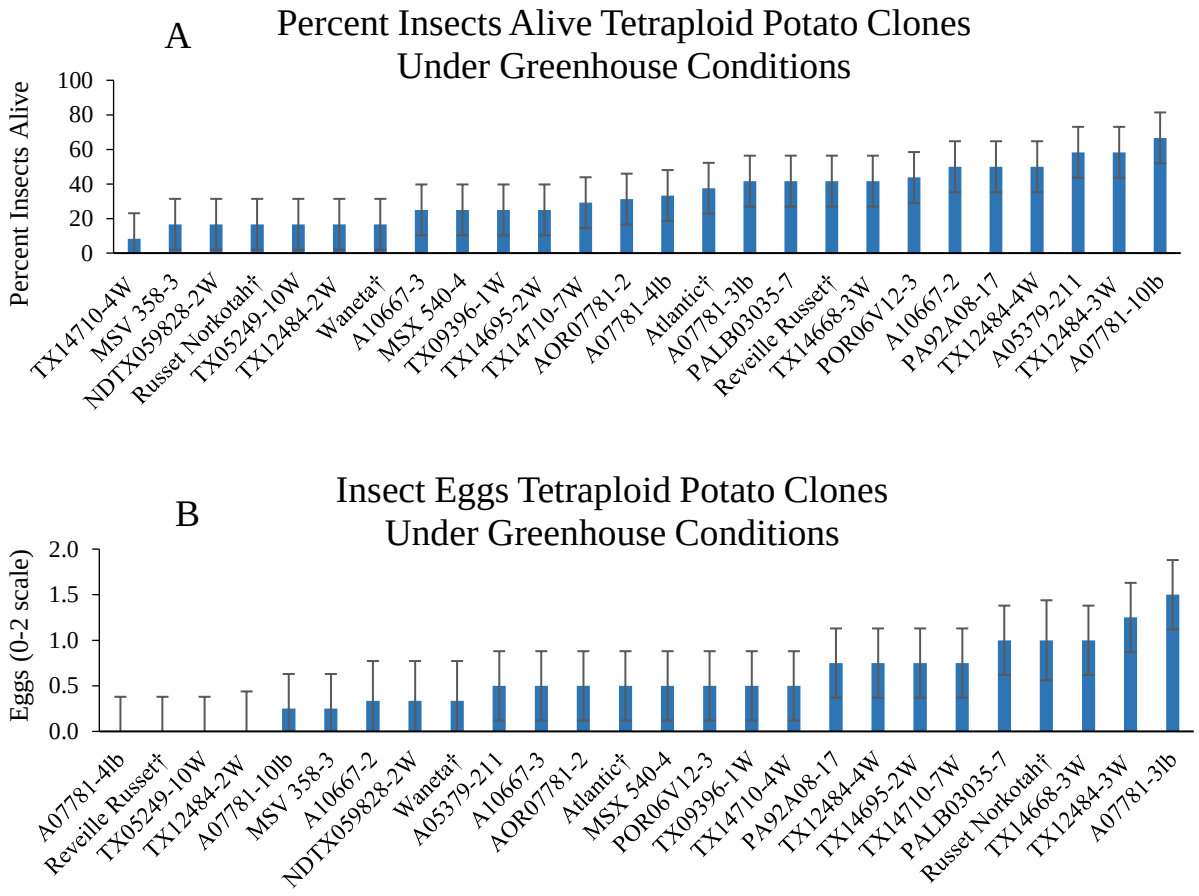

Figure 25. Survival and oviposition of psyllids on plants of tetraploid potato clones grown under greenhouse conditions near Snook, TX in 2017. Average percent insects alive after seven days (A) and insect eggs (0 = no eggs, 1 = few eggs, and 2 = many eggs) per plant (B). Values are least square means ± standard error. Insect egg numbers are shown based on a number code Clones were sorted from left to right for lowest percent insects alive (A) and fewest number of eggs (B). Atlantic† was used as the standard chipping variety check. Russet Norkotah† and Reveille Russet† were used as additional tetraploid checks.

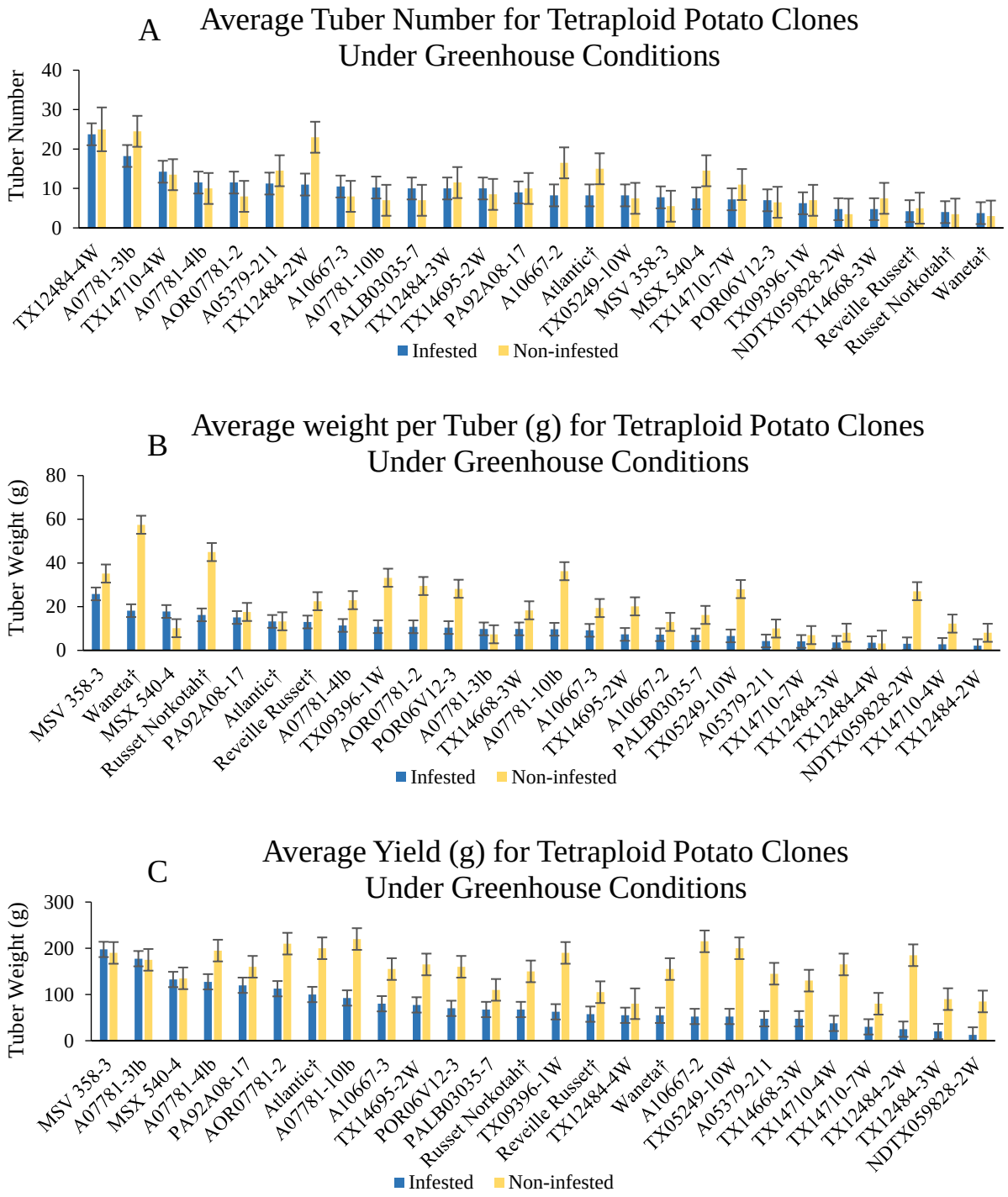

Figure 26. Production and size of tubers of tetraploid potato clones grown under greenhouse conditions near Snook, TX in 2017. Average tuber number per plant (A), Average weight per tuber (B), and average yield per plant (C). Values are least square means ± standard error. Clones were sorted from left to right for highest average tuber number (A), highest average weight per tuber (B), and highest average yield per plant (C). Atlantic† was used as the standard chipping variety check. Russet Norkotah† and Reveille Russet† were used as additional tetraploid checks.

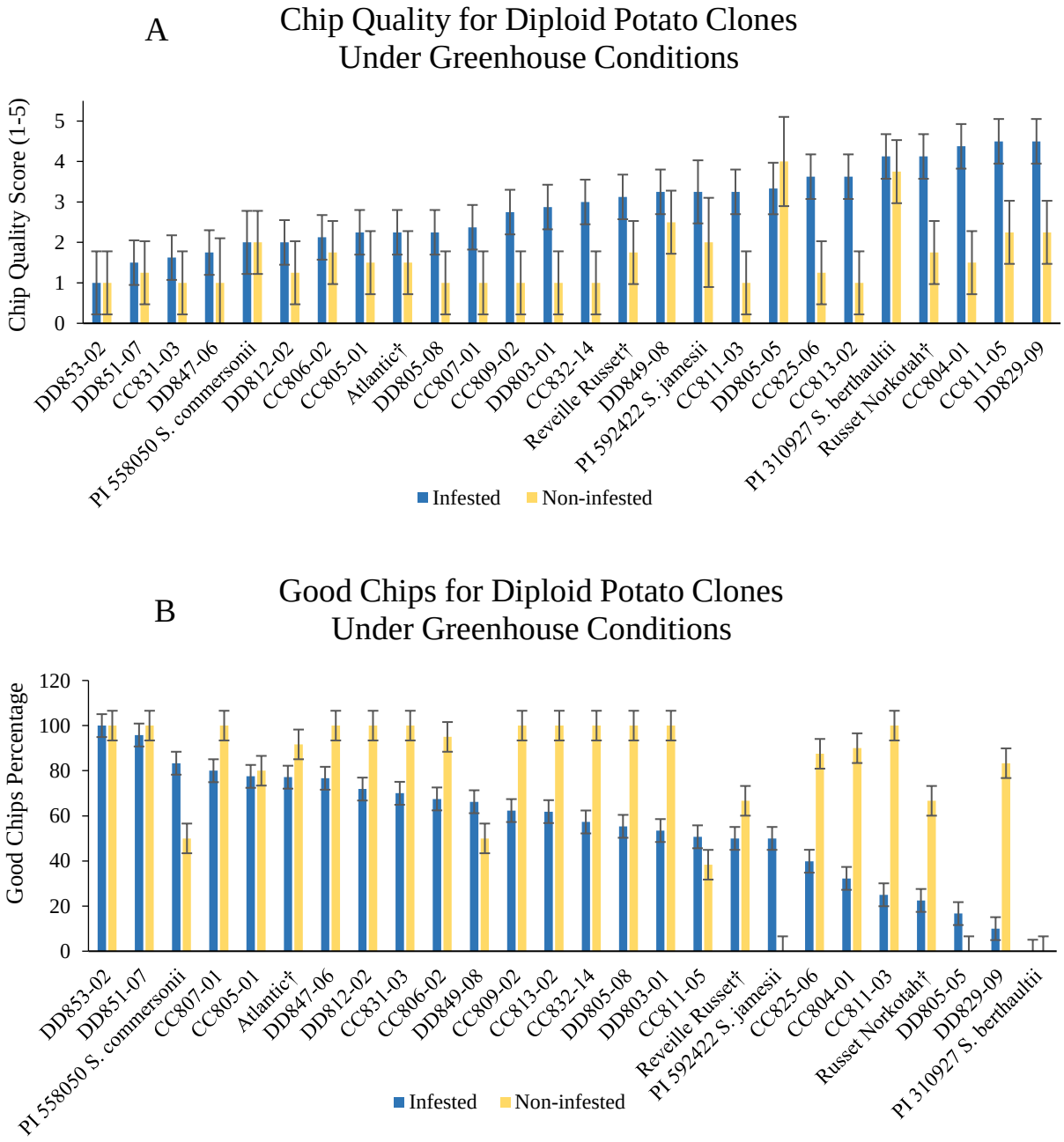

Figure 27. Quality of chips for diploid potato clones grown under greenhouse conditions near Snook, TX in 2017. Average chip quality scores (1 = light chip, 5 = very dark chip) (A) and percentage of good chips (B) from infested (psyllids from an Lso infected colony) and non-infested tubers fried immediately after harvest. Values are least square means ± standard error. Clones were sorted from left to right with best chip quality (A) on the left and highest percentage of good chips (B) on the left. Atlantic† was used as the standard chipping variety check. Russet Norkotah† and Reveille Russet† were used as additional tetraploid checks.

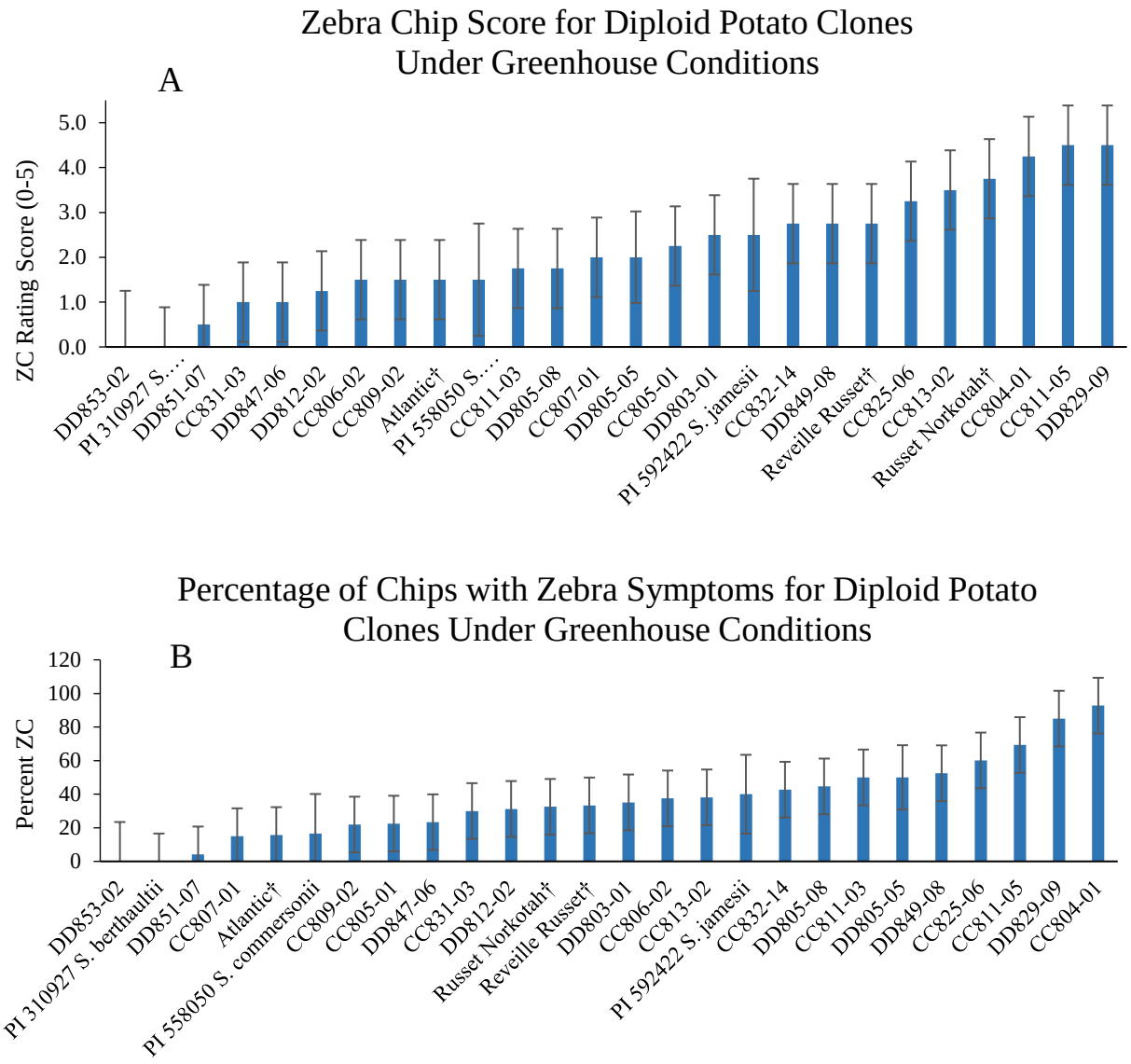

Figure 28. Level of ZC damage for diploid potato clones grown under greenhouse conditions near Snook, TX in 2017. Average ZC chip scores (A) and average percentage of chips with zebra symptoms per plant (B) from infested (psyllids from an Lso infected colony) tubers fried immediately after harvest. Values are least square means ± standard error. Clones were sorted from left to right with lowest ZC score (A) on the left and lowest percent ZC (B) on the left. Atlantic† was used as the standard chipping variety check. Russet Norkotah† and Reveille Russet† were used as additional tetraploid checks.

