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Palmer Amaranth (*Amaranthus palmeri* S. Wats.) and Waterhemp [*Amaranthus tuberculatus* (Moq.) J.D. Sauer] Biovigilance in Canadian Agro-ecosystems.

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Abstract

The evolution and spread of herbicide-resistant weeds threatens long-term sustainability of Canadian agro-ecosystems. Herbicide-resistant weeds increase management inputs and costs, increases off-target and environmental exposure to pesticides, reduces yield quality and quantity, and impedes harvest efficiency. *Amaranthus* species including Palmer amaranth (*Amaranthus palmeri* S. Wats.) and waterhemp [*Amaranthus tuberculatus* (Moq.) J.D. Sauer] are particularly concerning due to both their propensity towards herbicide resistance evolution, their history of invasion, and their spread in agro-ecosystems. A biovigilance approach is taken to build awareness of these pigweeds initial invasion and spread in the USA. Characteristics of their identification, potential hybridization, and known herbicide resistance evolution are reviewed. Fourteen species of *Amaranthus* are found in Canada, nine of which (including waterhemp) possess herbicide-resistant biotypes. A total of forty-five hybrids between various Canadian *Amaranthus* species with each other or Palmer amaranth have been noted. Hybrids have been experimentally produced or observed from herbarium specimens, with three cases of herbicide resistance transfer notably with Palmer amaranth or waterhemp. Mitigation strategies will depend on successful species identification and herbicide resistance status determination. Common pathways for Palmer amaranth introductions in the northern USA include both animal feed systems with grain screenings and crop production systems including seed and equipment contamination. Regional awareness campaigns will be critical to support Canadian farmers in identifying and quickly mitigating invasions of Palmer amaranth and waterhemp to prevent establishment and spread of infestations into new areas.

Keywords: Awareness; Detection; Assessment; Understanding; Mitigation; Appropriateness

Introduction

Biovigilance is a research approach which studies and anticipates the unintentional effects of climate change, pest introductions, and new agricultural productions and practices on pest populations, plant health, environmental health, and biodiversity, to adapt agricultural practices to cope with these changes (Carisse et al. 2017). The biovigilance research continuum includes six steps which are interconnected with cyclical feedback into the continuum: 1) awareness, 2) detection or identification, 3) assessment, 4) understanding, 5) mitigation, and 6) appropriateness (Figure 1). The end goal of the biovigilance continuum is to provide a framework for more rapid, flexible, and effective response to crop pests (Carisse et al. 2017). The purpose of this review is to adapt the biovigilance continuum to the invasive species Palmer amaranth (*Amaranthus palmeri* S. Wats.) which has yet to establish a stable foothold in Canada and the closely related species waterhemp [*A. tuberculatus* (Moq) J.D. Sauer] which is established in the provinces of Ontario and Quebec and spreading in Manitoba. This review will focus on developing awareness of the threat of these species to Canadian agriculture based on its history and ecology, identifying potential tools for detection and assessment activities, developing an understanding of how these weeds could be a threat in Canadian agro-ecosystems, some direction for potential mitigation options, and lastly, appropriateness considerations and future directions.

1. Awareness – Anticipating the Threat

Palmer Amaranth

Palmer amaranth is an annual C4 plant that was first described by Sereno Waston in 1877 as "dioecious, rather stout" from samples collected in California by Dr. E. Palmer and various other collectors from along the Rio Grande in Arizona and California. Sauer (1955) included the species in his revision of the dioecious *Amaranthus* species. He described the range of the species as encompassing the south-central USA, from California east to Oklahoma and, south into northern and central Mexico, to the Mexican states of Chilpancingo and Puebla but noted that records of the species suggested a recent "substantial" expansion both northeastward and southeastward (Sauer 1957). He, and others, indicated that the pre-colonial historical range (circa 1900) appeared to be largely confined within the Sonoran Desert ecoregion including Sonora, Mexico and the southwestern USA states of California, Arizona, New Mexico, and Texas (Ehleringer 1983; Sauer 1957; Welkie and Caldwell 1970). However, the species has now spread widely from this initial geographic range. Palmer amaranth is currently a high priority herbicide-resistant weed with a widespread distribution in the USA (Roberts and Florentine 2022; GBIF 2022). This represents approximately 125 Palmer amaranth lifecycles since the 1900s initial historical range accounting.

While the origins of Palmer amaranth remain elusive, prior to colonization it may have been either a grain amaranth for food or ceremony, or a weedy Vavlovian mimic to other grain amaranths. The species served as an important potherb and grain for several Indigenous groups in its range (Sauer 1955). Prior to Spanish contact, Palmer amaranth was sown or permitted to naturalize into maize fields (Sauer 1950). The initial historic range within the Sonoran Desert ecoregion may have been influenced by the aggressive punishments for amaranth cultivation established during the Spanish conquest of the Aztec Empire during the 1500s (Sauer 1950) which would be unaccounted for in herbarium records due to their later establishment. Notably,

while Sauer (1955) does indicate that there was no evidence of systematic cultivation of Palmer amaranth but the availability of such information may be limited due to the destruction of indigenous writing during Spanish conquest and colonization (Don 2012) many centuries before Sauer's writing. Anecdotally, the plant habit of Palmer amaranth at maturity, particularly the elongated, open seed head, does resemble a grain amaranth more so than other weedy amaranths, and was used in detection for eradication activities in Minnesota (Yu et al. 2021).

Comparative plant anatomy may support some degree of domestication of Palmer amaranth prior to Spanish contact, both as a grain and a potherb. Two important domestication traits considered for Levantine grain archaeobotany were increased seed size and indehiscence (pod/capsule/seed) (Weiss and Zohary 2011). Palmer amaranth seeds (1 to 1.25 mm diameter) (Sauer 1955) are similar to cultivate grain amaranths (*Amaranthus cruentus* L.) (1.1 to 1.24 mm diameter) (Abalone et al. 2004) whereas waterhemp [*A. tuberculatus* (Moq) J.D. Sauer] seed are smaller (0.75 to 1 mm in diameter) (Sauer 1955). Palmer amaranth has been shown to shatter (Schwartz-Lazaro et al. 2017), but many grain amaranth also have slight to severe shattering at maturity (Kauffman 1992). Reduced shattering was identified as an important grain amaranth breeding target in the early 2000s (Brenner 2002) suggesting this might not be as a reliable an indicator of previous selection this genus. Shattering is an identifying characteristic of two waterhemp biotypes, present in the more invasive form suggesting weediness adapations (Costea et al. 2005). Palmer amaranth stalks typically remain upright due to stem strength well after winter kill (Brenner 2002). This may be an ease of harvest adaption or selection from gathering itself in the fall after senescence. This trait may be more important to Palmer amaranth than shattering itself due to weedy and thinned amaranths being used as a potherb (Sauer 1967).

Palmer amaranth was used as a potherb by indigenous communities in its range (Sauer 1955). Young amaranth leaves and shoots are gathered from either thinned grain amaranth stands or weedy relatives and boiled when consumed as potherb (Sauer 1967). Spinach (*Spinacia oleracea* L.) is a leafy vegetable and it showed very little evidence of domestication syndrome compared to wild relatives, the most notable being flower morphology (Ribera et al. 2020). Kale (*Brassica oleraceae* L.) domestication syndrome traits included apical dominance, leaf morphology, delayed flowering, taste/defense, and nutritional value (Arias et al. 2021). Denham et al. (2020) described several domestication syndrome traits for grasses, herbs, and tuberous plants including yield of the edible portion, plant lifecycle, and defensive adaptions. Floral and lifecycle considerations may be convoluted due to dual-selection as a grain and potherb. Palmer amaranth leaves and stems are hairless compared to other pigweeds (Yu et al. 2021) which could be a taste/defense trade-off. Reports of gathering weedy amaranths and grain amaranth (Sauer 1967) may have produced selection similarities to spinach resembling its wild relatives (Ribera et al. 2020) since pigweed identification early in its growth cycle is challenging (Yu et al. 2021).