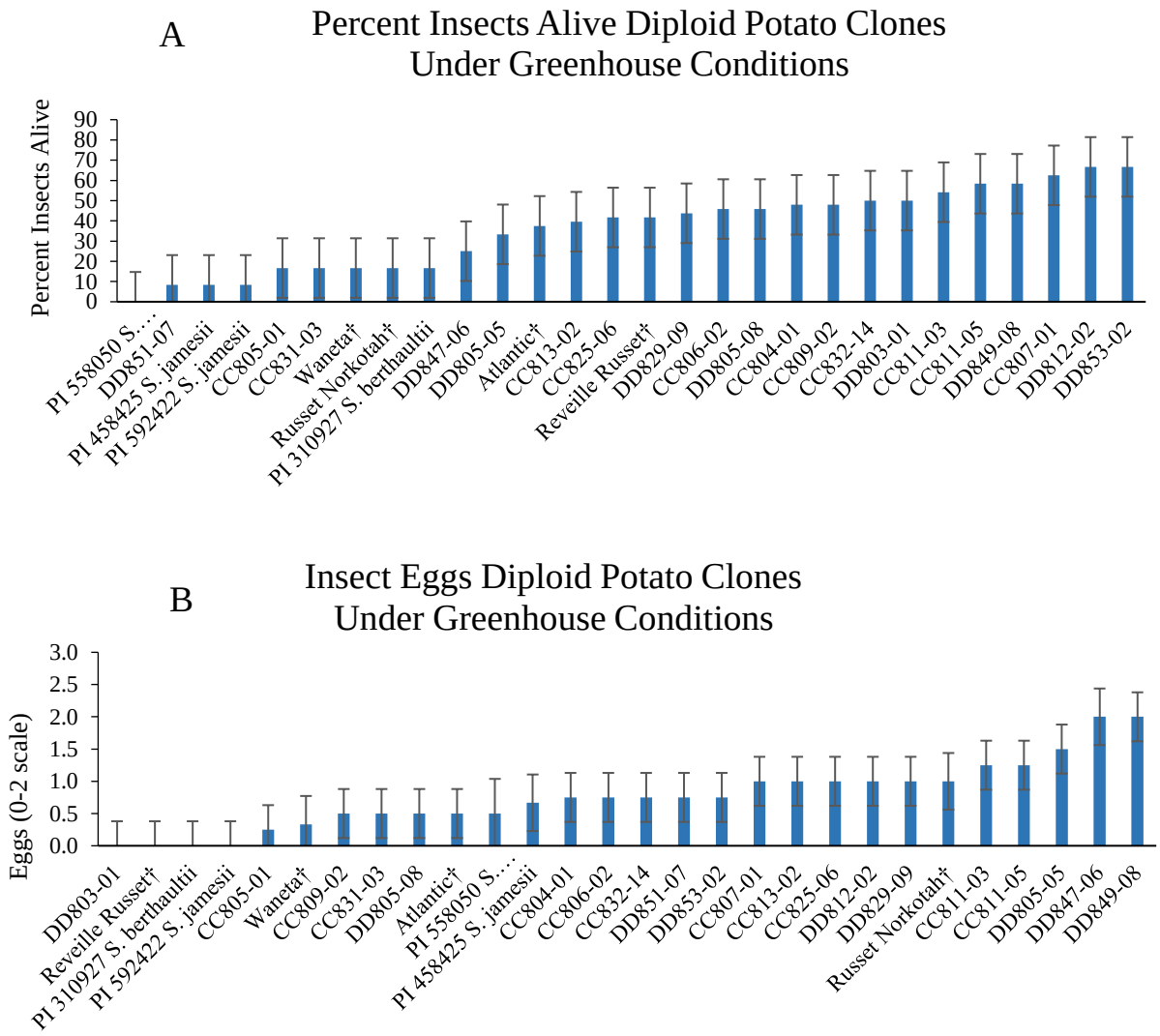

Figure 29. Survival and oviposition of psyllids on plants of diploid potato clones grown under greenhouse conditions near Snook, TX in 2017. Average percent insects alive (A) after seven days and insect eggs per plant (B). Values are least square means ± standard error. Insect egg numbers are shown based on a number code (0 = no eggs, 1 = few eggs, and 2 = many eggs) Clones were sorted from left to right for lowest percent insects alive (A) and fewest number of eggs (B). Atlantic† was used as the standard chipping variety check. Russet Norkotah† and Reveille Russet† were used as additional tetraploid checks

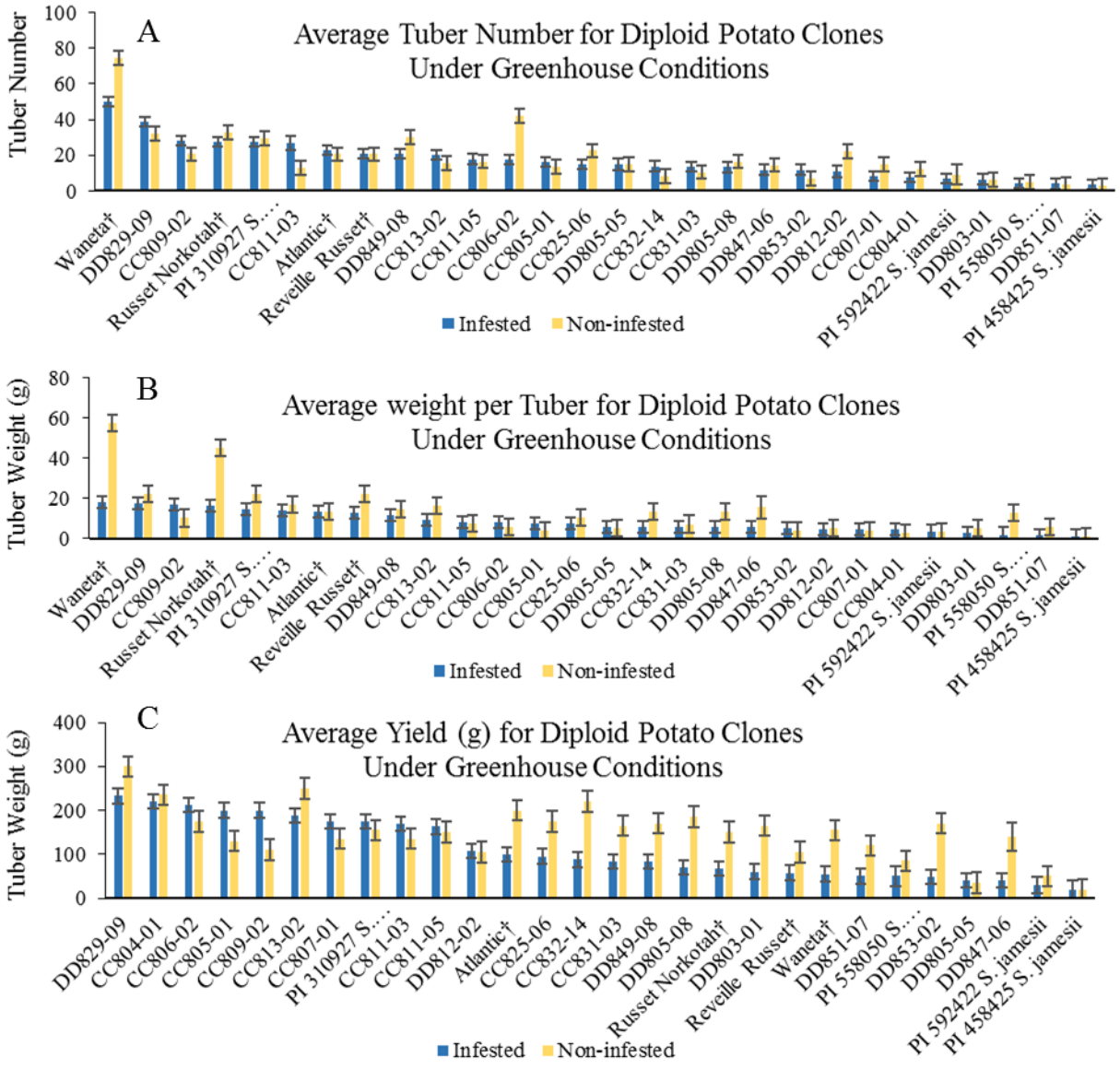

Figure 30. Production and size of tubers of diploid potato clones grown under greenhouse conditions near Snook, TX in 2017. Average tuber number per plant (A), Average weight per tuber (B), and average yield per plant (C). Values are least square means ± standard error. Clones were sorted from left to right for highest average tuber number (A), highest average weight per tuber (B), and highest average yield per plant (C). Atlantic† was used as the standard chipping variety check. Russet Norkotah† and Reveille Russet† were used as additional tetraploid checks.

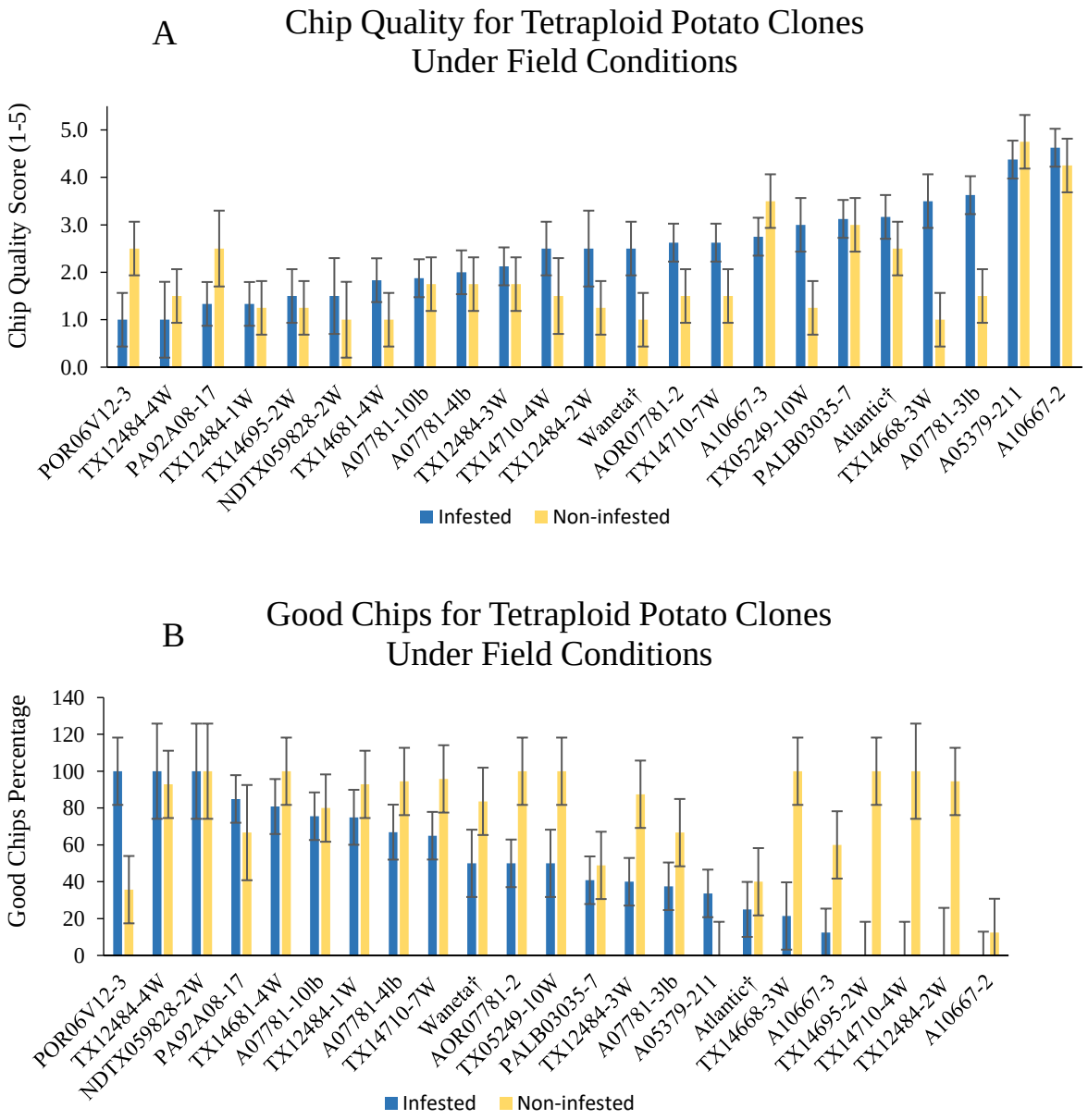

Figure 31. Quality of chips for tetraploid potato clones grown under field conditions near Springlake, TX in 2017. Average chip quality scores (1 = light chip, 5 = very dark chip) (A) and percentage of good chips (B) from infested (psyllids from an Lso infected colony) and non-infested tubers fried immediately after harvest. Values are least square means ± standard error. Clones were sorted from left to right with best chip quality (A) on the left and highest percentage of good chips (B) on the left. Atlantic† was used as the standard chipping variety check. Waneta† was used as an additional tetraploid check.

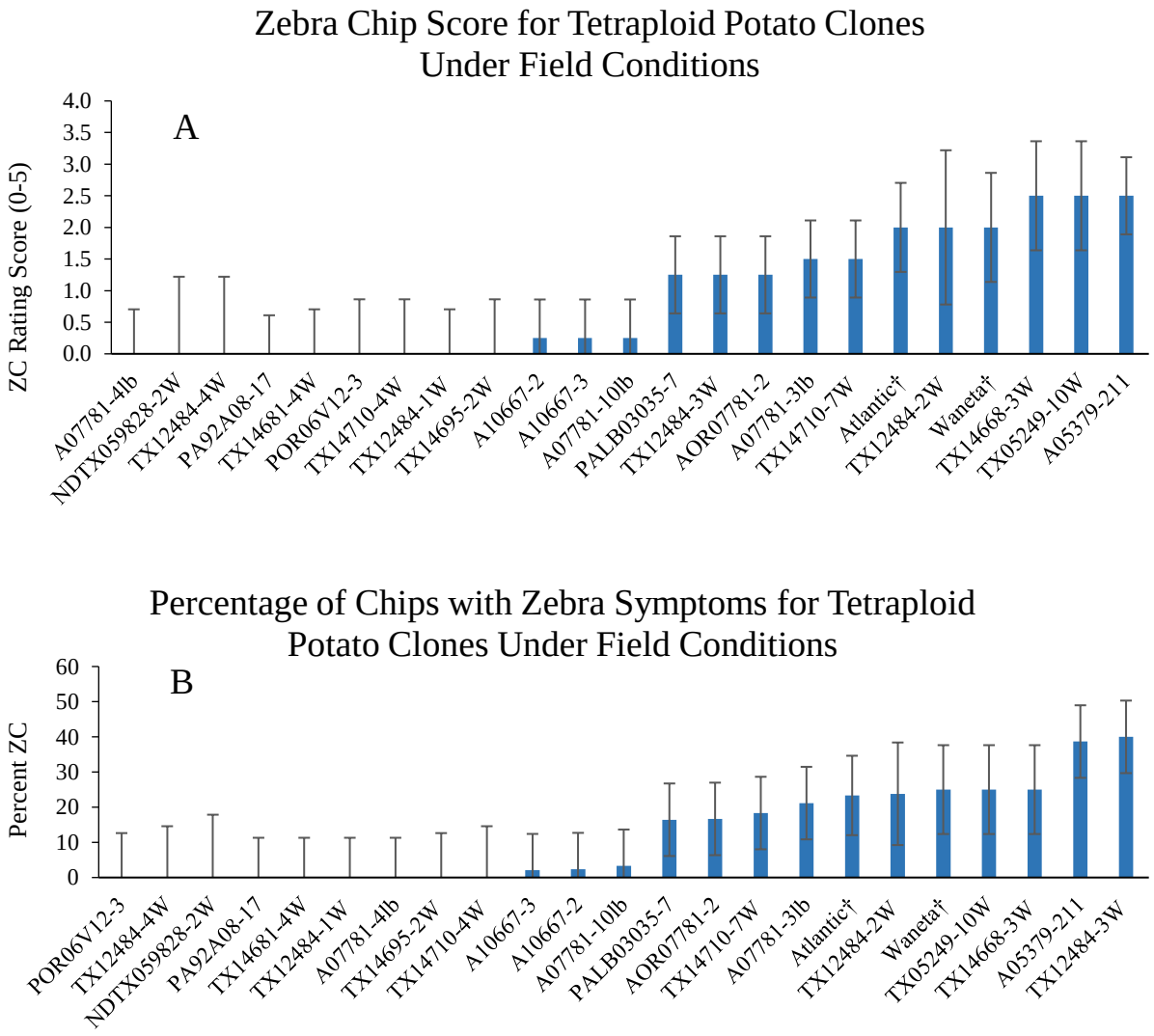

Figure 32. Level of ZC damage for tetraploid potato clones grown under field conditions near Springlake, TX in 2017. Average ZC chip scores (A) and average percentage of chips with zebra symptoms per plant (B) from infested (psyllids from an Lso infected colony) tubers fried immediately after harvest. Values are least square means ± standard error. Clones were sorted from left to right with lowest ZC score (A) on the left and lowest percent ZC (B) on the left. Atlantic† was used as the standard chipping variety check. Waneta† was used as an additional tetraploid check.