Using language and carbon dating techniques, the identified pre-colonial historic range of Palmer amaranth does overlap with the northern reaches of agricultural land from the domestication epicenter in central Mexico (Diamond and Bellwood 2003). This area overlaps with the furthest reaches of the diffusion pathway from the Meso-American epicenter (Diamond and Bellwood 2003; Larson et al. 2014). By the 1950s, Palmer amaranth's naturalized range moved south towards the central Mexico domestication epicenter, with nearly half the observed specimens in artificial environments (Sauer 1957). This may be indicative that this species was well adapted to invade and establish into these pre-colonial domesticated systems in proximity to

the epicenter itself, which dates approximately 4000 years before present (Diamond and Bellwood 2003).

Agriculture in the USA was rapidly expanding through the 1800s in response to colonialization, then slowed dramatically by 1900 (Coulter 1912). Early Palmer amaranth herbarium records prior to the 1910s show its limited range with additional observations within Utah in 1888, Kansas in 1895, Illinois in 1896, and Missouri in 1897 (Sauer 1955; Sauer 1957; GBIF 2022). The 1910's are notable for the gasoline-powered tractor agricultural expansion (Dieffenbach and Gray 1960). The distribution range of Palmer amaranth when assessed in 1956 included a substantial increase from its historic range northward, southward, and eastward, overlapping the range of two other *Amaranthus* species (Sauer 1957). Palmer amaranth was first identified in Oklahoma in 1926, in Pennsylvania in 1933, in New York in 1936 (Sauer 1955; Sauer 1957) reaching Arkansas in 1962, Florida in 1967 and West Virgina in 1970 (Sauer 1972). Palmer amaranth's southern invasion into Mexican states was more widespread. It was first identified in San Luis Potosi in 1876, Chihuahua in 1885, Jalisco in 1886, Baja California in 1887, Nayarit in 1892, Durango in 1897, Colima in 1897, Quertaro in 1913, Mexico in 1932, Guerrero in 1934, Coahuila in 1940, and Puebla in 1947 (Sauer 1955). Sauer (1972) also noted a seedless specimen from Lambton, Ontario collected in 1963, deeming it the first Canadian record, as well as records in Sweden, England, Netherlands, Luxembourg, Germany and Austria. Currently, the species is considered introduced across much of the USA, and in Argentina, China, Cuba, Czechoslovakia, Denmark, the Dominican Republic, Egypt, Ethiopia, Finland, France, Great Britain, Greece, Italy, Korea, Maderia, Norway, Palestine, Primorye, Spain, Sweden, Tunisia, and Turkey (POWO 2024).

Waterhemp

As a whole, the genus *Amaranthus* is afflicted with a variety of taxonomic challenges (see section 1.3.1). The taxon referred to as waterhemp, an annual, dioecious, C4 plant, is no exception. It has had various taxonomic names and circumscriptions resulting from the taxon's variability in height and form, its flexibility in flowering time, as well as its propensity to hybridize with other taxa (Sauer 1955{Sauer, 1972 #775)(Sauer 1955; Sauer 1957). Currently, some treatments recognize two varieties *A. tuberculatus* var. *tuberculatus* (Moq.) J. D Sauer and *A. tuberculatus* var. *rudis* (J. D. Sauer) Costea & Tardif. (Costea and Tardif 2003), but others do not (FNAEC 1993+; POWO 2024; Voss and Reznicek 2012) and the weed science literature is inconsistent in distinguishing between the varieties.

Sauer recognized ten dioecious species in his 1955 revision of the group including *A. tuberculatus* and *A. tamariscinus*. These two species were described as having overlapping ranges with A. *tuberculatus* reaching further north, into Ontario and Quebec, Canada, and further east, into Vermont, New York and south through western Ohio, Kentucky and Oklahoma into Missouri and northwestern Alabama. *Amaranthus tamariscinus*'s range was defined as more central and southern, spanning from North Dakota to Indiana down to Texas (Sauer 1957). He Sauer (1957) noted that the species hybridized where they overlapped and that, while the range of *A. tuberculatus* seemed to have been largely static over the last hundred years, the range of *A. tamariscinus* had been consistently expanding its eastern and northern range limits. Sauer (1972) later determined that the type specimen of *A. tamariscinus* (the material the taxonomic identity was officially based on) was a sterile hybrid and created the new name *A. rudis* Sauer. to refer to individuals of the taxon. The species were then reduced to a single species, *A. tuberculatus,* by Pratt and Clark (2001), who suggested that the two taxa represented ends of a morphological continuum of a single polymorphic taxon. Recently Costea and Tardif (2003) suggested division

of the taxon into two varieties based on differences in morphology and ecology with *A. tuberculatus* var. *rudis* the weedier lineage(Costea and Tardif 2003).

Recent population genomic studies have determined that there are two lineages corresponding to those recognized by Sauer and Costea and Tardif (Kreiner et al. 2019). Populations from non-agricultural lands in Ontario were homogenous for ancestry corresponding to *A. tuberculatus* var. *tuberculatus,* while populations from Missouri showed homogeneity for the *A. tuberculatus* var. *rudis* lineage and, over all, longitude and latitude explained a significant portion of the genetic variation observed. However, (Kreiner et al. 2019); Kreiner et al. (2021) also found evidence of introgression of genes resulting in admixture of the lineages in samples from areas of historical overlap in Illinois and in agricultural populations in Ontario. Further, glyphosate resistant populations in Ontario were determined to have two evolutionary origins, one showing derivation from the *rudis* lineage indicating an introduction from the USA, and the other showing derivation from the *tuberculatus* lineage with adaptation to agricultural environments potentially facilitated by genes from the *rudis* lineage. As a result, from a biovigilance perspective, genes for success in agricultural environments may predominantly originate from the *rudis* lineage and genes for adaptation to the species' current northern range limit may predominantly originate from the *tuberculatus* lineage, but weedy, herbicide resistant individuals could be derived from either lineage or a mixture of the two. Waterhemp has not spread as widely as Palmer amaranth, however it is currently recognized as having spread across much of the USA and have been introduced to Canada, Czechoslovakia, Italy, Palestine, and Spain (POWO 2024).

1.1 Resistance Evolution

Palmer Amaranth

Herbicide resistance cases for Palmer amaranth were first documented in the USA in 1989 (Heap 2023). Within ten years there was nine reports of Group 2-, 3-, or 5-resistant biotypes from, Kansas, Arkansas, Texas, Tennessee, North Carolina, and South Carolina, typically involving rotations of corn (*Zea mays* L.), soybean (*Glycine max* (L.) Marr.), and cotton (*Gossypium hirsutum* L. and *Gossypium barbadense* L.) production (Heap 2023). Glyphosate-resistance (Group 9) was first confirmed in Georgia and North Carolina in 2005, hydroxyphenyl pyruvate dioxygenase (HPPD) inhibitor resistance (Group 27) in Kansas in 2009, the emergence of Group 14 resistance was documented in Arkansas in 2011, 2,4-D (Group 4) resistance in Arkansas in 2015, *S*-metolachlor (Group 15) resistance was identified in Arkansas in 2016, and finally, the evolution of glufosinate resistance (Group 10) in 2020 in Arkansas (Heap 2023). Currently, many of the herbicide resistances are found as "stacked" traits with for examples, biotypes in Kansas showing six-way resistance to Groups: 2, 5, 6, 9, 14, and 27 (Shyam et al. 2021) and, in Arkansas, showing five-way resistance to Groups: 2, 3, 9, 14, and 15 (Schwartz-Lazaro et al. 2017).