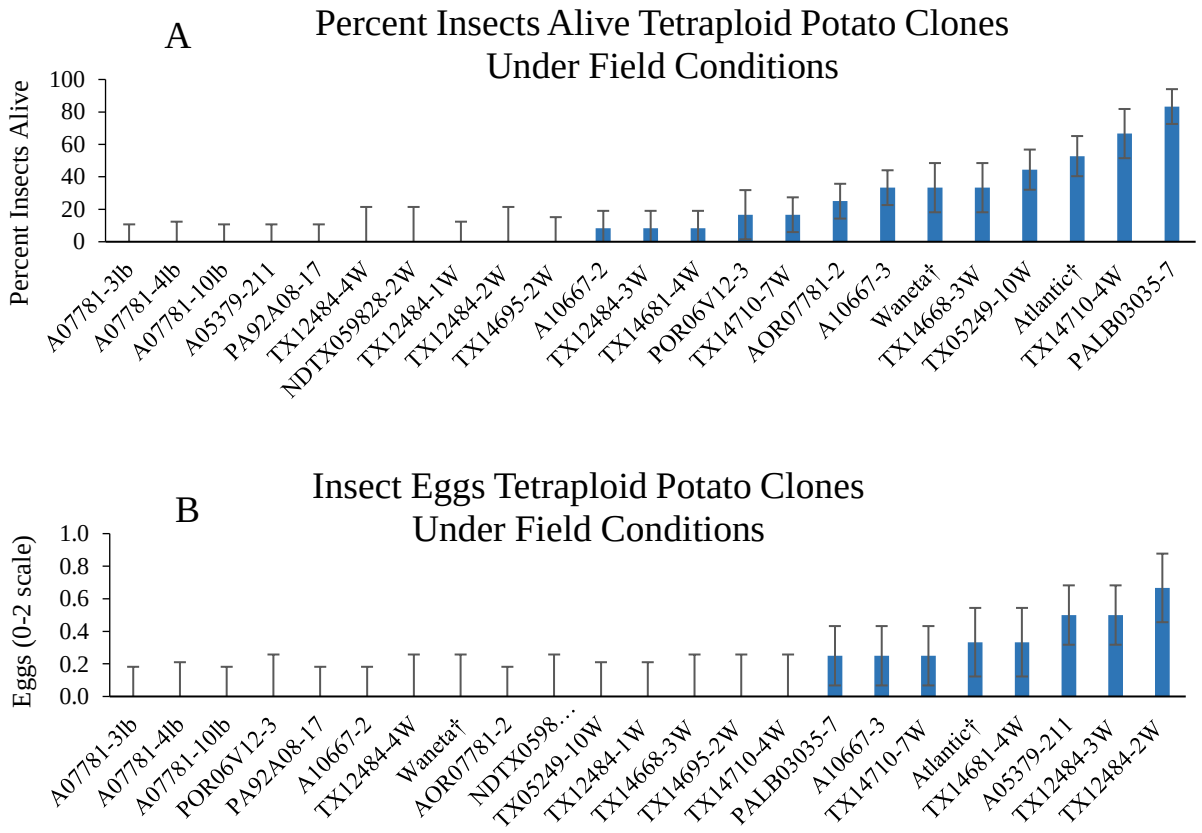

Figure 33. Survival and oviposition of psyllids on plants of tetraploid potato clones grown under field conditions near Springlake, TX in 2017. Average percent insects alive (A) after seven days and insect eggs per plant (B). Values are least square means ± standard error. Insect egg numbers are shown based on a number code (0 = no eggs, 1 = few eggs, and 2 = many eggs) Clones were sorted from left to right for lowest percent insects alive (A) and fewest number of eggs (B). Atlantic† was used as the standard chipping variety check. Waneta† was used as an additional tetraploid check.

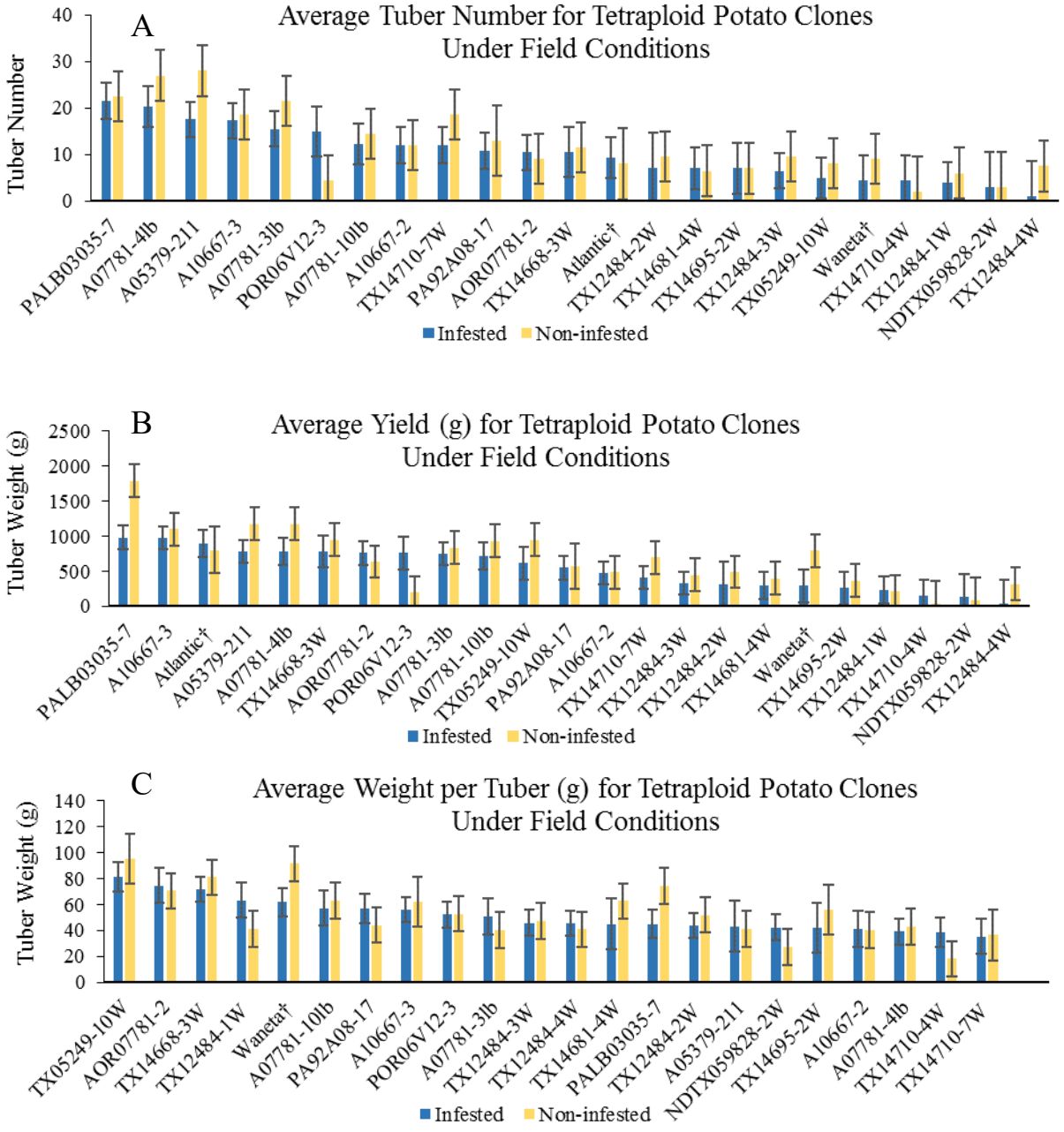

Figure 34. Production and size of tubers of tetraploid potato clones grown under field conditions near Springlake, TX in 2017. Average tuber number per plant (A), Average weight per tuber (B), and average yield per plant (C). Values are least square means ± standard error. Clones were sorted from left to right for highest average tuber number (A), highest average weight per tuber (B), and highest average yield per plant (C). Atlantic† was used as the standard chipping variety check. Waneta† was used as an additional tetraploid check.

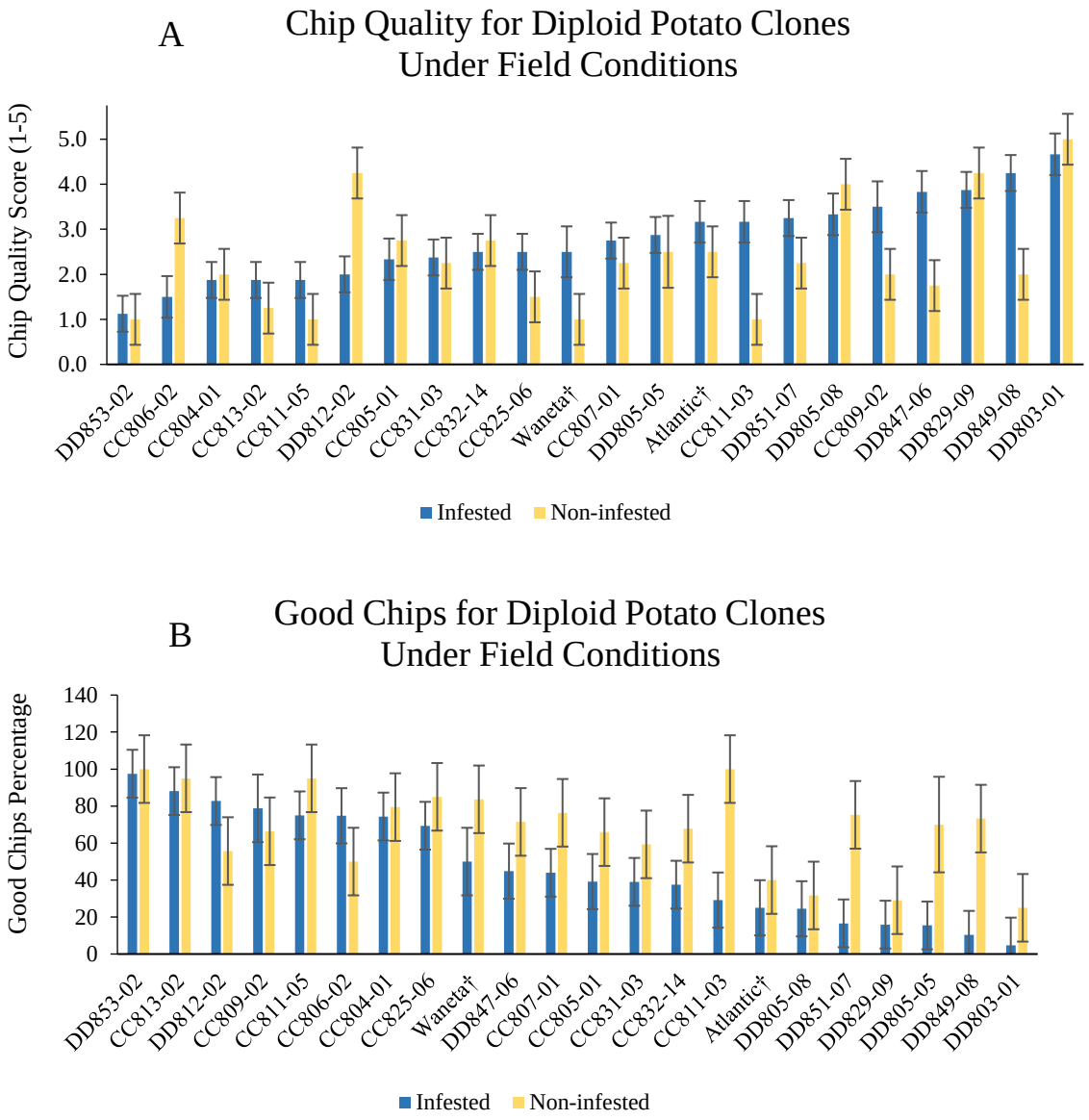

Figure 35. Quality of chips for diploid potato clones grown under field conditions near Springlake, TX in 2017. Average chip quality scores (1 = light chip, 5 = very dark chip) (A) and percentage of good chips (B) from infested (psyllids from an Lso infected colony) and non-infested tubers fried immediately after harvest. Values are least square means ± standard error. Clones were sorted from left to right with best chip quality (A) on the left and highest percentage of good chips (B) on the left. Atlantic† was used as the standard chipping variety check. Waneta† was used as an additional tetraploid check.

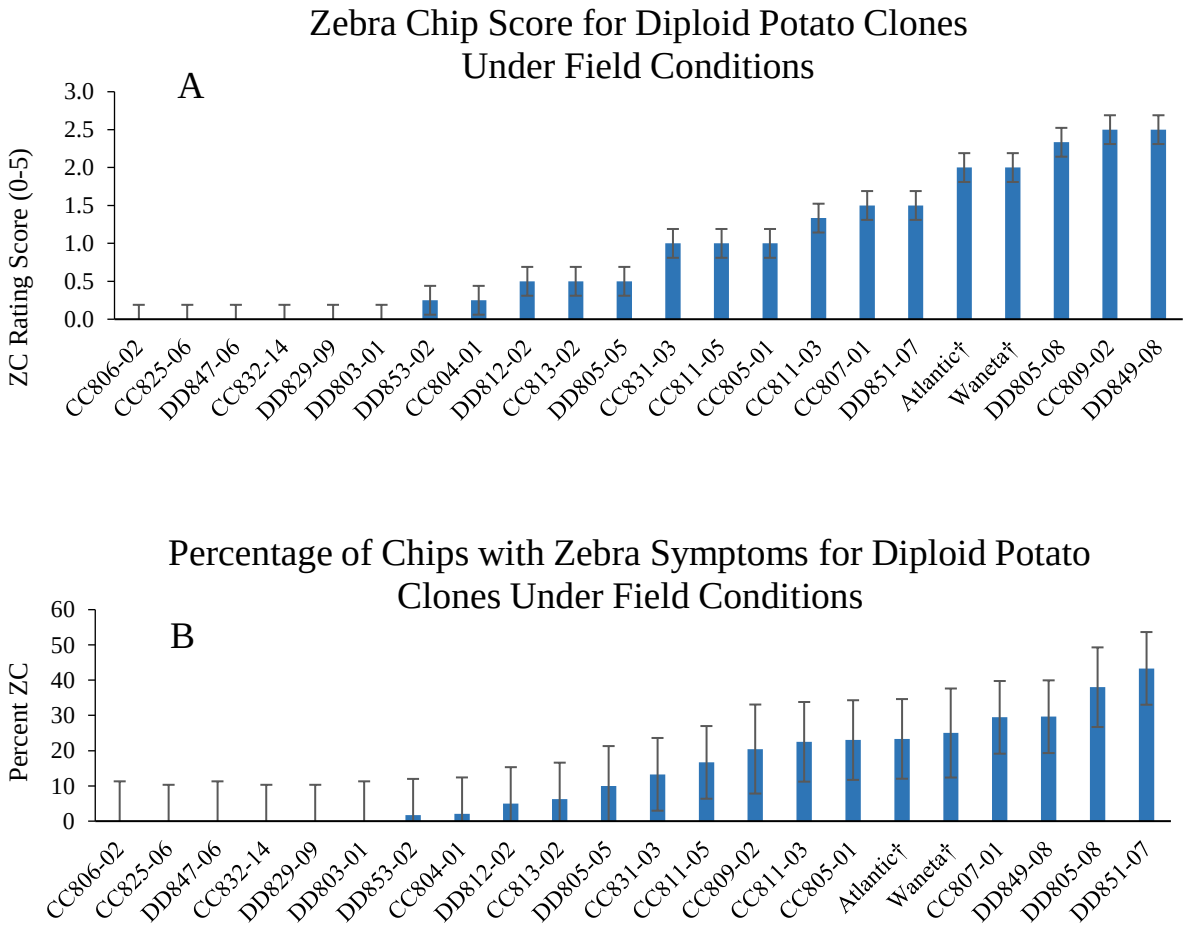

Figure 36. Level of ZC damage for diploid potato clones grown under field conditions near Springlake, TX in 2017. Average ZC chip scores (A) and average percentage of chips with zebra symptoms per plant (B) from infested (psyllids from an Lso infected colony) tubers fried immediately after harvest. Values are least square means ± standard error. Clones were sorted from left to right with lowest ZC score (A) on the left and lowest percent ZC (B) on the left. Atlantic† was used as the standard chipping variety check. Waneta† was used as an additional tetraploid check.

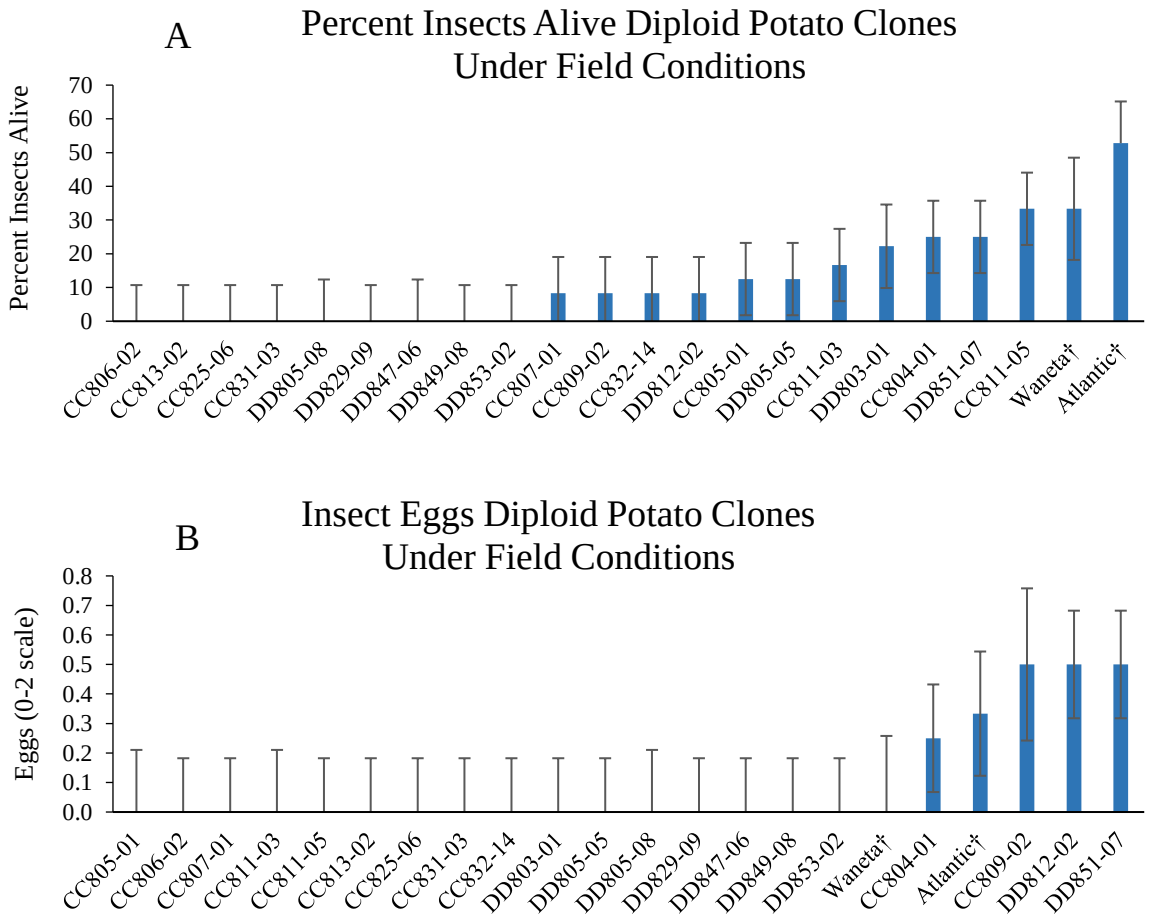

Figure 37. Survival and oviposition of psyllids on plants of diploid potato clones grown under field conditions near Springlake, TX in 2017. Average percent insects alive (A) after seven days and insect eggs per plant (B). Values are least square means ± standard error. Insect egg numbers are shown based on a number code (0 = no eggs, 1 = few eggs, and 2 = many eggs) Clones were sorted from left to right for lowest percent insects alive (A) and fewest number of eggs (B). Atlantic† was used as the standard chipping variety check. Waneta† was used as an additional tetraploid check.