Palmer amaranth first evolved resistance against triufluralin (Group 3) in 1989 in eight corn, soybean, or cotton fields within two South Carolina counties (Gossett et al. 1992; Heap 2023). Trifluralin was first publicly used in 1963 (Timmons 1970). Gossett et al. (1992) reports that trifluralin-resistant Palmer amaranth was suspected for several years on the Coastal Plains region of South Carolina and that the field had been treated for twenty-four consecutive years with trifluralin (Gossett et al. 1992). Group 3 (trifluralin) resistance also evolved in cotton and soybean production systems within Tennessee in 1998 (Heap 2023). Group 3 resistance in Arkansas was attributed to metabolism mediated by glutathione S-transferase (GST) but not

P450-mediated metabolism or due to target site mutations in α- and β- tubulin (González-Torralva and Norsworthy 2021).

Palmer amaranth became widespread in Kansas, with invasion into Missouri and Illinois cropping systems by 1995, while waterhemp was the dominant pigweed in the midwest (Wax 1995). Within five years in the mid-1990's, another eight resistant Palmer amaranth biotypes were reported: an atrazine-resistant (Group 5) population in Texas corn and sorghum (*Sorghum bicolor* (L.) Moench) in 1993, a Group 2-resistant biotype in Arkansas soybean in 1994, a Group 2-resistant biotype (chlorimuron-ethyl) in North Carolina soybean in 1995, and Group 2-resistant biotypes (imazapic, imazaquin, and imazethapyr) in South Carolina corn, cotton, soybean, and peanut (*Arachis hypogaea* L.) in 1997 (Heap 2023). Group 2 resistance in Palmer amaranth was due to target-site mutations (Franssen et al. 2001; Kohrt et al. 2017; Shyam et al. 2021; Singh et al. 2019) while Group 5 resistance was typically metabolism-based (Chahal et al. 2019; Kohrt et al. 2017; Nakka et al. 2017; Shyam et al. 2021). The reduction in soil applied herbicides, cultivation, and adoption of less effective postemergence herbicide applications reportedly favored pigweed escape in the midwest (Wax 1995). (Foes et al. 1998; Franssen et al. 2001; Shyam et al. 2021; Singh et al. 2019)

Glyphosate was first publicly available in the early 1970s (Appleby 2005). Glyphosate-resistant crops including corn, soybean, and cotton, became publicly available for planting in 1996 (Benbrook 2016). Glyphosate-resistant Palmer amaranth was first confirmed in Georgia and North Carolina in 2005, Arkansas, South Carolina, and Tennessee in 2006, and New Mexico in 2007 (Culpepper et al. 2006; Heap 2023). These reports are from corn, cotton, and soybean production systems. In 2012, Group 9- (glyphosate) and Group 2-resistant (imazapic) Palmer amaranth was confirmed in north west and north central Florida peanut and cotton (Berger et al.

2015). Glyphosate-resistance in Palmer amaranth can be a result of increased EPSPS copy number via gene amplification (Gaines et al. 2011; Kohrt et al. 2017; Oliveira et al. 2021). Gene amplification in Palmer amaranth is a result of an extrachromosomal circular DNA replicon which harbours the EPSPS gene and 59 others, 41 of which were transcribed during glyphosate stress (Molin et al. 2020). Alternatively, Palmer amaranth from Mexico evolved both target-site (amino acid substitutions) and differences in absorption and translocation as resistance mechanisms (Dominguez-Valenzuela et al. 2017).

In 2011, Group 14 resistance was documented in Arkansas, then in 2015 in Tennessee, 2016 in Illinois and Arkansas (Heap 2023). The resistance mechanism in an Arkansas population was found to be a target site mutation, with a glycine 210 deletion on the PPX2 gene (Salas et al. 2016). Alternatively, Tennessee biotypes contained two different amino acid substitutions in the PPX2 gene (Copeland et al. 2018). A six-way resistant biotype from Kansas (Groups 2, 4, 5, 9, 14, 27) where the biotype contained target site mutations for Group 2 (imazethapyr) resistance and metabolism via P450 or GST resulted in Group 4 (2,4-D), Group 14 (lactofen), and Group 27 (mesotrione) resistance (Shyam et al. 2021). Evolution of metabolic-resistant Palmer amaranth is a concerning development given the potential for resistance towards modes of action not previously employed.

Lastly, glufosinate-resistant Palmer amaranth was detected in cotton production in Arkansas in 2020 and North Carolina in 2022 (Heap 2023). Resistance ratios for two Arkansas populations ranged from 16.9 to 27.4 (Priess et al. 2022). Glufosinate-resistance was due to gene amplification and expression of chloroplastic glutamine synthase enzyme (Carvalho-Moore et al. 2022). Overall, Palmer amaranth has displayed a complex adaptation to agro-ecosystems, with resistance evolution against eight modes of action: Group 2, 3, 4, 5, 9, 10, 14, 15, and 27 through

a variety of mechanisms including metabolism, target-site mutations, altered absorption and translocation, and gene amplification.

Waterhemp

Herbicide-resistant waterhemp was first documented in the USA in 1993 in corn and soybean production (Horak and Peterson 1995; Sprague et al. 1997). Group 5 resistance was detected for this species in Missouri corn in 1993, and Group 14 resistance in Kansas soybean in 2001 (Heap 2023). Similar to Palmer amaranth, many resistances are found as "stacked" traits in this species. For example, the first 3-way resistant waterhemp biotype was identified in Missouri (Groups 2, 5, and 14) in 2005. Glyphosate-resistant (Group 9) waterhemp was first documented in Missouri in 2005, which was also three-way resistant (Groups 2, 9, and 14) biotype (Heap 2023). Resistance towards HPPD inhibitors (Group 27) was first documented in in 2009, Group 4 resistance in 2009, and Group 15 resistance in 2016 (Heap 2023). Recently, two waterhemp biotypes with 5-way resistance to these herbicides (Groups 2, 5, 9, 14, and 27) have been identified in Ontario and North Carolina (Heap 2023).

Multiple herbicide-resistant waterhemp (Groups 2 and 5) was first documented in soybean production in Ontario Canada in 2002 (Heap 2023). Waterhemp resistance mechanisms against Group 2 chemistry have been shown to be based on target site mutations via amino acid substitutions (Bell et al. 2013; Foes et al. 1998; Patzoldt and Tranel 2007; Schultz et al. 2015) and nontarget-site resistance has been noted (Guo et al. 2015). Waterhemp resistance mechanisms for Group 5 chemistry include target site mutations (Foes et al. 1998) and metabolism via GST (Ma et al. 2013; Vennapusa et al. 2018).

Glyphosate-resistant waterhemp was first detected in 2005 in Missouri corn and soybean systems, 2006 in Kansas, Illinois, Texas, and 2007 in in Minnesota (Heap 2023). Like Palmer amaranth, waterhemp populations have shown a diverse number of Group 9 resistance mechanisms including gene amplification (Chatham et al. 2015; Murphy et al. 2019), reduced translocation (Nandula et al. 2013), and target site mutations (Murphy et al. 2019; Nandula et al. 2013).

Group 14 resistant waterhemp was first documented in Kansas in 2001 (Shoup et al. 2003). Group 14 resistant waterhemp evolved due to a codon deletion in the PPO gene (Bell et al. 2013; Murphy et al. 2019; Patzoldt et al. 2006). Multiple herbicide-resistant waterhemp have shown to have multiple adaptations to various modes of action. For example, in a survey of Missouri waterhemp populations in 2012 showed at least 52% of samples were resistant two modes of action, 11% to three modes of action, and 2% to four modes of action, and 1 population with five-way resistance (Groups 2, 5, 9, 14, and 27) (Schultz et al. 2015). Resistance mechanisms found included: target site mutations providing Group 2 resistance ($Trp^{574}Leu$ substitution), Group 9 resistance ($Pro^{106}Ser$ amino acid substitution), Group 14 resistance (Δ210 deletion), and increased EPSPS transcript copy number for Group 9 resistance.

Group 27 resistance was first detected in Iowa in 2009 (Heap 2023). The mechanism of Group 27 resistance is through P450 metabolism (Ma et al. 2013). Group 4 resistance was first found in 2009 within a multiple-herbicide resistant waterhemp biotype in Nebraska (Heap 2023). This waterhemp biotype demonstrated a 10 fold increase in resistance for 2,4-D (Bernards et al. 2012). Waterhemp resistance to 2,4-D was found to be metabolism-based (Figueiredo et al. 2018). Lastly, Group 15 resistance was detected in Illinois corn and soybean in 2016 (Strom et al. 2019). The mechanism of Group 15 resistance in waterhemp was also metabolism-based

(Strom et al. 2020). Overall, waterhemp has evolved resistance towards seven modes of action: Groups 2, 4, 5, 9, 14, 15, and 27 and uses a variety of resistance mechanisms including metabolism, target site mutations, and gene amplification.

1.2 Canadian Border

Palmer amaranth distributions were modeled using CLIMEX to examine future climate projections of its suitable range (Kistner and Hatfield 2018). Both the GFDL-ESM2M and CNRM-CM5 2050 representative concentration pathway 8.5 emission scenario for 2050 showed that land north of the USA and Canadian border change from unsuitable to suboptimal growing conditions for Palmer amaranth. Palmer amaranth was first discovered in South Dakota in 2015 (Van De Stroet and Clay 2019). Palmer amaranth was first discovered in North Dakota in 2018 within five counties: McIntosh, Benson, Dickey, Foster, and Richland (Peters 2018; Peters and Jenks 2018). The extension service explained that the suspected means of dispersal into each county was different and included migratory birds, a used combine, alternative feedstock purchased out of state, custom combining, and contamination from grain cleaned out of railroad cars (Peters 2018). While there are no known persistent populations in Canada, viable seeds were transported in sweet potato [*Ipomoea batatas* (L.) Lam] slips in from North Carolina (Page et al. 2021) and recent "waifs" have been found in Manitoba (Booker 2021) and Ontario (Cowbourgh 2023).

1.3 Ecological Considerations

1.3.1 Hybridization

Amaranthus species pose challenges to biovigilance efforts from two main perspectives: 1) the ability of *Amaranthus* species to form hybrids and potentially transfer herbicide resistance or

other weedy traits through introgression; and 2) a lack of information on which *Amaranthus* species are present in the Canadian landscape due to a lack of collection and difficulties in identification with either morphological or molecular characteristics.

Hybridization among *Amaranthus* species in North America has long been recognized by taxonomists with specimens identified as hybrids over 150 years ago (Sauer 1957). Hybrids often exhibit a mixture of morphological traits from each parent. The frequency of these hybrid individuals and significant phenotypic plasticity or environment induced variation with *Amaranthus* species results in substantial difficulties identifying specimens to species level. This has led to "nomenclatural disorder and confusion" and has caused at least one author to despair that the literature on *Amaranthus* only preserves scattered bits of usable information because of doubtful taxonomy (Sauer 1957). This, and changes to names, changes in species status, and a lack of identification of material to sub-specific taxon, leads to difficulties in interpreting results in both the historical and recent literature. This difficulty in identifying species and their hybrids, especially advanced generation hybrids (Costea and Tardif 2003; Sauer 1957) and under collection of the genus, will mean that some hybrids and hybrid combinations have not been recognized in herbaria collections. Further, the parentage of hybrid material has usually been inferred based on familiarity with the morphological characteristics and observed presence of the parental species. This may frequently lead to the correct conclusion, but in some cases the true parentage of hybrids or even the very hybridity of the specimen would not be supported by further analysis. As a result, the level of hybridization and number of potential combinations, as extensive as it appears, may be under appreciated. This and the “speedy transition from flagrant to subtle hybridity" noted by Sauer (1957) may mean that the gene pools of many *Amaranthus* species have strong genetic connections that allow for introgression of key traits such as

herbicide resistance. The overall ability to hybridize among *Amaranthus* species has been described by breeders as "erratic" (Brenner et al. 2000) and is likely strongly influenced by the evolutionary relationships of the species involved in the cross and the sub-genome composition of these older polyploid lineages (only one species in *Amaranthus* is known to be a recent polyploid from the base chromosome number (2n = 16, 17) *A. dubious* Mart. ex Thell. (2n=32)). Despite the extensive previous work, our understanding of the systematics of the genus still requires further elucidation.

Amaranthus includes approximately 70 to 75 annual plant species including pseudocereals, vegetable crops and their wild relatives (Bayón 2015; Brenner et al. 2000; Costea and Tardif 2003). The majority of species are native to North or South America while the rest are distributed through Africa, Asia, Australia, and Europe. In North America the majority of taxa are monecious, with separate male and female flowers on the same plant, while fewer are dioecious, with male and female flowers on separate plants (Costea et al. 2001b). The genus has been divided into three subgenera *Acnida*, *Amaranthus*, and *Albersia* with all dioecious species assigned to *Acnida* and North American monecious taxa included in both *Amaranthus* and *Albersia* (Costea et al. 2001a; Mosyakin and Robertson 1996). However, taxonomists working with this difficult genus have noted their dissatisfaction with elements of this system and hybridization between dioecious and monoecious taxa suggests some are more closely related than indicated by this classification system. Recent molecular work using chloroplast and low copy nuclear markers has borne up these reservations indicating that placing all dioecious species together in the sub-genus *Acnida* oversimplifies evolution within *Amaranthus* (Waselkov et al. 2018). Only a handful of the species, mostly the crop species and their wild relatives, have been investigated to determine their sub-genome composition (Brenner et al.

2000). Additional genome sequencing and population level genome comparisons are needed to fill this gap and clarify the evolutionary relationships among taxa, their reticulate allopolyploid origins, and the degree of historical introgression among the species (e.g. (Kreiner et al. 2019)). In the absence of this information or other experimental work, species that form mixed populations within Canada or which come into contact within Canada should be considered likely to form hybrids.