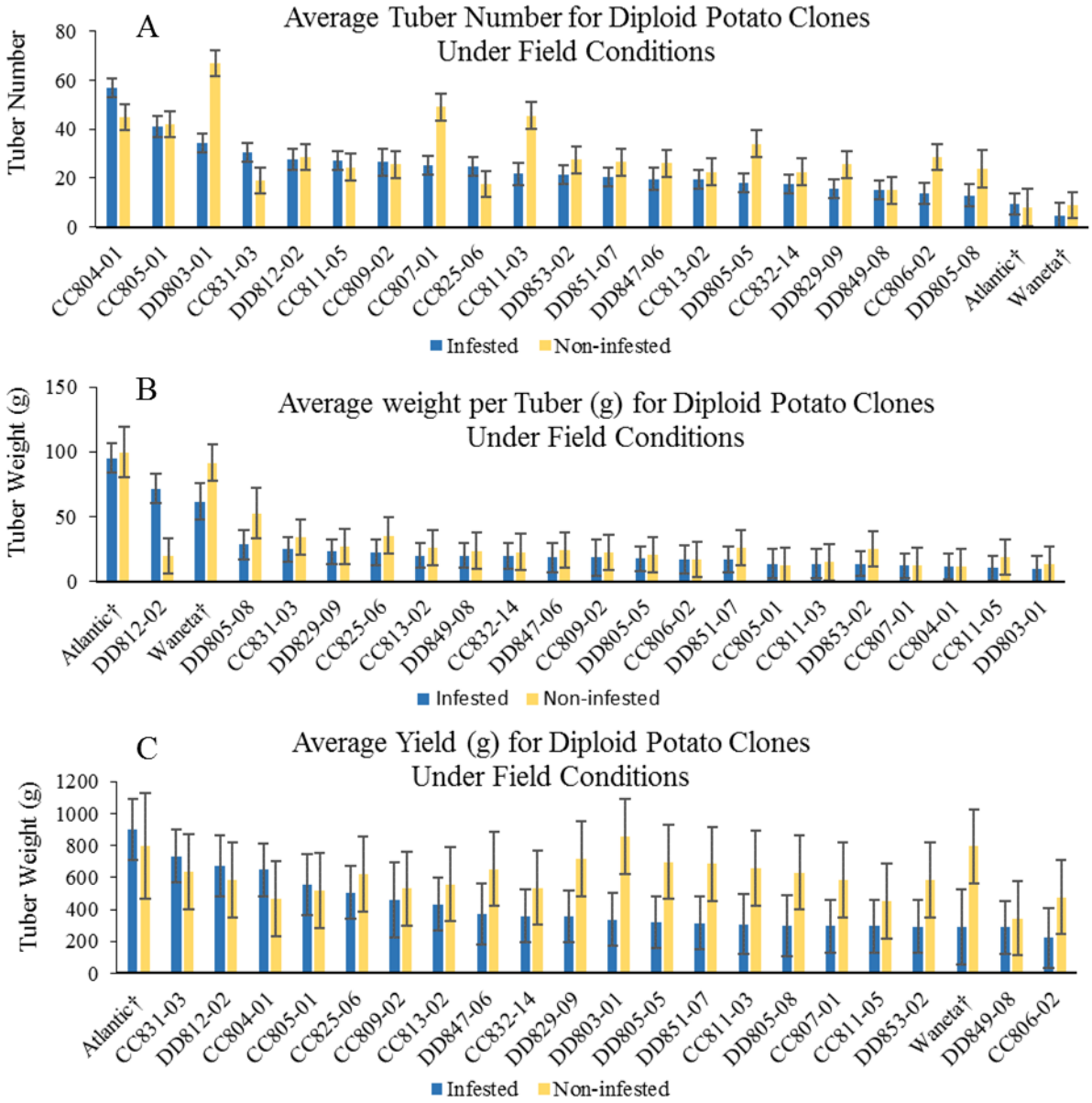

Figure 38. Production and size of tubers of diploid potato clones grown under field conditions near Springlake, TX in 2017. Average tuber number per plant (A), Average weight per tuber (B), and average yield per plant (C). Values are least square means ± standard error. Clones were sorted from left to right for highest average tuber number (A), highest average weight per tuber (B), and highest average yield per plant (C). Atlantic† was used as the standard chipping variety check. Waneta† was used as an additional tetraploid check.

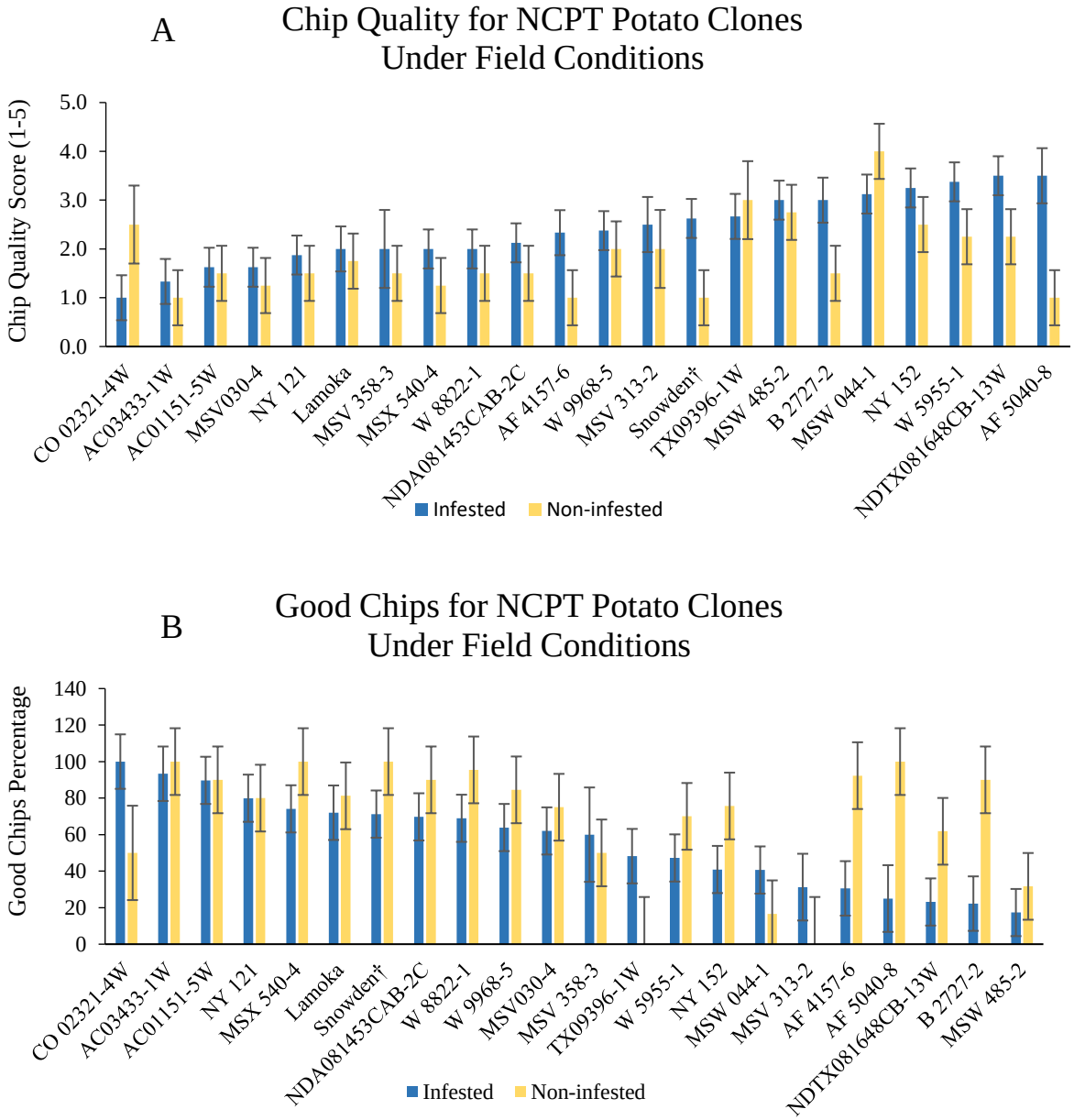

Figure 39. Quality of chips for NCPT potato clones grown under field conditions near Springlake, TX in 2017. Average chip quality scores (1 = light chip, 5 = very dark chip) (A) and percentage of good chips (B) from infested (psyllids from an Lso infected colony) and non-infested tubers fried immediately after harvest. Values are least square means ± standard error. Clones were sorted from left to right with best chip quality (A) on the left and highest percentage of good chips (B) on the left. Snowden† was used as the standard chipping variety check.

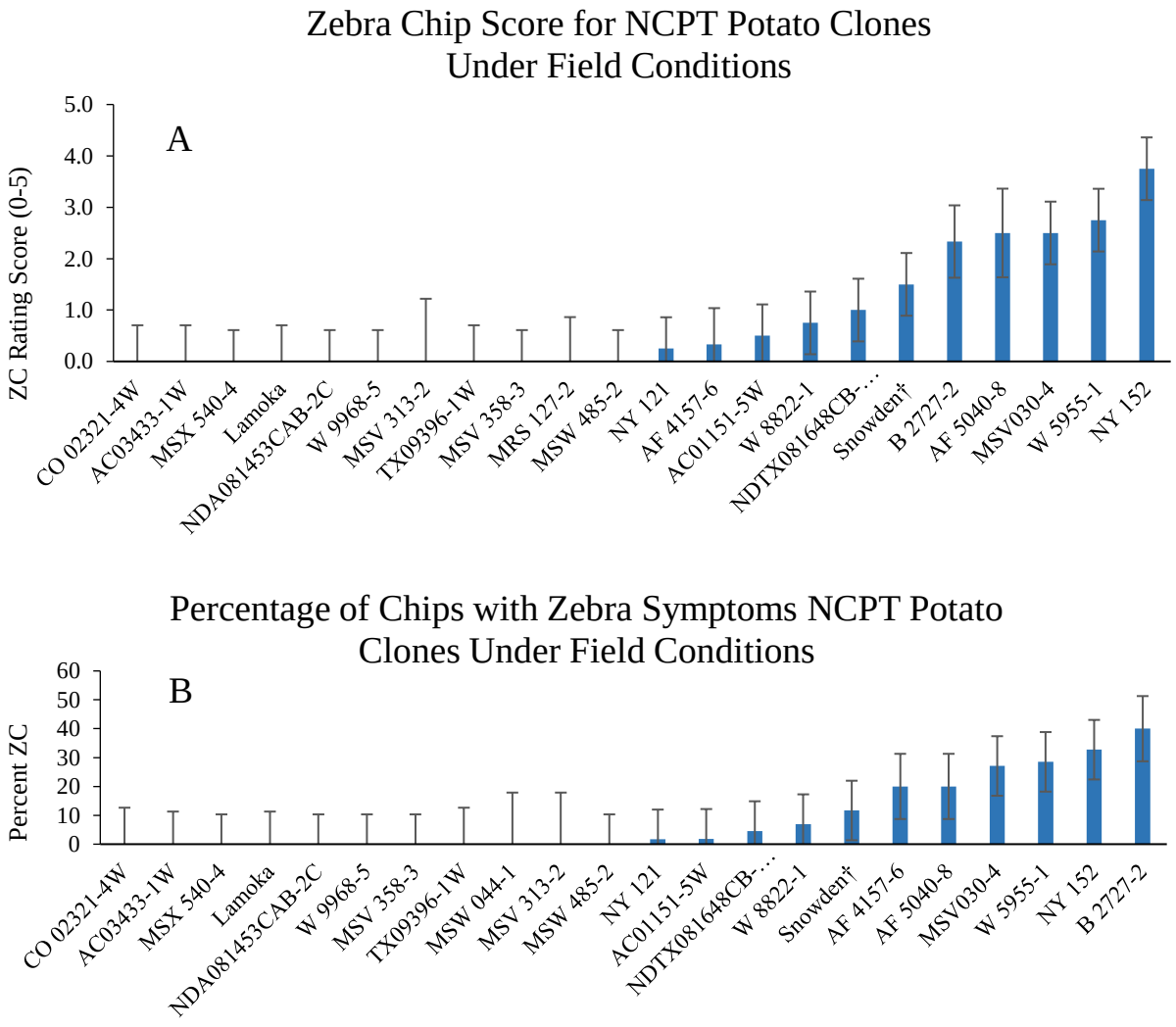

Figure 40. Level of ZC damage for NCPT potato clones grown under field conditions near Springlake, TX in 2017. Average ZC chip scores (A) and average percentage of chips with zebra symptoms per plant (B) from infested (psyllids from an Lso infected colony) tubers fried immediately after harvest. Values are least square means ± standard error. Clones were sorted from left to right with lowest ZC score (A) on the left and lowest percent ZC (B) on the left. Snowden† was used as the standard chipping variety check.

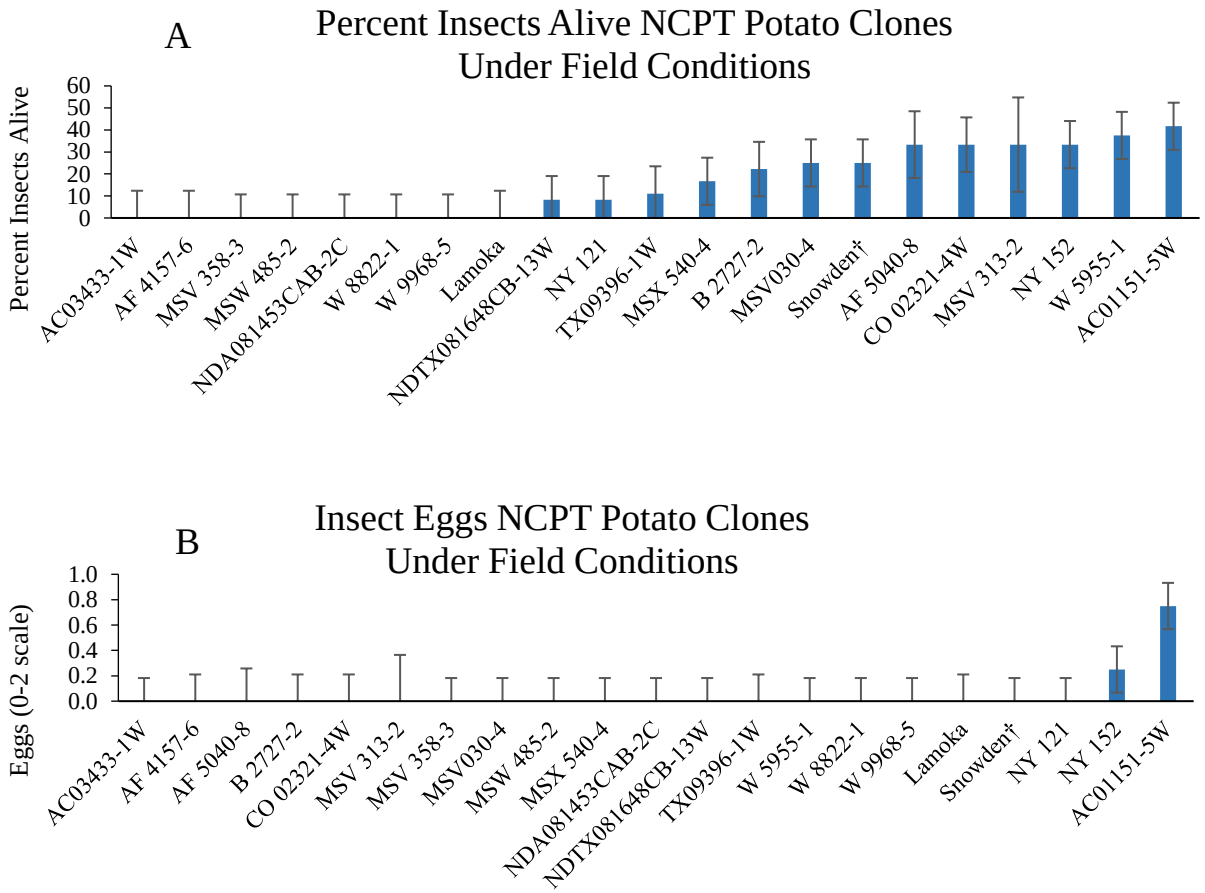

Figure 41. Survival and oviposition of psyllids on plants of NCPT potato clones grown under field conditions near Springlake, TX in 2017. Average percent insects alive (A) after seven days and insect eggs per plant (B). Values are least square means ± standard error. Insect egg numbers are shown based on a number code (0 = no eggs, 1 = few eggs, and 2 = many eggs) Clones were sorted from left to right for lowest percent insects alive (A) and fewest number of eggs (B). Snowden† was used as the standard chipping variety check.