Costea and Tardif (2003) reviewed herbarium collections and determined that 14 species have been collected in Canada and that eight of these are native or naturalized (Table 1). However, they highlight that the genus is under collected and poorly represented in herbaria collections echoing previous statements calling collections seriously deficient (Sauer 1957). This is unlikely to have changed in the 20 years since their work as few resources are dedicated to collection, herbaria continue to close or limit acceptance of new collections due to space constraints, and plant taxonomists continue to retire and not be replaced. Further, resources often considered as having replaced the need for taxonomists with boots on the ground, such as iNaturalist, include few observations of these frequently uncharismatic species and, when they do, do not include the detailed, often magnified, observations of female flower's floral morphology required to confirm species identification. As a result, the identifications applied to reports of *Amaranthus* species on these platforms is frequently suspect, if not erroneous. It is therefore certain that a lack of observational data continues to underlie a significant gap in our understanding of the distribution of *Amaranthus* species in Canada representing a significant risk for biovigilance efforts. Costea and Tardif (2003) suggest more *Amaranthus* species are likely present in Canada than is currently known. Specifically, several weedy species such as sand amaranth (*A. arenicola* Johnst.) and large-fruit amaranth (*A. deflexus* L.) occur in or have

invaded USA states sharing a border with Canada or are invasive elsewhere in the world with similar climates (Table 2). These species may have undiscovered populations within Canadian provinces or territories. An example of this type of addition to the Canadian flora from the USA is Palmer amaranth which was recently detected in Manitoba (Booker 2021) and in Ontario (Cowbrough 2023). Climate change may also bring new species not currently considered invasive into Canada such as salt marsh pigweed (*A. cannabinus* (L.) Sauer) and open new possibilities for hybridization. Finally, it is worth considering that even a species present only ephemerally in Canada could contribute to hybrid formation.

Six hybrids were documented by Costea and Tardif (2003) as present within collections from Canada (Table 3). Most of these hybrid taxa are combinations of redroot pigweed (*A. retroflexus* L.), Powell amaranth (*A. powellii* S. Wats.), and smooth pigweed (*A. hybridus* L.) which can create hybrids in any combination, but also includes hybrids between tumble pigweed (*A. albus* L.) and prostrate pigweed (*A. blitoides* S. Wats.). Numerous other hybrids have also been documented in material collected outside of Canada or generated artificially in experimental work involving species that are either currently present in Canada or are potential invaders. Further, three of the *Amaranthus* species most frequently grown for grain, *A. caudatus* L., *A. cruentus* L. and *A. hypochondriacus* L., can be grown in Canada. All are reported to have some crossing compatibility with eighteen currently recognized *Amaranthus* taxa (Table 4). Beyond these combinations breeders have also used bridge species and polyploidization to transfer traits between species with greater incompatibility (Brenner et al. 2000). Brenner et al. (2000) note that while fertility is expected to be lower in hybrids it is generally high enough to allow transfer of traits between species – a consequence, perhaps, of 5% fertility still potentially resulting in 5,000 seeds/plant. As a result, in addition to the currently documented cases of

transfer of herbicide resistance genes between *Amaranthus* species (noted in Table 3), numerous hybridization pathways likely exist for these genes to enter weedy *Amaranthus* populations.

Unsurprisingly, given the number of species of interest, many potentially important reproductive combinations have not been tested. For example, key combinations for Canada, such as Palmer amaranth's ability to cross with the common weedy species tumble pigweed or the potentially problematic species purple amaranth (*A. blitum* S. Wats.) do not appear to have been tested. In other cases follow up work is needed: previous work by Murray (1940) determined waterhemp varieties can cross with redroot pigweed, but the potential for introgression of herbicide resistance into redroot pigweed populations still needs to be explored. It is important that future work on hybridization in *Amaranthus* use molecular markers to document hybridity (Trucco et al. 2007). Additionally, herbarium records of parental or hybrid material, which includes the features need for identification – mature female flowers (Costea and Tardif 2003) should be created, deposited at a herbarium, and cited the paper. This will ensure that the value of the work will be maintained even if significant nomenclatural changes occur within the genus and clarification of the taxa used in the study is needed (Carter et al. 2017). These types of experiments would support future biovigilance work and focus attention on potentially problematic combinations, especially if combined with programs focused on maintaining plant taxonomy skills and collection efforts in Canada.

1.3.2 Population Dynamics

Palmer amaranth and waterhemp are known to produce a substantial amount of seed in the absence of plant interference. Both species can produce up to and in excess of 1 million seeds plant^{-1}. Seed production can occur through both sexual reproduction and apomixis for both Palmer amaranth (Roberts and Florentine 2022) and waterhemp (Franssen et al. 2001; Sarangi et

al. 2017). As dioecious species, pollination must occur between a male and a female plant for reproductive development to occur in both Palmer amaranth (Sosnoskie et al. 2012) and waterhemp. Palmer amaranth typically produces between 200,000 and 1 million seeds plant^{-1} in uncompetitive environments (Roberts and Florentine 2022). Palmer amaranth at a density of 5.2 plants m^{-1} row produced 1.2 billion seeds ha^{-1} (Burke et al. 2007). High densities of Palmer amaranth produced up to 1.5 million seeds m^{-2} in wide-row soybean in Arkansas (Korres and Norsworthy 2017). Waterhemp plants produced about 300,000 to 2.3 million seeds plant^{-1} in Iowa soybean production, dependent on location (Hartzler et al. 2004).

Fecundity of Palmer amaranth and waterhemp both decline with later emergence dates (Hartzler et al. 2004; Keeley et al. 1987; Spaunhorst et al. 2018). In California, Palmer amaranth plants that emerged in March or June produced about 600,000 seeds plant^{-1}, while those that emerged between July and September produced 115 to 80,000 seeds plant^{-1} (Keeley et al. 1987). Flowering hastened as daylength decreased. For example, plants had produced 181 seeds on average by 6 weeks after planting Palmer amaranth seeds on August 01, while those planted on March 01 had not produced seeds by 12 weeks after planting. The first cohort of glyphosate-resistant Palmer amaranth that emerged in Georgia produced 446,000 seeds plant^{-1} in the absence of competition, and fecundity declined by 50% when plants emerged about six weeks later (Webster and Grey 2015). In the same study, interference from a cotton crop reduced fecundity of the first Palmer amaranth cohort to 312,000 seeds plant^{-1} and also shifted time to 50% seed production about 1 month earlier compared with the absence of competition. The fecundity of multiple Palmer amaranth accessions tended to decline with later emergence dates in Indiana and Arkansas, however, this effect depended on the site-year and accession (Spaunhorst et al. 2018). Among years and accessions, Palmer amaranth produced 44,988 seeds plant^{-1} when emerging in

early June in Indiana and 34,266 seeds plant^{-1} when emerging in mid-June. In Arkansas, Palmer amaranth seed production averaged 170,399, 137,852, and 53,872 seeds plant^{-1} when transplanted into the field in mid-May, mid-June, and the beginning of August, respectively. In contrast, waterhemp established in May, June, and July produced on average 926,629, 828,905, and 276,258 seeds plant^{-1} in Indiana (Heneghan and Johnson 2017). Waterhemp cohorts that emerged in Iowa in early July produced 50-75% fewer seeds compared with the most-fecund, earlier-emerging cohorts (Wu and Owen 2014). Mean Palmer amaranth seed production in soybean ranged among midwest and upper-south USA states and years from 11,833 to 60,221 seeds plant^{-1} with a grand mean of 33,888 seeds plant^{-1} (Schwartz et al. 2016). Tall waterhemp seed production was numerically greater than Palmer amaranth, however. For example, state-wide mean tall waterhemp fecundity in soybean ranged from 17,459 to 82,811 seeds plant^{-1} with a grand mean of 40,372 seeds plant^{-1}. Palmer amaranth and waterhemp plants retained 95% to 100% of their seeds at soybean harvest among several states in the midwest and upper-south USA (Schwartz et al. 2016), suggesting that these species may be good targets for harvest weed seed control.

Palmer amaranth and waterhemp are characterized by slight-to-moderately persistent seedbanks which tend to persist for about 4 to 5 years. For example, waterhemp seeds in the soil seedbank declined to 39%, 28%, 10%, and 0.004% after preventing seed return to the soil seedbank for 1, 2, 3, and 4 years, respectively, in Illinois (Steckel et al. 2007). In Iowa, however, an artificial waterhemp seedbank declined to 65%, 45%, 28%, and 12% of the original seedbank 1, 2, 3, and 4 years, respectively, after burial in the top 5 cm of soil (Buhler and Hartzler 2001). Six years of limiting seed return to the soil seedbank reduced Palmer amaranth seedbank density by 98% compared with untreated control plots (Menges 1987). In South Carolina, the surface

soil seedbank (top 5 cm) of Palmer amaranth declined by 80-99% during a single growing season where herbicidal control and conventional tillage were implemented (Norsworthy 2008). Much less is known about long-term (>5 year) persistence of seeds of these invasive *Amaranthus* spp. in the soil seedbank.

Several studies suggest that Palmer amaranth and waterhemp seed burial depth in soil affects the persistence in the soil seedbank where deeper burial leads to slightly greater seed longevity. A seed ecotype burial study in the midwest and upper-south USA concluded that rates of palmer amaranth and waterhemp seed mortality were directly proportional to burial depth (Korres et al. 2018). After 36 months, 4.1% of Palmer amaranth seeds remained viable when placed on the soil surface compared with 5.0% when buried at 15 cm depth. About 4.3% of waterhemp seeds remained viable on the soil surface after 36 months compared with 5.3% when buried at 15 cm depth. After 12 months, Palmer amaranth seed mortality averaged 85.0% and 80.0% for unburied seeds and buried seed, respectively. These rates of seed mortality were roughly similar to those for waterhemp, averaging 84.6% and 78.2% seed mortality for unburied and buried seeds, respectively, after 12 months. Seed viability declined by >50% after one year of burial in soil at depths between 1 and 10 cm in Georgia (Sosnoskie et al. 2013). However, seed viability was greater for seeds buried at deeper depths within the soil (up to 40 cm). Seed viability after three years in the soil seedbank ranged from 9% to 22% between seeds buried at 1 cm and 40 cm depths, respectively. Greater germination and emergence of waterhemp was observed under no-till compared with tillage in Illinois, resulting in a more-rapid decline in the shallow (0–6 cm) seedbank under no-till systems (Steckel et al. 2007).

Both Palmer amaranth and waterhemp tend to germinate and emerge later in the growing season and exhibit season-long emergence patterns compared with most summer-annual weeds

in western Canada. Germination of Palmer amaranth typically occurs in a two-month period in late-spring to early-summer (Roberts and Florentine 2022). Palmer amaranth is characterized as being highly opportunistic in response to available soil moisture (Ward et al. 2013). Among nine *Amaranthus* spp., Palmer amaranth and smooth pigweed germinated within 1 day after being exposed to alternating temperatures around 30°C, while the other seven species took between three and eight days to reach 50% cumulative emergence (Steckel et al. 2004). Steinmaus et al. (2000) estimated the base temperature for phenological development of Palmer amaranth to be about 16.6°C. However, delayed and reduced cumulative germination of Palmer amaranth has been observed at temperatures as low as 14°C (Wright et al. 1999). Palmer amaranth seed germination declined above 35°C (Steckel et al. 2004) and ceased at 45-50°C (Guo and Al-Khatib 2003). Germination rates are often lower later in the growing season because warmer temperatures can induce secondary seed dormancy in Palmer amaranth (Jha et al. 2010a; Roberts and Florentine 2022). Primary seed dormancy in waterhemp can limit germination shortly after maturation and is released by after-ripening within about 4 months of maturity (Wu and Owen 2015).

Both Palmer amaranth and waterhemp germinate and emerge more-readily from the shallow seedbank (Keeley et al. 1987; Steckel et al. 2007), suggesting that no-till systems are well-suited to growth and development of these invasive *Amaranthus* spp. Palmer amaranth emerged more rapidly from shallow depths in the soil seedbank in California where about 36% to 44% emergence was documented at depths ≤ 2.5 cm while emergence was ≤ 7.2% at depths ≥ 7.6 cm (Keeley et al. 1987). Far-red light suppressed Palmer amaranth germination after nine to 12 months of burial in soil while red light stimulated germination (Jha et al. 2010a). Sensitivity of Palmer amaranth seed to germination in light or dark environments was predisposed by the

quantity of light experienced by the maternal plant (Jha et al. 2010b). For example, 87% shading of maternal plants decreased germination of progeny seeds in darkness from 21–25% to 12% compared with no shade. It was hypothesized that this could be an adaptive mechanism to mitigate fatal germination of Palmer amaranth seeds in environments deprived of light. In addition, seeds from the top two thirds of the mother plant had 67–87% higher germination than those on the bottom third of the plant, potentially related to the same adaptive mechanism.

The Palmer amaranth damage niche, otherwise known as the as the geographic area in which the weed causes economic crop yield losses (McDonald et al. 2009), was seed-limited in Illinois soybean production suggesting a critical need for extension and outreach efforts to focus on proper identification of this species such that seed immigration could be prevented (Davis et al. 2015). Male plants of Palmer amaranth can disperse pollen over 300 m from the source (Sosnoskie et al. 2012). Seed dispersal of Palmer amaranth can take place via barochory (gravity), hydrochory (water), amenochory (wind), and several anthropochory (human-mediated) pathways (Kistner and Hatfield 2018; Roberts and Florentine 2022; Sauer 1957). Zoochory (animals and waterfowl) also plays a role in dispersal of Palmer amaranth seed over short and long distances. A study in Missouri evaluated the potential for waterfowl to transport weed seed including Palmer amaranth and waterhemp, through endozoochory (Farmer et al. 2017). Palmer amaranth survived only in the esophagus and proventriculus (2%) of waterfowl while 11 to 38% of waterhemp seed survived in the esophagus and proventriculus, gizzard, and intestines. The authors further estimated a potential dispersal range of 2964 km via long-distance transport in waterfowl, potentially reaching the Maritime provinces, Quebec, Ontario, and the Prairie provinces from Missouri (Farmer et al. 2017).

2. Detection / Identification and Assessment Steps

Detection of Palmer amaranth may be challenging due to the similarity of many pigweed species. Extension and outreach are important considerations, demonstrated in the eradication of Palmer amaranth in Minnesota (Yu et al. 2021). Anticipating where to find Palmer amaranth or waterhemp may be more challenging. Both species are highly adapted to anthropochory, spreading as both a seed mimic in plant seed, a contaminant in biproducts such as screenings for animal feed, and contamination of agricultural equipment, where Palmer amaranth ended up infesting both agricultural fields and conservation plantings (Yu et al. 2021). Many identifiable features for Palmer amaranth reportedly persist past typical timings for chemical intervention into maturity including: a much longer seed head; female seed heads with distinctive sharp bracts; the leaves, stems, and petioles are completely hairless; the leaves are oval to diamond-shaped and in a rosette-like arrangement pattern; and most distinctly and reliably, the petiole length (Yu et al. 2021). Species differences can also be distinguished through genetic testing, where sex-specific markers for waterhemp and Palmer amaranth have been identified (Montgomery et al. 2019). Multiple genetic tests were developed in response to Palmer amaranth invasion into Minnesota and seed company adoption of genetic tests was credited with reducing of contamination through seed pathways (Yu et al. 2021). Genetic testing to evaluate herbicide resistance status is also advisable if chemical control is sought.