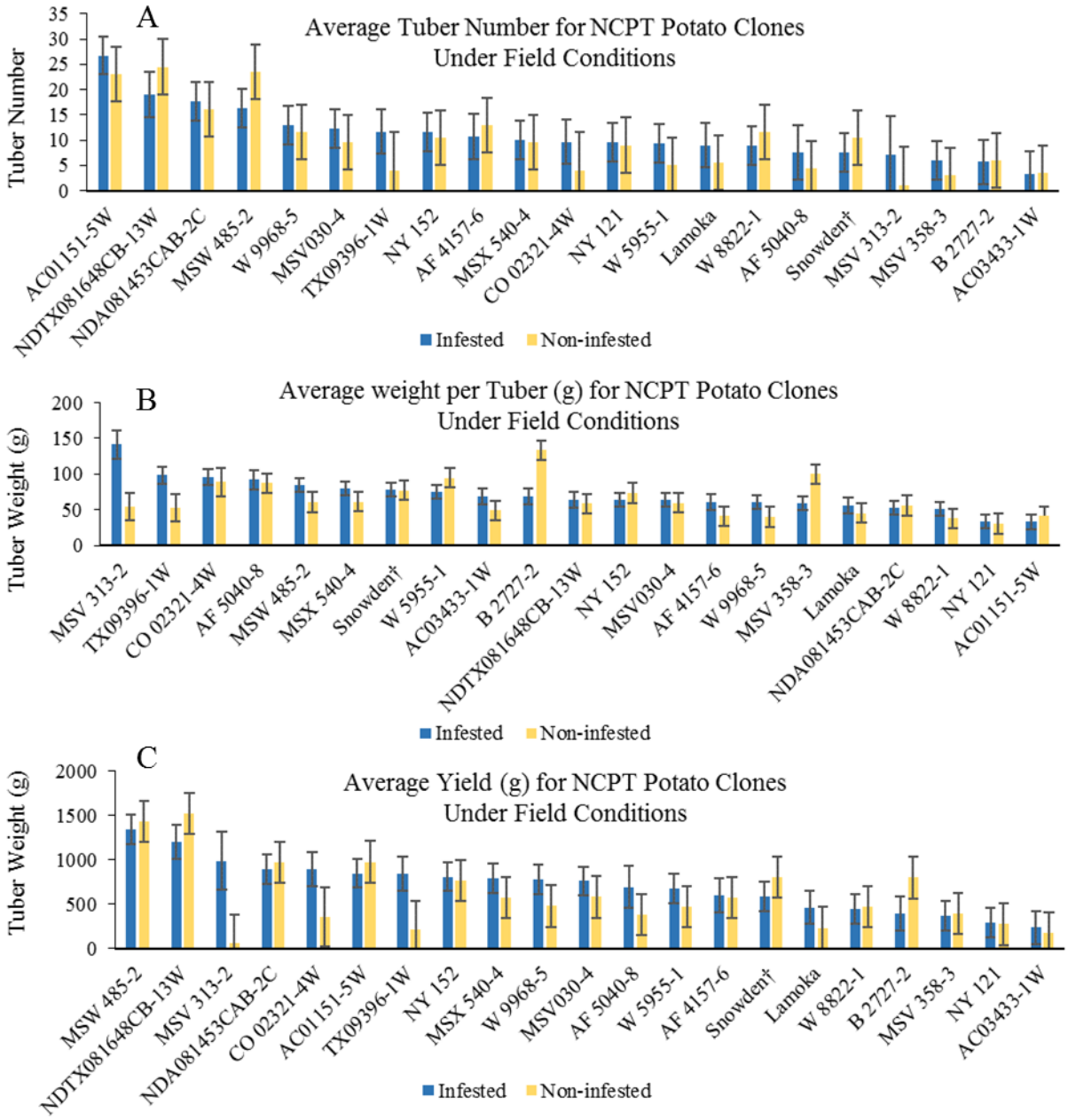

Figure 42. Production and size of tubers of NCPT potato clones grown under field conditions near Springlake, TX in 2017. Average tuber number per plant (A), Average weight per tuber (B), and average yield per plant (C). Values are least square means ± standard error. Clones were sorted from left to right for highest average tuber number (A), highest average weight per tuber (B), and highest average yield per plant (C). Snowden† was used as the standard chipping variety check.

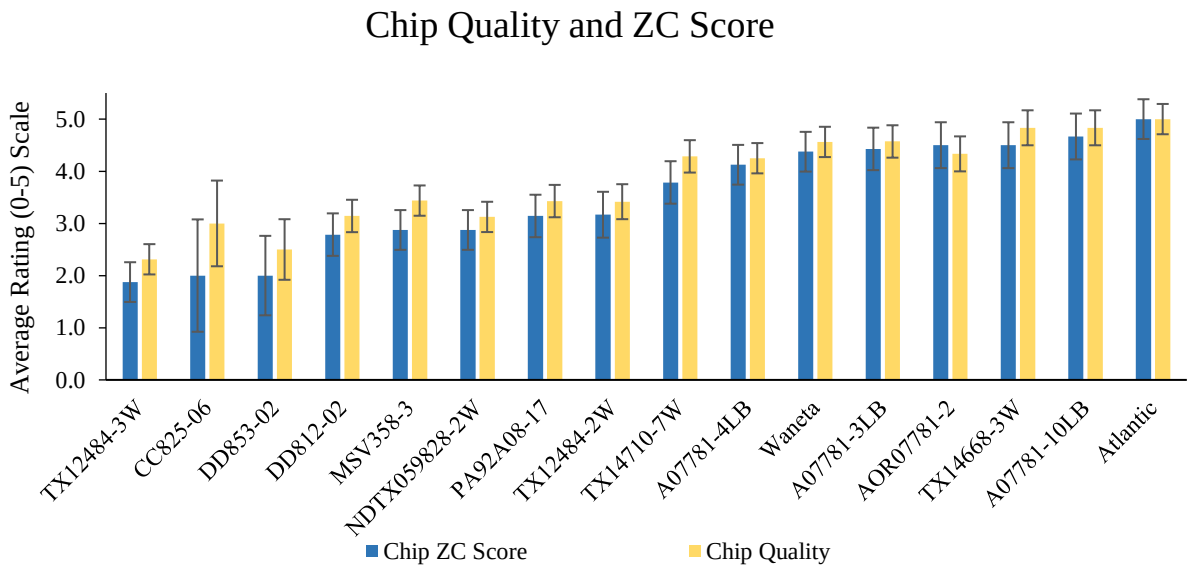

Figure 43. Quality of chips and ZC score of potato clones grown in the field validation study near Bushland, TX in 2018. Average chip quality scores (1 = light chip, 5 = very dark chip). Values are least square means ± standard error. Clones were sorted from left to right for lowest ZC score. Atlantic† was used as the standard chipping variety check. Waneta† was used as an additional tetraploid check.

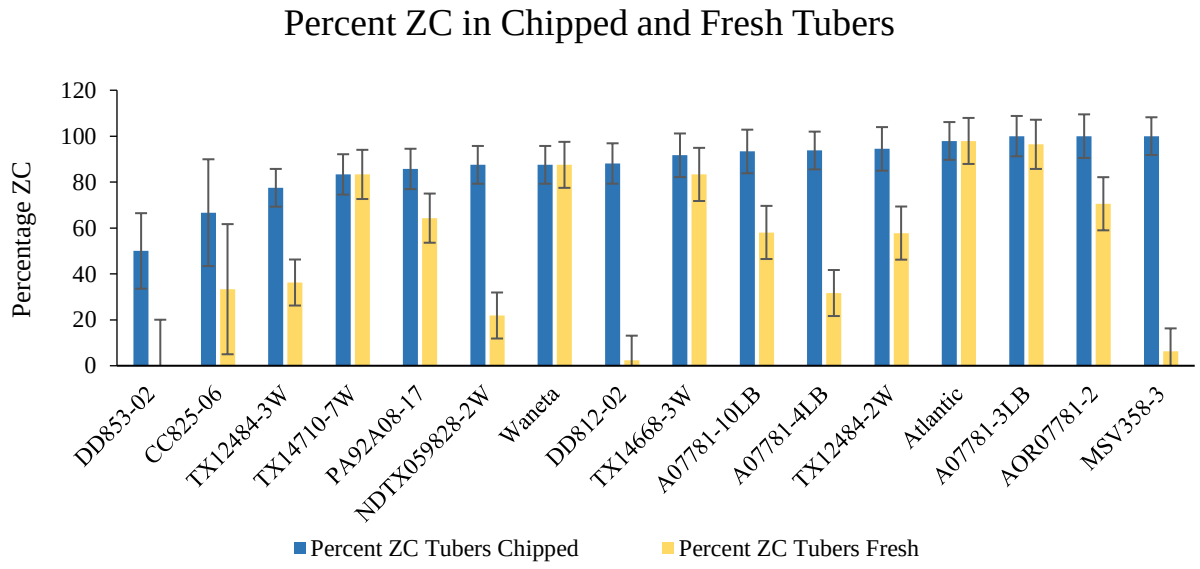

Figure 44. Percent ZC in chipped and fresh potato clones grown in the field validation study near Bushland, TX in 2018. Values are least square means ± standard error. Clones were sorted from left to right for lowest percent ZC in chipped. Atlantic† was used as the standard chipping variety check. Waneta† was used as an additional tetraploid check.

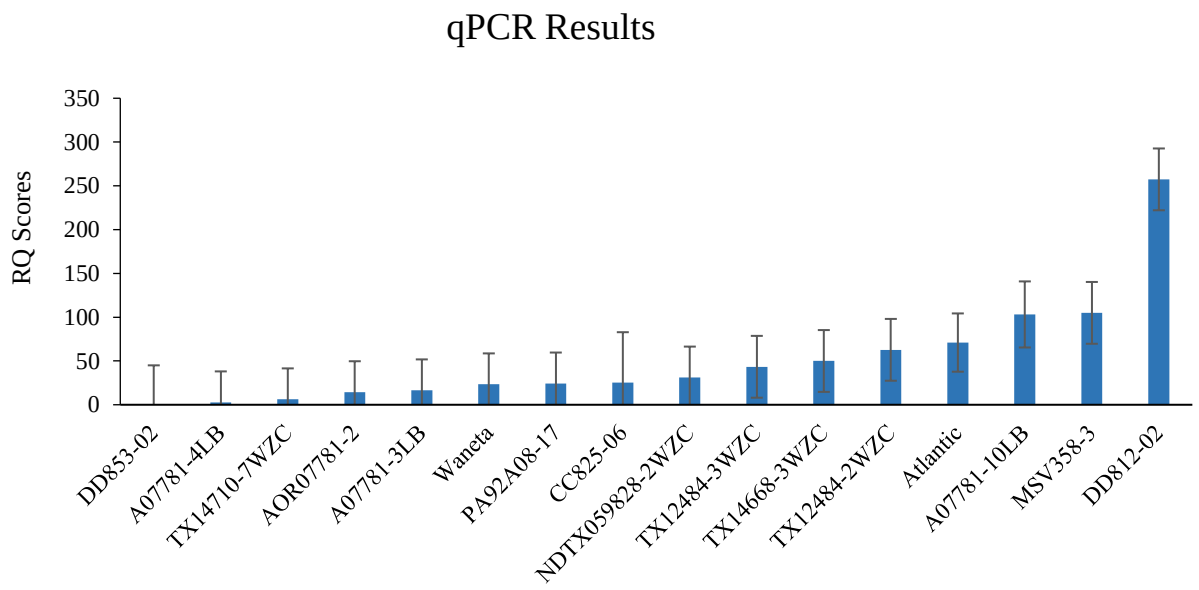

Figure 45. RQ values indicating the level of Lso in the tuber using qPCR for the field validation study near Bushland, TX in 2018. (RQ) was normalized to the Lso endogenous reference and quantified in relation to the calibrator containing 6,250 genome copies. Values are least square means ± standard error. Clones were sorted from left to right for lowest RQ value. Atlantic† was used as the standard chipping variety check. Waneta† was used as an additional tetraploid check.

CHAPTER IV

DISCUSSION

4.1 Tolerance in the Field and Greenhouse

Genotypic variability in symptom expression in response to ZC (infested trials) indicated that screening for ZC tolerance was a valuable effort to identify sources of tolerance to ZC. Clones with no disease symptoms (zero ZC score) were found. From a breeder's perspective those with a very low or no symptoms of ZC are declared resistant. However, very low ZC score could represent escapes or non-efficient infection, thus the term highly tolerant is used. It is possible that tolerance could be monogenic or polygenic and could explain the reaction to ZC. Results indicating tolerance to ZC in the first screening (greenhouse) were followed up with additional field experiments. Field studies included artificially infested trials (using cages) at two locations, the first near Springlake, TX including many clones and the second was considered as a validation experiment near Bushland, TX, with a subset of promising tolerant clones and checks.

ZC tolerance had previously been found using fresh tuber symptoms as the indicator, (Rubio-Covarrubias et al., 2015; Rubio-Covarrubias et al., 2017) but the analysis was not conducted on fried potato chips. In the present study, ZC symptoms were clearly visible in some of the fresh tubers but the ZC symptoms were more evident in chipped tubers (Figure 11). Tubers with clear symptoms in the fresh state showed ZC in the chips, but there were instances when the symptoms were not easy to see in the fresh state but showed ZC symptoms after frying.

The same set of clones was used in the greenhouse and first field studies in infested and non-infested trials with the same experimental design. This allowed for comparison of

consistency of results between greenhouse and field and also comparison of the effect of ZC on a number of traits. The greenhouse screening had higher and more consistent infection levels than the first field screening. In the field, reduced insect survival, insect eggs, and percentage of ZC infection (18.0% field compared to 32.9% for the greenhouse) was observed. The lower ZC incidence level under field conditions made results more difficult to interpret compared to the greenhouse. Additional browning was observed in fried potato chips from the field study that was not related to ZC (browning due to other chip defects) that was not seen under greenhouse conditions. Since the artificially-infested field experiment was conducted under insect-proof cages, tuber defects were likely not caused by other insects or viruses transmitted by insects in season. Since certified seed was not used, it cannot be guaranteed that the tubers were free from viruses which could cause tuber defects. However, the same seed source was used for the greenhouse and first field experiment. It is possible that some bruising was caused at harvest time but all tubers were treated in a similar way thus this should not bias the results. Under greenhouse conditions, harvest was gentler to the tubers since the pots were simply turned over to harvest instead of digging (by hand using a fork) in the field. The temperatures were more stable under greenhouse conditions with a mean of 20.2°C and range of 13.9 °C to 31.1°C compared to a mean 24.3 °C and a range of 7.2 °C to 47.2 °C under field conditions. Thus, it is believed that chip defects observed in field-harvested tubers not caused by ZC were likely due to internal heat necrosis. Previous research indicated the difficulty of field-testing in finding consistent results. Some potato clones would initially show tolerance to ZC but after two years of field studies none of the selections could be confirmed as tolerant because of contradicting results, (Levy et al., 2018). Several years of field cage screenings of clones at Texas A&M have been used to separate potentially tolerant from more susceptible clones. Several of those clones

were included along with selected progenies in the field and greenhouse studies. The greenhouse screening increase the level of confidence because it allowed assigning each clone a specific ranking for ZC tolerance which was not always possible under field conditions, where a zero ZC score could represent escape or non-efficient infection.. Non-efficient infection could possibly be due to heat sensitivity of Lso to high temperatures. Temperatures above 32 °C were reported to affect Lso (Munyaneza, 2015). Soon after placing the insects in the field there were spikes of high temperatures that could have affected psyllid survival. Despite the difficulties associated with field screening, field evaluation is still an important element of ZC screening, especially if used in combination with greenhouse screening. Ideally, two field studies should be conducted to validate results in different locations with different levels of disease pressure to be able to see variation for disease expression and differentiate tolerant from susceptible. Since, if the incidence is very low most of the clones could appear tolerant but if the incidence is very high most of the clones could appear susceptible. This was the intent when the second field screening was conducted with a subset of clones. Triangulation screening (greenhouse, first field screening and second field) would enable better filtering of the clones in order to identify those (very few in our case) that can more reliably be declared tolerant to ZC.