Once a detection is made, it is important to assess what the extent of the invasion is through additional surveillance activities. Typically, this can involve targeted surveys of the surrounding areas. A good comparison can be drawn with the discovery of glyphosate-resistant kochia in Alberta (Beckie et al. 2013). Here, the authors conducted a targeted survey with a 20 km radius from the origin of detection, using primary and secondary roadways. Kochia is a

tumbleweed and already infesting the area so the scope of the survey may be more than necessary for environmental movement of invasive pigweeds. The type of assessment to conduct may depend on if the origin of the plant can be elucidated. A targeted survey of agricultural land may be more appropriate if a seed or equipment contamination is determined. Seed may also be found in dockage used as animal feed and may persist in manure (Yu et al. 2021) so targeted surveys for where manure was applied, pasture and rangeland where animals grazed, and if possible, land where screenings were generated. Should detections be linked to waterfowl or other animals, more targeted surveys for natural and artificial areas where these animals may frequent could be devised though this may be complicated by long-distance transport in waterfowl (Farmer et al. 2017). Assessments may be aided by remote sensing operations using drones and transfer learning previous research (Chen et al. 2022) given the public availability of images of Palmer amaranth and waterhemp in this dataset but additional training for Canadian cropping systems will be needed.

3.0 Understanding – How is it a Threat?

Like many weed species, Palmer amaranth and waterhemp affect farming by reducing yield, increasing input costs due to herbicide resistance, reducing harvest efficiencies and grain quality. Understanding how a detection may be a threat in Canadian agro-ecosystems will be reliant on communication of detections to weed science extension and research specialists for additional diagnosis. These professionals can execute single dose screening and subsequent dose response assays to determine if the populations are herbicide-resistant. Given the challenges with *Amaranthus* identification, species identification can be verified through weed science

professionals and molecular tests are available to confirm species identification and herbicide resistance status to some modes of action.

To assist in understanding of the threat of potential invasions, a few case studies are evaluated. A northern biotype was used to evaluate Palmer amaranth interference in soybean in South Dakota (Van De Stroet and Clay 2019). This biotype induced 33% yield loss in soybean at densities of 15 plants m^{-2}. These seedlings were not controlled in the greenhouse by thifensulfuron (Group 2), glyphosate (Group 9), mesotrione (Group 27), or atrazine (Group 5) while control was achieved with dicamba (Group 4), *S*-metolachlor (Group 15), and glufosinate (Group 10) (Van De Stroet and Clay 2019). Waterhemp from twenty-five locations in Ontario and Quebec were confirmed resistant to imazethapyr, while 80% of the samples demonstrated multiple resistance to Group 2 (imazethapyr), Group 5 (atrazine), Group 9 (glyphosate), and Group 14 (lactofen) (Benoit et al. 2020). A waterhemp population in Nebraska found in a native grass field for seed production was resistant to Group 4 (2,4-D and dicamba) chemistry (Bernards et al. 2012).

Pyroxasulfone was evaluated in Georgia and provided very good to excellent Palmer amaranth control with 90 to 120 g ai ha^{-1} (Grey et al. 2013). These values do correspond to maximum label rates for pyroxasulfone in western Canada (Anonymous 2022), but caution is advised due to different soil textures and moisture availability scenarios. Resistance towards Group 15 chemistry was found in Arkansas populations and the mechanism was associated with GST metabolism (Brabham et al. 2019). In Kansas, a six-way herbicide-resistant Palmer amaranth biotype was identified (Groups 2, 4, 5, 9, 14, 27), where resistance was linked to both EPSP gene amplification and metabolic resistance via cytochrome P450 and GST (Shyam et al. 2021). In Arkansas, a glufosinate-resistant (Group 10) Palmer amaranth biotype was found, and

the resistance mechanism was both gene amplification and chloroplastic glutamine synthetase activity (Carvalho-Moore et al. 2022). The discovery of metabolic-linked resistance with Groups 10 and 14 in particular is concerning due to reliance on these herbicide Groups to mitigate ongoing glyphosate-resistance concerns in kochia in the Prairie cropping systems (Geddes et al. 2022; Geddes et al. 2023; Sharpe et al. 2023) and Canada fleabane (*Erigeron canadensis* L. (syn. *Conyza canadensis)*) in Ontario corn/soybean systems (Langdon et al. 2020).

Herbicide resistance impacts producers in several ways: increasing production costs through alternative herbicides, yield reductions due to incomplete control of problem weeds, reductions in harvest efficiency, and reductions in grain quality due to contamination with weed seed. Glyphosate-resistant Palmer amaranth infestations in Georgia cotton production was first detected in 2005 (Sosnoskie and Culpepper 2014). As a result of the glyphosate-resistant Palmer amaranth biotypes: 1) cotton acres treated with alternative herbicides doubled from 2000-2005 to 2006-2010, 2) herbicide input costs doubled, 3) Palmer amaranth control was inadequate with 52% of the crop hand-weeded, 4) an increased overall cost of at least 475% compared to non-resistance managed years, and 5) growers utilized tillage pre-plant, in-crop, and post-harvest for management (Sosnoskie and Culpepper 2014). Economic analysis for management solutions for glyphosate-resistant Palmer amaranth in Alabama cotton showed that herbicide layering with alternative POST herbicides cost between \$64.49 to \$112.05 USD ha^{-1} from 2009 to 2011 while layering with PRE and POST herbicides cost \$105.11 to \$152.67 USD ha^{-1} (Duzy et al. 2016). Comparatively, costs for glyphosate applied post-emergence in 2010 were approximately \$16.04 ha^{-1}, assuming approximately 0.45 kg per acre application rate, \$14.42 USD per kg of glyphosate, and 1 post-emergence application (Livingston et al. 2015).

4.0 Mitigation – How do we Counter the Threat in Canada?

Mitigation of Palmer amaranth will certainly involve a chemical component for integrated management strategies. The propensity for this weed to develop resistance to phloem-mobile, translocating herbicides such as Groups 2, 4, and 9 leaves spray coverage as paramount to ensure proper dosing and control with contact herbicides such as Group 10, 14, and 22 (Berger et al. 2014). This scenario does have parallels to kochia management considerations on the Canadian Prairies due to the evolution of multiple herbicide-resistant biotypes (Beckie et al. 2019). Unfortunately, many Canadian agro-ecosystems do not currently benefit from an availability of herbicide-resistant crops for applying broad-spectrum herbicides in-crop, nor many have many options for registered herbicides overall. Even in those cropping systems where herbicide-resistant crops are available, such as in eastern Canadian row cropping systems, herbicide control of multiple-resistant *Amaranthus* species can be challenging. For example, farmers in Ontario are currently faced with managing waterhemp biotypes that can have resistance to up to six distinct herbicide modes of action (Heap 2023; Symington et al. 2023; Symington et al. 2022). In this case, resistance has already been reported to inhibitors of protoporphyrinogen oxidase (PPO) and 4-hydroxyphenylpyruvate dioxygenase-(HPPD) (Groups 14 and 27, respectively), effectively reducing some of the potential value of planned PPO- and HHPD-resistant cropping systems even before their launch.