4.2 Tetraploid Clones

A recent study screened in the greenhouse a few of the same clones (members of the A07781 full sib family: A07781-3lb, A07781-4lb, and A07781-10lb) that were included in our experiment (Rashidi et al., 2017). These full sibs were derived from *S. chacoense* and all showed some degree of tolerance. In our study, A07781-10lb was found to be more tolerant in both the greenhouse and field compared to A07781-4lb; A07781-3lb had inconsistent ZC symptoms when greenhouse and field results were compared. The previous study (Rashidi et al., 2017)

indicated that A07781-3lb and A07781-4lb were the more tolerant members of the full-sib family. This seems to indicate that many factors influence the extent of ZC chip infestation and multiple screenings or larger experimental sizes are needed to have a clearer picture. Nevertheless, A07781-10lb (although having higher Lso titer) was the most tolerant for this full sib family based on greenhouse and field results and focusing on ZC symptoms of chipped tubers; however A07781-3lb and A07781-4lb had lower Lso titer (second field study). Another member of the same family, AOR07781-2 (same female and male, but selected in Oregon) was also screened. This clone was not included in the (Rashidi et al., 2017) study. AOR07781-2 and A07781-10lb were among the most ZC tolerant tetraploid clones based on greenhouse evaluations. A07781-10lb had lower ZC score than AOR07781-2 in the first field screening, and similar in the second field screening (both had very higher percentage of zebra symptoms in the tubers (90%) in the second field trial) however the RQ values (the amount of Lso DNA in the sample) of AOR07781-2 was lower than that of A07781-10lb. Several members of another family segregating for ZC tolerance, TX12484 were screened, and some of its members showed tolerance under greenhouse and first field screening. TX12484-2W and TX12484-3W were re-tested in the second field screening. TX12484-3W had the lowest ZC score indicating tolerance; TX12484-2W could also be considered as tolerant, taking into account the very high pressure of Lso the plants were subjected to. Lso was present as shown by the RQ scores indicated Lso titer. There was no correlation between ZC scores and Lso titer, which contradicts previous research that concluded that Lso titers were correlated to both fresh and fried ZC symptoms (Wallis et al., 2015a). Atlantic had the maximum ZC score in the second field study but the RQ values were equivalent to other clones declared tolerant to ZC. It was concluded that evaluating tubers based

on visual symptoms after chipping is likely a much better approach to screen for ZC tolerance when comparing results from infested and non-infested experiments.

4.3 Diploid Clones

This study looked at the potential of diploid clones from a recurrent selection program (Michigan State University) for ZC tolerance in respect to each other and to a range of tetraploid clones. Improved diploid clones were used in this study in hopes that if tolerance for ZC was found it would be easier to incorporate them as parents in breeding programs. Previous studies indicated resistance to psyllids in diploids, (Cooper and Bamberg, 2014; Cooper and Bamberg, 2016; Levy et al., 2018; Novy et al., 2010a); however, data was not collected on ZC chip score or chip quality of fried potato chips. The wide ranges of variation for ZC chip scores and chip quality observed in the diploid clones that were screened indicated that careful selection would be needed to combine ZC tolerance and good chip quality. It was encouraging to find several clones with good chip quality that met the criteria outlined herein for ZC tolerance. There were some clones, such as DD805-05, tolerant to ZC but produced dark chips. One diploid clone (DD853-02) from Michigan State University was declared most tolerant based on ZC score in greenhouse and field studies and absence of Lso despite overwhelming infestation (second field study).

Clone DD853-02 and PI 310927 *S. berthaultii* (Figure 22) (from the Potato Introduction Center, WI and included in a previous study screening the potato mini-core collection) (Levy et al., 2018) were both potentially tolerant to ZC due to no difference between infested and control fried tubers for ZC score and chip quality and had the lowest ZC score in the greenhouse and first field study. DD853-2 had among the lowest values for ZC score, good chipping quality in the second field study, and low RQ. PI 310927 *S. berthaultii* was not included in the field

screening because of bad chip quality in the non-infested. *S. berthaultii* is one of the wild species present in the pedigree background all of the diploids developed by recurrent selection at Michigan State University of *S. tuberosum* Grp. Tuberosum, *S. tuberosum* Grp. Phureja, *S. microdontum*, and *S. berthaultii*, *S. chacoense*. In the clone from PI 310927, the fried tubers were dark and did not have acceptable chip quality but DD853-02 was among the highest in chip quality. DD853-02 had small tuber size of 5.3 g for infested and 4.1 g for non-infested in the greenhouse and 13.6 g for infested and 24.9 g for non-infested for the field. This clone had evenly round shape and high tuber number per plant at 42 per plant for the non-infested (the second highest of all clones) and 18 per plant for the infested. Improving tuber size is a must but at least it has good chipping quality and round tubers, which are desirable quality traits for the chipping market class.

4.4 Wild Species

The diploid accession PI310927 (*S. berthaultii*) confirmed previous screening showing absence of eggs and low percentage of live insects; however, it had had bad chip quality. PI558050 (*S. commersonii*) also confirmed previous screening showing (based on no insects alive and few eggs) and it had good chip quality. This validated prior research that showed that these two accessions both exhibited the insect resistance and had lower yield reduction than most accessions in the mini-core collection (Levy J., Personal Communication, 2018). In the greenhouse study, the PI310927 (*S. berthaultii*) was the healthiest and greenest out of all clones tested when the plants were harvested. It was noted that there is likely variation among members of PI accessions. Tubers of plants were included that were previously screened and indicated as potentially tolerant. Our PI's represent clones within the accession that should be preserved individually. Further study is needed to investigate this accession more closely.

There were no correlations between insect eggs or insects alive with ZC score or any of the other traits measured. There was a weak correlation between alive insects and insect eggs. Since there were only three insects, it is possible that more plants are needed to evaluate insects and eggs. Interestingly, out of all tolerant diploid clones tested, PI558050 *S. commersonii* had 0% insects alive even though there was a moderate level of eggs and *S. berthaultii* had 0 eggs even though there was 16.7 % average alive insects on the plants after seven days. It seems that ultimate insect survival has little influence on egg laying, but survival of insects among wild species may be from a completely different mechanism. One may target the feeding or survival of the insect while the other affects egg laying but not insect survival. Absence of eggs was an indication of insect resistance, however, since a small number of insects were used there is no guarantee that both males and females were present. It is also possible that some females were too old or too young to lay eggs. All four species clones tested from the mini-core collection (PI 310927 *S. berthaultii*, PI 558050 *S. commersonii*, PI 592422 *S. jamesii*, and PI 458425 *S. jamesii*) had less insect eggs and live insects than the mean of all the other diploids tested. This seems to confirm the data presented previously about insect survival and oviposition on these accessions from the mini-core collection, (Levy et al., 2018). Surprisingly, clone DD853-02 that is most tolerant had the highest percent of live insects and an average number of insect eggs. This indicates that previous work, (Cooper and Bamberg, 2014; Cooper and Bamberg, 2016) which found resistance to the psyllid is not in necessarily related to tolerance to ZC as both can be separate characteristics. The other diploids that were determined to be tolerant ranged all over the spectrum from having few live insects to many live insects and from have few eggs to many eggs. Live insects and numbers of eggs do not correlate to ZC tolerance based on our

observations. However, lower insect survival could contribute to reduced transmission of the Lso to the plant and consequently lower infestation rates in a natural field setting.

4.5 Evaluating Screening Methods

Standard methodology to evaluate tolerance to ZC has not been established. The number of psyllids (infected with Lso) feeding on the plant with other factors including time and duration of infection could influence the degree of infection and intensity of the ZC chip score on the fried tubers (Rashed et al., 2013). When 20 psyllids per plant were used in a previous study, all clones tested had significant yield loss over 49.9%, with almost 100% of the plants developing severe symptoms with a ZC chip score of 4 or higher (Munyaneza et al., 2011). This led to the conclusion that all types of tetraploid potatoes were severely affected. Our results indicated that using three psyllids per plant, instead of 20, the level of symptoms was not as severe and allowed us to see a wide range of symptom expression. Most of the plants did not die from ZC and many did not show aboveground symptoms. In the greenhouse, non-infested plants had an average yield of 150.9 g/plant, an average weight per tuber of 15.7 g/tuber, and 15.3 tubers/plant. Infested plants had an average yield of 95.5 g/plant (36.7% loss in relation to non-infested plants), average tuber weight was 8.6 g/tuber (45.2% loss in relation to non-infested) and tuber number was 14.0 per plant (10.8% loss in relation to non-infested) (Table 1). The greenhouse experiments (infested versus non-infested) were conducted in separate greenhouses. The greenhouse where the infested experiment was conducted had occasional problems with thrips and one episode of gray mold. Those factors could interfere with yield loss assessments. The field study had low ZC incidence rate 18.3% for the field compared to 32.9% for the greenhouse. Non-infested plants had an average yield of 592.5 g/plant, an average weight per tuber of 46.8 g/tuber, and 16.6 tubers/plant. Infested plants had an average yield of 548.4 g (7.4% loss in

relation to non-infested plants), average weight per tuber of 48.5 g, (3.6% gain in relation to non-infested) and tuber number of 14.9 (10.2% loss in relation to non-infested). All of these comparisons between infested and non-infested were not significant for the field but were significant for average yield and average weight per tuber for the greenhouse. Among previously declared susceptible clones such as Atlantic there was a ZC chip score of 1.5 (on a 0 – 5 scale) in the greenhouse and a ZC chip score of 2.0 in the first field study (three Lso infected psyllids per plant), respectively, but a score of 5.0 for ZC score when six Lso infected psyllids were used per plant (second field study). The second field study had much higher incidence of ZC of 87.3% and it was more difficult to determine differences between the clones with the average ZC score of 3.5 and a range of 1.9 to 5.0. Despite that, some clones had relatively lower ZC score, good chip quality and low RQ values. Using a very low number of psyllids (or screening under conditions that do not favor psyllid viability – like in the first field study) generally causes low levels of ZC infection. However, increasing the number of psyllids is a delicate aspect since the plants could be easily overwhelmed and do not allow much variation of ZC symptoms. In the second study with six psyllids per plant, most plants had ZC symptoms. Variation was noted, but the range of ZC symptom intensity was narrower.

From this research, it is clear that the collection of traits on chip quality for infested and non-infested tubers and ZC score are the key traits valuable for making a decision on a clone breeding value for tolerance to ZC. Especially helpful was the difference between trait values of the control and the infested chips. Percent of good chips is inversely correlated with the ZC chip score ($r = -0.61$) greenhouse and ($r = -0.39$) field. Correlation was also observed between ZC score and chip quality score ($r = 0.89$) in the greenhouse and ($r = 0.63$) in the field (Table 5 and 6). Scoring for chip quality is easier than providing a ZC score, as sometimes it is difficult to

determine if browning is caused by ZC or other causes. Thus, chip quality could be used as an indirect trait to evaluate ZC, especially when combined with the difference between chip quality of non-infested and infested.

Insect eggs and numbers do not correlate to the tolerance of susceptibility in the plant to ZC. Tuber size, tuber weight, and yield help to determine the potential of the cultivar but are not helpful in assessing ZC tolerance.

The second field study (validation) using higher numbers of psyllids (6 instead of 3) resulted in much higher levels of disease symptoms on the chips (percent ZC average 87.3% compared to 32.9% in the greenhouse and 18.0% in the field). The Atlantic check variety for example had a ZC chip score of 5.0 compared to 2.5 in the greenhouse. Although this is useful to see the extent of maximum damage from ZC for all clones, it seems to overwhelm the plants causing the tolerant clones to have higher symptoms than the other studies but less than the checks. TX12484-3W still had acceptable chip quality and low ZC chip score even at this high infestation level. This indicated that intense screening might be useful for indicating which clones would still be acceptable in an extreme disease outbreak. Symptoms of ZC in fresh tubers were shown to not predict symptoms in fried chips in our second field screening. This confirms what was seen in the greenhouse and first field studies as there where very few fresh tuber symptoms. This indicates that determination of tolerance needs to be done with frying to determine symptoms correctly. Previous studies that only looked at fresh tuber symptoms are likely not applicable for chipping tolerance. The RQ values measuring Lso titer were not able to predict the ZC score or chip quality as the R^2 of the regression value was very low ($R^2 = 0.007$) and ($R^2 = 0.008$) respectively. This indicates that for evaluating tolerance, Lso titer cannot be used as a primary method. In a recent study it was found that there was no significant correlation

between ZC symptom severity and Lso titer for fresh cut tubers (Rashidi et al., 2017). This was in contrast to previous research indicating that Lso titer was correlated to fresh and friend ZC symptoms (Wallis et al., 2015a). However, since some of the lowest RQ scores were from clones with lighter symptoms, it still is useful to look at the values are RQ in combination with the other phenotypic traits.

It is very limiting if the industry has zero tolerance for ZC; however, there are a few potential tolerant clones, both diploid and tetraploid, if some level of ZC damage is acceptable. The NCPT field trial indicated what a moderate level of ZC incidence (14.0%) may result in terms of ZC damage to tubers. It is suggested that in future screenings, a multi-level (greenhouse and field) evaluations should be used. The field screen indicates if the clones that performed well under greenhouse conditions also hold up in the field environment. The greenhouse gives a more consistent data set that allows for ranking and detailed comparison of the clones for ZC score, chip quality, and trait difference between infested and non-infested. Under field conditions, variable and unpredictable weather conditions, temperature, precipitation, management practices, digging individual plants by hand with tools, etc. add possible confounding effects to the screening for ZC tolerance. However, evaluation of tuber quality and yield traits under field conditions is necessary to select clones and advance them to eventually be released as varieties.

Chip quality alone is not a direct indicator of ZC tolerance, thus using it as part of a filtering system, could eliminate potential ZC tolerant clones. Clones from PI310927 *S. berthaultii* (Figure 22) and DD805-05 are examples of genotypes with low ZC but still very dark chips. Potentially tolerant clones could be discarded because of chip quality. Ideally the results should be separated into both dark ZC tolerant chips and light ZC tolerant chips and the breeder would have to treat those separately in the breeding program. Clones with ZC tolerance

producing dark chips would need multiple rounds of recurrent selection in pre-breeding programs for light chip color combined with ZC tolerance in order to be useful by main stream breeding programs directed to develop varieties for the processing markers (chippers, French fries).

CHAPTER V

CONCLUSION

5.1 Summary

In summary, a few potato clones were found that consistently had tolerance in both greenhouse and field infested trials and also had good chipping quality. Diploid and tetraploid potato clones with tolerance (and high tolerance) to ZC and good processing quality are potential sources of ZC tolerance for future potato breeding efforts, mainly for the chipping and French fry market classes. High tolerance in one diploid clone and one wild species accession was found. It was determined that greenhouse screening is more consistent than field screening and that chip quality, chip quality difference, ZC score, and percentage of ZC are best used in combination to determine the associated level of disease symptoms to indicate tolerance.

5.2 Lessons Learned

- ZC is a very difficult disease to work with because of environmental effects, genetics, and GxE affecting the potato plant, the psyllid, and the Lso bacteria at the same time
- The most important traits to assess ZC tolerance are ZC chip score (0 – 5 scale), chip quality and chip quality difference (chip quality of infested versus non-infested chipped tubers)
- Chip quality score (1 – 5 scale) is needed to assess the relevance of tolerance for practical breeding programs for the processing market (chips and French fries)
- Live insects and number of eggs are not directly associated with ZC tolerance
- Both diploids and tetraploids evaluated had some level of tolerance

- A few diploids with good chip quality and ZC tolerance are available, but most do not have both attributes
- A few tetraploids with good chip quality and ZC tolerance have been found, but most tetraploid are susceptible to ZC
- One diploid clone was highly tolerant but none of the tetraploid clones could be considered as highly tolerant
- Low chip quality (dark chips) interferes with the evaluation of ZC symptoms
- Clones tolerant to ZC, but producing dark chips would require pre-breeding efforts before they can be used by main-stream breeding programs
- High numbers of psyllids tend to overwhelm the plants and most looked susceptible
- Intermediate level of psyllids would allow to see a wide range of symptoms and better help to identify tolerance
- Additional screening of wild species is needed
- Introgressing tolerance from crop wild relatives will require several rounds of recurrent selection
- Greenhouse screening is a lot more reliable than field screening, but the field component is useful to confirm greenhouse results and to assess agronomic and quality potential
- RQ values from qPCR do not predict ZC tolerance but some tolerant clones have a low RQ

5.3 Future Work

Several of the most tolerant high chip quality clones from both the tetraploid and the diploid clones were planted in a crossing block in the greenhouse. The goal is to make crosses

and then evaluate the resulting progeny. The identified clones were placed in tissue culture to maintain them for future work. One of the most promising diploid clones did not grow well in the field validation study so it will be grown again in the greenhouse to verify the previous results.

This ZC evaluation has only scratched the surface of potato diversity since there are at least 219 wild species on the planet, and more than 7,000 accessions located in germplasm banks around the world, (Bradshaw et al., 2006). Based on the results of this diploid screen, it is recommended that clones be screened that are similar to *S. chacoense*, *S. berthaultii*, and *S. commersonii*. Also, *S. guerroense* is present in the background of the 7781 family and should also be tested (Brown, C., Personal Communication, 2018). However, it is expected that many more species could contain potential tolerance or resistance that have not yet been tested.

Developing molecular markers to track ZC tolerance could be a valuable next step to breeding for tolerance or resistance. However, good phenotyping is essential to link ZC tolerance traits with molecular markers. Based on this study, the recommendation is to use chip quality (overall quality based on the level of browning) under infested conditions as the key trait to evaluate ZC tolerance, ideally in combination with chip quality of the same clones under control non-infested conditions. Screening under greenhouse conditions should be the first evaluation step. Validation under field conditions will be necessary to confirm results. The number of Lso infected psyllids used for infestation studies is also very important, a number between three and six seems appropriate to detect differences. It is hoped that the screening guidelines developed in the present study will be a valuable tool for phenotyping clones from the breeding program derived from crosses involving tolerant/resistant genotypes and for future mapping studies

aligned towards the identification of markers and genes responsible for ZC tolerance or resistance.

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APPENDIX

Tetraploid Greenhouse

Table A1. Least square means of chip quality and percentage of good chips of infested (psyllids from an Lso infected colony) and non-infested; percentage of zebra chip (ZC) and ZC score from chipped tetraploid potato clones grown under greenhouse conditions near Snook, TX in 2017.

	Chip Quality (1-5)		Good Chips (%)			
Clone	Infested	Non-infested	Infested	Non-infested	ZC (%)	ZC Score (0-5)
AOR07781-2	1.4	1.0	81.7	91.7	13.3	1.0
A05379-211	2.4	1.8	86.7	100.0	47.5	2.8
A07781-10lb	1.6	1.0	52.5	100.0	37.5	1.8
A07781-3lb	3.3	1.0	57.5	100.0	43.6	3.8
A07781-4lb	2.4	1.0	51.4	0.0	20.8	2.0
A10667-2	4.1	2.8	72.9	50.0	8.3	0.3
A10667-3	2.5	1.8	77.1	91.7	15.7	1.5
MSV 358-3	1.6	1.0	62.5	75.0	54.4	3.8
MSX 540-4	4.3	1.5	12.5	87.5	37.5	2.5
NDTX059828-2W	3.5	1.5	43.8	100.0	56.3	3.0
PA92A08-17	3.6	1.3	29.9	100.0	64.6	3.5
PALB03035-7	4.0	1.3	60.4	50.0	35.4	2.3
POR06V12-3	2.6	1.8	50.0	66.7	33.3	2.8
TX05249-10W	1.9	1.3	54.2	100.0	45.8	2.5
TX09396-1W	3.0	1.0	75.0	100.0	8.3	0.3
TX12484-2W	1.1	1.0	91.7	100.0	18.3	2.0
TX14668-3W	3.5	1.0	70.0	100.0	25.0	3.0
TX14695-2W	3.3	1.0	68.8	100.0	31.3	3.0
TX14710-7W	2.0	1.0	66.7	100.0	33.3	1.0
Reveille Russet†	3.1	1.8	22.5	66.7	32.5	3.8
Russet Norkotah†	4.1	1.8	70.8	100.0	29.2	1.3
Atlantic†	2.3	1.5	76.9	100.0	20.0	0.5
Mean	*2.8*	*1.4*	*60.7*	*85.4*	*32.4*	*2.2*
St. error	0.2	0.1	4.2	5.3	3.2	0.2
Min	1.1	1.0	12.5	0.0	8.3	0.3
Max	4.3	2.8	91.7	100.0	64.6	3.8
Count	22.0	22.0	22.0	22.0	22.0	22.0

†Reveille Russet and †Russet Norkotah were used as fresh market checks.
†Atlantic was used as the standard chipping variety check.

Table A2. Survival and oviposition of psyllids on plants of tetraploid potato clones grown under greenhouse conditions near Snook, TX in 2017. Least square means of insect egg numbers based on a number code (0 = no eggs, 1 = few eggs, and 2 = many eggs) and average percent insects alive after seven days.

	Oviposition and survival of psyllids	
Clone	Eggs (0-2 scale)	Insects Alive %
A05379-211	0.5	58.3
A07781-10lb	0.3	66.7
A07781-3lb	1.5	41.7
A07781-4lb	0.0	33.3
A10667-2	0.3	50.0
A10667-3	0.5	25.0
AOR07781-2	0.5	31.3
MSV 358-3	0.3	16.7
MSX 540-4	0.5	25.0
NDTX059828-2W	0.3	16.7
PA92A08-17	0.8	50.0
PALB03035-7	1.0	41.7
POR06V12-3	0.5	43.8
TX05249-10W	0.0	16.7
TX09396-1W	0.5	25.0
TX12484-2W	0.0	16.7
TX12484-3W	1.3	58.3
TX12484-4W	0.8	50.0
TX14668-3W	1.0	41.7
TX14695-2W	0.8	25.0
TX14710-4W	0.5	8.3
TX14710-7W	0.8	29.2
Reveille Russet†	0.0	41.7
Russet Norkotah†	1.0	16.7
Atlantic†	0.5	37.5
Waneta†	0.3	16.7
Mean	*0.5*	*34.0*
Std error	0.1	3.0
Min	0.0	8.3
Max	1.5	66.7
Count	26.0	26.0

†Reveille Russet and †Russet Norkotah were used as fresh market checks.
†Atlantic and †Waneta were used as the standard chipping variety checks.

Table A3. Production and size of tubers of tetraploid potato clones grown under greenhouse conditions near Snook, TX in 2017. Least square means of average tuber number per plant, average weight per tuber, and average yield per plant.

	Average Tuber Number		Average Weight per Tuber (g)		Average Yield (g)	
Clone	Infested	Non-infested	Infested	Non-infested	Infested	Non-infested
A05379-211	11.3	14.5	4.3	10.0	47.5	145.0
A07781-10lb	10.3	7.0	9.7	36.3	92.5	220.0
A07781-3lb	18.3	24.5	9.8	7.4	177.5	175.0
A07781-4lb	11.5	10.0	11.4	23.0	127.5	195.0
A10667-2	8.3	16.5	7.2	13.0	52.5	215.0
A10667-3	10.5	8.0	9.2	19.4	80.0	155.0
AOR07781-2	11.5	8.0	10.8	29.5	112.5	210.0
MSV 358-3	7.8	5.5	25.8	35.2	197.5	190.0
MSX 540-4	7.5	14.5	17.8	10.2	132.5	135.0
NDTX059828-2W	4.8	3.5	3.0	27.1	12.5	85.0
PA92A08-17	9.0	10.0	15.0	17.6	120.0	160.0
PALB03035-7	10.0	7.0	7.1	16.2	67.5	110.0
POR06V12-3	7.0	6.5	10.4	28.2	70.0	160.0
TX05249-10W	8.3	7.5	6.6	28.1	52.5	200.0
TX09396-1W	6.3	7.0	10.8	33.3	62.5	190.0
TX12484-2W	11.0	23.0	2.2	8.0	25.0	185.0
TX12484-3W	10.0	11.5	3.7	8.1	20.0	90.0
TX12484-4W	23.8	25.0	3.5	3.2	55.0	80.0
TX14668-3W	4.8	7.5	9.8	18.3	47.5	130.0
TX14695-2W	10.0	8.5	7.3	20.1	77.5	165.0
TX14710-4W	14.3	13.5	2.7	12.3	37.5	165.0
TX14710-7W	7.3	11.0	4.1	7.0	30.0	80.0
Reveille Russet†	4.3	5.0	13.0	22.5	57.5	105.0
Russet Norkotah†	4.0	3.5	16.3	45.0	67.5	150.0
Atlantic†	8.3	15.0	13.3	13.3	100.0	200.0
Waneta†	3.8	3.0	18.2	57.5	55.0	155.0
Mean	*9.4*	*10.6*	*9.7*	*21.1*	*76.1*	*155.8*
Std error	0.8	1.2	1.1	2.5	8.8	8.3
Min	3.8	3.0	2.2	3.2	12.5	80.0
Max	23.8	25.0	25.8	57.5	197.5	220.0
Count	26.0	26.0	26.0	26.0	26.0	26.0

†Reveille Russet and †Russet Norkotah were used as fresh market checks.
†Atlantic and †Waneta were used as the standard chipping variety checks.

Diploid Greenhouse

Table A4. Least square means of chip quality and percentage of good chips of infested (psyllids from an Lso infected colony) and non-infested; percentage of zebra chip (ZC) and ZC score from chipped diploid potato clones grown under greenhouse conditions near Snook, TX in 2017.

	Chip Quality (1-5)		Good Chips (%)			
Clone	Infested	Non-infested	Infested	Non-infested	ZC (%)	ZC Score (0-5)
CC804-01	4.4	1.5	32.3	90.0	92.7	4.3
CC805-01	2.3	1.5	77.5	80.0	22.5	2.3
CC806-02	2.1	1.8	67.5	95.0	37.5	1.5
CC807-01	2.4	1.0	80.0	100.0	15.0	2.0
CC809-02	2.8	1.0	62.3	100.0	21.9	1.5
CC811-03	3.3	1.0	25.0	100.0	50.0	1.8
CC811-05	4.5	2.3	50.7	38.3	69.3	4.5
CC813-02	3.6	1.0	61.9	100.0	38.1	3.5
CC825-06	3.6	1.3	39.9	87.5	60.1	3.3
CC831-03	1.6	1.0	70.0	100.0	30.0	1.0
CC832-14	3.0	1.0	57.3	100.0	42.7	2.8
DD803-01	2.9	1.0	53.5	100.0	35.2	2.5
DD805-05	3.3	4.0	16.7	0.0	50.0	2.0
DD805-08	2.3	1.0	55.4	100.0	44.6	1.8
DD812-02	2.0	1.3	71.9	100.0	31.3	1.3
DD829-09	4.5	2.3	10.0	83.3	85.0	4.5
DD847-06	1.8	1.0	76.7	100.0	23.3	1.0
DD849-08	3.3	2.5	66.3	50.0	52.5	2.8
DD851-07	1.5	1.3	95.8	100.0	4.2	0.5
DD853-02	1.0	1.0	100.0	100.0	0.0	0.0
PI 310927 S. berthaultii	4.1	3.8	0.0	0.0	0.0	1.5
PI 558050 S. commersonii	2.0	2.0	83.3	50.0	16.7	2.5
PI 592422 S. jamesii	3.3	2.0	50.0	0.0	40.0	2.8
Reveille Russet†	3.1	1.8	50.0	66.7	33.3	3.8
Russet Norkotah†	4.1	1.8	22.5	66.7	32.5	1.5
Atlantic†	2.3	1.5	77.1	91.7	15.7	0.0
Mean	*2.9*	*1.6*	*55.9*	*76.9*	*36.3*	*2.2*
St. error	0.2	0.2	5.0	6.5	4.5	0.2
Min	1.0	1.0	0.0	0.0	0.0	0.0
Max	4.5	4.0	100.0	100.0	92.7	4.5
Count	26.0	26.0	26.0	26.0	26.0	26.0

†Reveille Russet and †Russet Norkotah were used as fresh market checks.
†Atlantic and †Waneta were used as the standard chipping variety checks.

Table A5. Survival and oviposition of psyllids on plants of diploid potato clones grown under greenhouse conditions near Snook, TX in 2017. Least square means of insect egg numbers based on a number code (0 = no eggs, 1 = few eggs, and 2 = many eggs) and average percent insects alive after seven days.

	Oviposition and survival of psyllids	
Clone	Eggs (0-2 scale)	Insects Alive %
CC804-01	0.8	47.9
CC805-01	0.3	16.7
CC806-02	0.8	45.8
CC807-01	1.0	62.5
CC809-02	0.5	47.9
CC811-03	1.3	54.2
CC811-05	1.3	58.3
CC813-02	1.0	39.6
CC825-06	1.0	41.7
CC831-03	0.5	16.7
CC832-14	0.8	50.0
DD803-01	0.0	50.0
DD805-05	1.5	33.3
DD805-08	0.5	45.8
DD812-02	1.0	66.7
DD829-09	1.0	43.8
DD847-06	2.0	25.0
DD849-08	2.0	58.3
DD851-07	0.8	8.3
DD853-02	0.8	66.7
PI 310927 S. berthaultii	0.0	16.7
PI 458425 S. jamesii	0.7	8.3
PI 558050 S. commersonii	0.5	0.0
PI 592422 S. jamesii	0.0	8.3
Reveille Russet†	0.0	41.7
Russet Norkotah†	1.0	16.7
Atlantic†	0.5	37.5
Waneta†	0.3	16.7
Mean	*0.8*	*36.6*
Std error	0.1	3.7
Min	0.0	0.0
Max	2.0	66.7
Count	28.0	28.0

†Reveille Russet and †Russet Norkotah were used as fresh market checks.
†Atlantic and †Waneta were used as the standard chipping variety checks.

Table A6. Production and size of tubers of diploid potato clones grown under greenhouse conditions near Snook, TX in 2017. Least square means of average tuber number per plant, average weight per tuber, and average yield per plant.

	Average Tuber Number		Average Tuber Weight (g)		Average Yield (g)	
Clone	Infested	Non-infested	Infested	Non-infested	Infested	Non-infested
CC804-01	50.0	74.5	4.5	3.2	220.0	235.0
CC805-01	27.5	32.5	7.6	3.9	200.0	130.0
CC806-02	27.3	29.5	8.0	5.9	212.5	175.0
CC807-01	38.8	32.0	4.7	4.3	175.0	135.0
CC809-02	13.5	10.5	17.0	10.3	200.0	110.0
CC811-03	13.8	8.0	14.0	16.7	170.0	135.0
CC811-05	20.8	20.5	8.3	7.4	162.5	150.0
CC813-02	20.0	15.5	9.6	16.3	187.5	250.0
CC825-06	13.3	16.5	7.4	10.6	95.0	175.0
CC831-03	15.0	22.5	6.0	7.3	82.5	165.0
CC832-14	17.8	16.5	6.1	13.3	87.5	220.0
DD803-01	20.8	30.0	2.8	5.5	60.0	165.0
DD805-05	6.5	6.0	6.1	5.5	40.0	35.0
DD805-08	11.8	14.5	5.9	13.5	70.0	185.0
DD812-02	22.8	20.5	4.7	5.2	107.5	105.0
DD829-09	16.0	13.5	17.4	22.3	232.5	300.0
DD847-06	6.8	9.0	5.7	15.6	40.0	140.0
DD849-08	7.5	12.0	11.7	14.4	82.5	170.0
DD851-07	28.0	20.5	1.8	5.6	50.0	120.0
DD853-02	17.5	42.0	5.3	4.1	47.5	170.0
PI 310927 S. berthaultii	11.8	7.0	14.9	22.1	175.0	155.0
PI 458425 S. jamesii	15.0	15.0	1.4	1.4	20.0	20.0
PI 558050 S. commersonii	26.5	13.0	1.8	13.0	50.0	85.0
PI 592422 S. jamesii	10.7	22.0	3.5	3.3	30.0	50.0
Reveille Russet†	4.3	5.0	13.0	22.5	57.5	105.0
Russet Norkotah†	4.0	3.5	16.3	45.0	67.5	150.0
Atlantic†	8.3	15.0	13.3	13.3	100.0	200.0
Waneta†	3.8	3.0	18.2	57.5	55.0	155.0
Mean	*17.1*	*18.9*	*8.5*	*13.2*	*109.9*	*149.6*
Std error	2.0	2.7	1.0	2.3	12.6	11.4
Min	3.8	3.0	1.4	1.4	20.0	20.0
Max	50.0	74.5	18.2	57.5	232.5	300.0
Count	28.0	28.0	28.0	28.0	28.0	28.0

†Reveille Russet and †Russet Norkotah were used as fresh market checks.
†Atlantic and †Waneta were used as the standard chipping variety checks.

Tetraploid Field

Table A7. Least square means of chip quality and percentage of good chips of infested (psyllids from an Lso infected colony) and non-infested; percentage of zebra chip (ZC) and ZC score from chipped tetraploid potato clones grown under field conditions near Springlake, TX in 2017.

	Chip Quality (1-5)		Good Chips (%)			
Clone	Infested	Non-infested	Infested	Non-infested	ZC (%)	ZC Score (0-5)
A05379-211	4.4	4.8	33.7	0.0	38.7	2.5
A07781-10lb	1.9	1.8	75.6	80.0	3.3	0.3
A07781-3lb	3.6	1.5	37.6	66.7	21.2	1.5
A07781-4lb	**2.0**	**1.8**	**66.9**	**94.4**	**0.0**	**0.0**
A10667-2	4.6	4.3	0.0	12.5	2.4	0.3
A10667-3	2.8	3.5	12.5	60.0	2.1	0.3
AOR07781-2	2.6	1.5	50.0	100.0	16.7	1.3
NDTX059828-2W	**1.5**	**1.0**	**100.0**	**100.0**	**0.0**	**0.0**
PA92A08-17	**1.3**	**2.5**	**84.9**	**66.7**	**0.0**	**0.0**
PALB03035-7	3.1	3.0	40.8	48.9	16.4	1.3
POR06V12-3	**1.0**	**2.5**	**100.0**	**35.7**	**0.0**	**0.0**
TX05249-10W	3.0	1.3	50.0	100.0	25.0	2.5
TX12484-1W	**1.3**	**1.3**	**75.0**	**92.9**	**0.0**	**0.0**
TX12484-2W	2.5	1.3	0.0	94.4	23.8	2.0
TX12484-3W	2.1	1.8	40.0	87.5	40.0	1.3
TX12484-4W	**1.0**	**1.5**	**100.0**	**92.9**	**0.0**	**0.0**
TX14668-3W	3.5	1.0	21.4	100.0	25.0	2.5
TX14681-4W	**1.8**	**1.0**	**80.8**	**100.0**	**0.0**	**0.0**
TX14695-2W	**1.5**	**1.3**	**0.0**	**100.0**	**0.0**	**0.0**
TX14710-4W	**2.5**	**1.5**	**0.0**	**100.0**	**0.0**	**0.0**
TX14710-7W	2.6	1.5	65.0	95.8	18.3	1.5
Atlantic†	3.2	2.5	25.0	40.0	23.3	2.0
Waneta†	2.5	1.0	50.0	83.7	25.0	2.0
Mean	*2.5*	*1.9*	*48.2*	*76.2*	*12.2*	*0.9*
St. error	0.2	0.2	6.9	6.1	2.7	0.2
Min	1.0	1.0	0.0	0.0	0.0	0.0
Max	4.6	4.8	100.0	100.0	40.0	2.5
Count	23.0	23.0	23.0	23.0	23.0	23.0

Clones in bold were likely not infected with ZC and showed no symptoms.
†Atlantic and †Waneta were used as the standard chipping variety checks.

Table A8. Survival and oviposition of psyllids on plants of tetraploid potato clones grown under field conditions near Springlake, TX in 2017. Least square means of insect egg numbers based on a number code (0 = no eggs, 1 = few eggs, and 2 = many eggs) and average percent insects alive after seven days.

	Oviposition and survival of psyllids	
Clone	Eggs (0-2 scale)	Insects Alive %
A05379-211	0.5	0.0
A07781-10lb	0.0	0.0
A07781-3lb	0.0	0.0
A07781-4lb	0.0	0.0
A10667-2	0.0	8.3
A10667-3	0.3	33.3
AOR07781-2	0.0	25.0
NDTX059828-2W	0.0	0.0
PA92A08-17	0.0	0.0
PALB03035-7	0.3	83.3
POR06V12-3	0.0	16.7
TX05249-10W	0.0	44.4
TX12484-1W	0.0	0.0
TX12484-2W	0.7	0.0
TX12484-3W	0.5	8.3
TX12484-4W	0.0	0.0
TX14668-3W	0.0	33.3
TX14681-4W	0.3	8.3
TX14695-2W	0.0	0.0
TX14710-4W	0.0	66.7
TX14710-7W	0.3	16.7
Atlantic†	0.3	52.8
Waneta†	0.0	33.3
Mean	*0.1*	*18.7*
St. error	0.0	4.9
Min	0.0	0.0
Max	0.7	83.3
Count	23.0	23.0

†Atlantic and †Waneta were used as the standard chipping variety checks.

Table A9. Production and size of tubers of tetraploid potato clones grown under field conditions near Springlake, TX in 2017. Least square means of average tuber number per plant, average weight per tuber, and average yield per plant.

	Average Tuber Number		Average Weight per Tuber (g)		Average Yield (g)	
Clone	Infested	Non-infested	Infested	Non-infested	Infested	Non-infested
A05379-211	17.5	28.0	43.2	41.3	784.7	1174.8
A07781-10lb	12.3	14.5	57.1	62.9	719.7	929.9
A07781-3lb	15.5	21.5	50.7	40.1	748.4	834.6
A07781-4lb	20.3	27.0	39.0	42.9	780.2	1170.3
A10667-2	12.0	12.0	41.2	40.1	469.5	485.3
A10667-3	17.3	18.5	55.7	62.2	970.7	1097.7
AOR07781-2	10.5	9.0	74.6	70.6	759.8	635.0
NDTX059828-2W	3.0	3.0	42.3	27.2	127.0	81.6
PA92A08-17	10.8	13.0	56.9	44.0	546.6	571.5
PALB03035-7	21.5	22.5	45.0	74.3	982.0	1782.6
POR06V12-3	15.0	4.5	52.2	52.8	757.5	199.6
TX05249-10W	5.0	8.0	81.2	95.3	612.3	943.5
TX12484-1W	4.0	6.0	63.3	41.3	229.8	208.7
TX12484-2W	7.0	9.5	44.1	52.0	308.4	489.9
TX12484-3W	6.5	9.5	45.9	47.1	326.6	449.1
TX12484-4W	1.0	7.5	45.4	40.7	45.4	317.5
TX14668-3W	10.5	11.5	71.6	81.0	780.2	943.5
TX14681-4W	7.0	6.5	45.1	62.6	299.4	394.6
TX14695-2W	7.0	7.0	42.2	56.0	258.5	362.9
TX14710-4W	4.5	2.0	38.6	18.1	145.1	36.3
TX14710-7W	12.0	18.5	35.3	36.4	406.0	694.9
Atlantic†	9.3	8.0	95.0	99.8	898.1	798.3
Waneta†	4.5	9.0	61.7	91.6	290.3	793.8
Mean	*10.2*	*12.0*	*53.3*	*55.7*	*532.4*	*669.4*
St. error	1.2	1.5	3.1	4.4	59.1	84.8
Min	1.0	2.0	35.3	18.1	45.4	36.3
Max	21.5	28.0	95.0	99.8	982.0	1782.6
Count	23.0	23.0	23.0	23.0	23.0	23.0

†Atlantic and †Waneta were used as the standard chipping variety checks.

Diploid Field

Table A10. Least square means of chip quality and percentage of good chips of infested (psyllids from an Lso infected colony) and non-infested; percentage of zebra chip (ZC) and ZC score from chipped diploid potato clones grown under field conditions near Springlake, TX in 2017.

	Chip Quality (1-5)		Good Chips (%)			
Clone	Infested	Non-infested	Infested	Non-infested	ZC (%)	ZC Score (0-5)
CC804-01	1.9	2.0	74.4	79.4	2.1	0.3
CC805-01	2.3	2.8	39.2	65.9	23.0	1.0
CC806-02	**1.5**	**3.3**	**74.7**	**50.0**	**0.0**	**0.0**
CC807-01	2.8	2.3	44.0	76.4	29.4	1.5
CC809-02	3.5	2.0	78.8	66.4	20.5	2.5
CC811-03	3.2	1.0	29.2	100.0	22.5	1.3
CC811-05	1.9	1.0	75.0	95.0	16.7	1.0
CC813-02	1.9	1.3	88.1	95.0	6.3	0.5
CC825-06	**2.5**	**1.5**	**69.4**	**85.0**	**0.0**	**0.0**
CC831-03	2.4	2.3	39.0	59.3	13.3	1.0
CC832-14	**2.5**	**2.8**	**37.5**	**67.8**	**0.0**	**0.0**
DD803-01	**4.7**	**5.0**	**4.8**	**25.0**	**0.0**	**0.0**
DD805-05	2.9	2.5	15.5	70.0	10.0	0.5
DD805-08	3.3	4.0	24.4	31.7	38.0	2.3
DD812-02	2.0	4.3	82.7	55.7	5.0	0.5
DD829-09	**3.9**	**4.3**	**15.9**	**29.1**	**0.0**	**0.0**
DD847-06	**3.8**	**1.8**	**44.8**	**71.4**	**0.0**	**0.0**
DD849-08	4.3	2.0	10.4	73.2	29.6	2.5
DD851-07	3.3	2.3	16.6	75.3	43.3	1.5
DD853-02	1.1	1.0	97.5	100.0	1.7	0.3
Atlantic†	3.2	2.5	25.0	40.0	23.3	2.0
Waneta†	2.5	1.0	50.0	83.7	25.0	2.0
Mean	*2.8*	*2.4*	*47.1*	*68.0*	*14.1*	*0.9*
St. error	0.2	0.2	5.9	4.6	2.9	0.2
Min	1.1	1.0	4.8	25.0	0.0	0.0
Max	4.7	5.0	97.5	100.0	43.3	2.5
Count	22.0	22.0	22.0	22.0	22.0	22.0

Clones in bold were likely not infected with ZC and showed no symptoms.
†Atlantic and †Waneta were used as the standard chipping variety checks.

Table A11. Survival and oviposition of psyllids on plants of diploid potato clones grown under field conditions near Springlake, TX in 2017. Least square means of insect egg numbers based on a number code (0 = no eggs, 1 = few eggs, and 2 = many eggs) and average percent insects alive after seven days.

	Oviposition and survival of psyllids	
Clone	Eggs (0-2 scale)	Insects Alive %
CC804-01	0.3	25.0
CC805-01	0.0	12.5
CC806-02	0.0	0.0
CC807-01	0.0	8.3
CC809-02	0.5	8.3
CC811-03	0.0	16.7
CC811-05	0.0	33.3
CC813-02	0.0	0.0
CC825-06	0.0	0.0
CC831-03	0.0	0.0
CC832-14	0.0	8.3
DD803-01	0.0	22.2
DD805-05	0.0	12.5
DD805-08	0.0	0.0
DD812-02	0.5	8.3
DD829-09	0.0	0.0
DD847-06	0.0	0.0
DD849-08	0.0	0.0
DD851-07	0.5	25.0
DD853-02	0.0	0.0
Atlantic†	0.3	52.8
Waneta†	0.0	33.3
Mean	*0.1*	*12.1*
St. error	0.0	3.0
Min	0.0	0.0
Max	0.5	52.8
Count	22.0	22.0

†Atlantic and †Waneta were used as the standard chipping variety checks.

Table A12. Production and size of tubers of diploid potato clones grown under field conditions near Springlake, TX in 2017. Least square means of average tuber number per plant, average weight per tuber, and average yield per plant.

	Average Tuber Number		Average Weight per Tuber (g)		Average Yield (g)	
Clone	Infested	Non-infested	Infested	Non-infested	Infested	Non-infested
DD812-02	57.0	45.0	71.7	19.7	648.6	467.2
CC804-01	41.0	42.0	11.3	11.1	554.9	517.1
CC805-01	13.7	28.5	13.7	12.4	220.7	476.3
CC806-02	25.3	49.0	16.9	16.9	294.8	585.1
CC807-01	26.5	25.5	12.0	11.9	458.1	530.7
CC809-02	21.7	45.5	18.3	22.5	308.4	657.7
CC811-03	27.3	24.5	13.6	14.8	294.8	453.6
CC811-05	19.5	22.5	10.2	18.7	433.2	557.9
CC813-02	24.8	17.5	20.0	25.8	505.8	621.4
CC825-06	30.5	19.0	22.4	35.3	732.6	635.0
CC831-03	17.8	22.5	24.6	34.0	358.3	535.2
CC832-14	34.3	67.0	19.4	22.7	335.7	857.3
DD803-01	18.3	34.0	9.7	12.9	319.8	696.3
DD805-05	13.0	24.0	17.5	20.5	296.3	630.5
DD805-08	27.7	28.5	28.5	52.5	671.3	585.1
DD829-09	15.8	25.5	22.8	26.9	356.1	716.7
DD847-06	19.7	26.0	18.6	24.0	371.9	653.2
DD849-08	15.0	15.0	19.9	23.6	288.0	344.7
DD851-07	20.3	26.5	16.8	26.2	315.2	684.9
DD853-02	21.5	27.5	13.6	24.9	292.6	585.1
Atlantic†	9.3	8.0	95.0	99.8	898.1	798.3
Waneta†	4.5	9.0	61.7	91.6	290.3	793.8
Mean	*22.9*	*28.8*	*25.4*	*29.5*	*420.3*	*608.3*
St. error	2.3	2.9	4.5	4.9	36.8	25.6
Min	4.5	8.0	9.7	11.1	220.7	344.7
Max	57.0	67.0	95.0	99.8	898.1	857.3
Count	22.0	22.0	22.0	22.0	22.0	22.0

†Atlantic and †Waneta were used as the standard chipping variety checks.

NCPT Field

Table A13. Least square means of chip quality and percentage of good chips of infested (psyllids from an Lso infected colony) and non-infested; percentage of zebra chip (ZC) and ZC score from chipped NCPT potato clones grown under field conditions near Springlake, TX in 2017.

	Chip Quality (1-5)		Good Chips (%)			
Clone	Infested	Non-infested	Infested	Non-infested	ZC (%)	ZC Score (0-5)
AC01151-5W	1.6	1.5	89.7	90.0	1.9	0.5
AC03433-1W	**1.3**	**1.0**	**93.3**	**100.0**	**0.0**	**0.0**
AF 4157-6	2.3	1.0	30.6	92.3	20.0	0.3
AF 5040-8	3.5	1.0	25.0	100.0	20.0	2.5
B 2727-2	3.0	1.5	22.2	90.0	40.0	2.3
CO 02321-4W	**1.0**	**2.5**	**100.0**	**50.0**	**0.0**	**0.0**
Lamoka	**2.0**	**1.8**	**72.0**	**81.3**	**0.0**	**0.0**
MSV 313-2	**2.5**	**2.0**	**31.3**	**0.0**	**0.0**	**0.0**
MSV 358-3	**2.0**	**1.5**	**60.0**	**50.0**	**0.0**	**0.0**
MSV030-4	1.6	1.3	62.0	75.0	27.1	**0.0**
MSW 044-1	**3.1**	**4.0**	**40.6**	**16.7**	**0.0**	2.5
MSW 485-2	**3.0**	**2.8**	**17.3**	**31.7**	**0.0**	**0.0**
MSX 540-4	**2.0**	**1.3**	**74.1**	**100.0**	**0.0**	**0.0**
NDA081453CAB-2C	**2.1**	**1.5**	**69.7**	**90.0**	**0.0**	**0.0**
NDTX081648CB-13W	3.5	2.3	23.1	61.8	4.5	1.0
NY 121	1.9	1.5	79.9	80.0	1.7	0.3
NY 152	3.3	2.5	40.9	75.7	32.7	3.8
TX09396-1W	**2.7**	**3.0**	**48.2**	**0.0**	**0.0**	**0.0**
W 5955-1	3.4	2.3	47.2	70.0	28.5	2.8
W 8822-1	2.0	1.5	69.0	95.5	6.9	0.8
W 9968-5	**2.4**	**2.0**	**63.9**	**84.5**	**0.0**	**0.0**
Snowden†	2.6	1.0	71.3	100.0	11.7	1.5
Mean	*2.4*	*1.8*	*56.0*	*69.7*	*8.9*	*0.8*
St. error	0.1	0.2	5.2	6.7	2.7	0.2
Min	1.0	1.0	17.3	0.0	0.0	0.0
Max	3.5	4.0	100.0	100.0	40.0	3.8
Count	22.0	22.0	22.0	22.0	22.0	22.0

Clones in bold were likely not infected with ZC and showed no symptoms.
†Snowden was used as the standard chipping variety check.

Table A14. Survival and oviposition of psyllids on plants of NCPT potato clones grown under field conditions near Springlake, TX in 2017. Least square means of insect egg numbers based on a number code (0 = no eggs, 1 = few eggs, and 2 = many eggs) and average percent insects alive after seven days.

	Oviposition and survival of psyllids	
Clone	Eggs (0-2 scale)	Insects Alive %
AC01151-5W	0.8	41.7
AC03433-1W	0.0	0.0
AF 4157-6	0.0	0.0
AF 5040-8	0.0	33.3
B 2727-2	0.0	22.2
CO 02321-4W	0.0	33.3
Lamoka	0.0	0.0
MSV 313-2	0.0	33.3
MSV 358-3	0.0	0.0
MSV030-4	0.0	25.0
MSW 485-2	0.0	0.0
MSX 540-4	0.0	16.7
NDA081453CAB-2C	0.0	0.0
NDTX081648CB-13W	0.0	8.3
NY 121	0.0	8.3
NY 152	0.3	33.3
TX09396-1W	0.0	11.1
W 5955-1	0.0	37.5
W 8822-1	0.0	0.0
W 9968-5	0.0	0.0
Snowden†	0.0	25.0
Mean	*0.0*	*15.7*
St. error	0.0	3.3
Min	0.0	0.0
Max	0.8	41.7
Count	21.0	21.0

†Snowden was used as the standard chipping variety check.

Table A15. Production and size of tubers of NCPT potato clones grown under field conditions near Springlake, TX in 2017. Least square means of average tuber number per plant, average weight per tuber, and average yield per plant.

	Average Tuber Number		Average Weight per Tuber (g)		Average Yield (g)	
Clone	Infested	Non-infested	Infested	Non-infested	Infested	Non-infested
AC01151-5W	26.8	23.0	32.7	40.7	848.2	975.2
AC03433-1W	3.3	3.5	68.8	49.1	232.8	172.4
AF 4157-6	10.7	13.0	61.1	41.0	595.7	576.1
AF 5040-8	7.5	4.5	91.9	87.3	694.0	381.0
B 2727-2	5.7	6.0	68.3	133.1	396.1	798.3
CO 02321-4W	9.7	4.0	95.9	88.5	889.0	353.8
Lamoka	9.0	5.5	55.7	45.0	462.7	231.3
MSV 313-2	7.0	1.0	141.3	54.4	988.8	54.4
MSV 358-3	6.0	3.0	59.3	99.8	362.9	390.1
MSV030-4	12.3	9.5	63.3	59.4	759.8	580.6
MSW 485-2	16.3	23.5	84.9	60.4	1342.6	1428.8
MSX 540-4	10.0	9.5	79.8	61.0	793.8	576.1
NDA081453CA B-2C	17.8	16.0	52.3	55.8	895.8	970.7
NDTX081648C B-13W	19.0	24.5	64.4	58.6	1197.5	1519.5
NY 121	9.5	9.0	33.5	30.2	292.6	272.2
NY 152	11.5	10.5	63.4	73.4	809.7	762.0
TX09396-1W	11.7	4.0	98.1	52.2	843.7	208.7
W 5955-1	9.3	5.0	75.3	94.3	675.9	471.7
W 8822-1	9.0	11.5	51.0	37.7	444.5	467.2
W 9968-5	13.0	11.5	60.4	40.0	773.4	476.3
Snowden†	7.5	10.5	78.3	77.2	587.4	802.9
Mean	*11.1*	*9.9*	*70.5*	*63.8*	*708.9*	*593.8*
St. error	1.1	1.5	5.1	5.4	60.7	82.4
Min	3.3	1.0	32.7	30.2	232.8	54.4
Max	26.8	24.5	141.3	133.1	1342.6	1519.5
Count	21.0	21.0	21.0	21.0	21.0	21.0

†Snowden was used as the standard chipping variety check