Layering of cultural practices can be incorporated to build towards diverse, resilient agro-ecosystems that are rich in carbon, competitive for space, and smother invasions. Increased seeding rates have been studied in multiple species for suppressing weed biomass including field peas (Baird et al. 2009). In western Canada, small statured pulse crops such as lentil, dry bean, and chickpea may be at risk given research in Arkansas showed neither soybean seeding rate and

row spacing affected Palmer amaranth densities (Bell et al. 2015). Eastern Canadian production of soybean is also vulnerable to competition from Palmer amaranth, with soybean yield reported to decline by up to 48% when in competition with Palmer amaranth at a density of two plants per m^{-1} of row (Klingaman and Oliver 1994). Integrated weed management strategies including but not limited to cover crops, harvest weed seed control (HWSC),alternative crops and cropping systems may help limit the potential for the establishment of Palmer amaranth in Canadian cropping systems, thereby mitigating its impact on the more vulnerable components of crop rotations (Eure et al. 2015; Norsworthy et al. 2016; Palhano et al. 2018).

4.1 Agronomic Cropping Systems

Wheat and canola are important western Canadian agronomic crops, with 8.9 million hectares of canola and 10.7 million hectares of wheat harvested in 2023 (Statistics Canada 2023a). Weed management in these systems typically involves reliance on cultivar selection for herbicide-resistant traits for canola (Beckie et al. 2006) and selective post-emergence chemistry in Groups 1, 2, and 4 for wheat production (Anonymous 2022). Due to the evolution of herbicide-resistant kochia among other weeds, Group 14 chemistry is an important mode of action for resistance management both pre-seeding and in-crop. Given the vast area in which these crops are grown [reviewed in McCallum et al. (2021)] and the evolution of resistance to glyphosate and Group 14 chemistry in Palmer amaranth and waterhemp, these systems are at risk for invasion, particularly with long-distance transport via waterfowl (Farmer et al. 2017). These production systems also occur in the northern USA so caution is advised if equipment is transferred across the border for use and should be sanitized to prevent introductions.

While these crops are also produced in eastern Canada, row crop systems in this region are focused on corn and soybean. As discussed previously, the introduction and establishment of

Palmer amaranth in this region is likely to differentially impact soybean production more so than corn. Not only are there more options for the chemical control of Palmer amaranth in corn but previous research has demonstrated that yield loss in corn was greatly reduced when Palmer amaranth emerges after the 4th-6th leaf stage of development (Massinga et al. 2001). The observation that, once established, corn is more competitive with Palmer amaranth than soybean agrees with the well-defined concept of the critical period for weed control in these crops (Hall et al. 1992; Van Acker et al. 1993). Indeed, a parallel could be drawn between the development of giant ragweed (*Ambrosia trifida* L.) as a weed of arable land in the USA corn belt and Ontario and the potential for the establishment of Palmer amaranth in this region (Page and Nurse 2015; Regnier et al. 2016). In both cases, the production of soybean and the associated cropping practices that are heavily reliant on chemical weed control appear to be the weak link in the crop rotation. In their review of certified crop advisors' perceptions of managing giant ragweed in the USA corn belt, Regnier et al. (2016) highlight the need for more diverse combination of crop species, including the incorporation of a cereal grain into the crop rotation in order to suppress early giant ragweed emergence and provide chemical or mechanical control options for late-emerging giant ragweed.

In the mid-south USA, peak Palmer amaranth emergence occurs between late April and early June (Liu et al. 2022). In Ontario, related Amaranth species emerge from late May to mid-July (Moore et al. 1994; Oryokot et al. 1997); a period which overlaps with the normal range of seeding dates for corn and soybean crops throughout the province (Ontario Ministry of Agriculture, Food and Rural Affairs (OMAFRA) 2017). The suppression of Palmer amaranth emergence during this period could be accomplished with a renewed emphasis on competitive winter crops such as winter wheat (*Triticum aestivum* L.) and winter canola (*Brassica napus* L.)

or through the use of novel production practices that incorporate overwintering cover crops, such as winter rye (*Secale cereale* L.) (Page et al. 2020; Vanhie et al. 2021; Webster et al. 2016; Wiggins et al. 2016). Double cropping and relay intercropping are also practices that have the potential to maintain a competitive crop canopy during the peak season for *Amaranthus* spp. emergence and facilitate the production of less competitive crops, such as soybean, at points in the growing season when Palmer amaranth pressure is waning (Gesch et al. 2014; Hood et al. 1991; Page et al. 2019a; Wallace et al. 1992).

4.2 Horticultural Cropping Systems

The top Canadian commodities in 2020 for marketed berry production when giving equal weight to area harvested, total production, and productivity (tonnes/ha) were: 1) apples (385,452 metric tonnes on 17,566 ha), 2) cranberries (161,903 metric tons on 7,476 ha), 3) blueberries (146,370 tonnes, 76,968 ha), and 4) grapes (101,095 tonnes, 12,541 ha) (Statistics Canada 2023c). These are all perennial, specialty cropping systems producing high value, fresh market products. Production of all four crops lays primarily in eastern Canada and the coastal regions. Apples are produced within eastern Canada (64%), the Coastal province of British Columbia (22%), and in Nova Scotia (11%). Most grape production takes place in British Columbia and Ontario, while most cranberry production is located within Quebec (63%) and British Columbia (29%). While perennial horticultural systems have more limited herbicide options, these systems often benefit from cultural advantages in weed control with good crop competition for canopy closure and belowground competition. Palmer amaranth, though not a frequent weed of concern in perennial horticultural systems, has been reported to reduce the growth of young saplings in pecan (*Carya illinoinensis* (Wangenh.) K. Koch) orchards (Wolf and Smith 1999). Renewed interest in cover crops and integrated weed management in orchards and vineyards will help reduce the potential

for the establishment of new weeds should species such as Palmer amaranth be introduced into these systems (Haring and Hanson 2022; Minville et al. 2022).

For vegetable production, the top commodities when giving equal weight to area harvested, total production, and productivity (tonnes/ha) were: 1) tomatoes (492,211 metric tonnes on 5,942 ha), 2) carrots (350,614 metric tonnes on 7,531 ha), 3) onions (229,481 metric tonnes on 5,496 ha), 4) cabbage (165,070 metric tonnes on 4,875 ha), and 5) pumpkins (93,244 metric tonnes on 3,341 ha) (Statistics Canada 2023b). Within eastern Canada are grown 76% (41% in ON / 35% in QB) of carrots, 83% of cabbage (38%/45%), and 81% (40/41%) of the onions within Canada. Ontario produces the majority of pumpkins (72%) and tomatoes (97%). As with perennial horticultural systems, herbicide options are more limited in annual horticultural cropping systems. There are, however, some herbicide modes of actions used in field vegetable production to which resistance in Palmer amaranth is limited or has yet to evolve. In sweet potato production, for example, herbicides from Groups 3, 13, 14, and 15 are often used for in-crop for weed control (Page et al. 2021). At present, there are only a few reported cases where Palmer amaranth has evolved resistance to these modes of action. Most concerningly however, is the report of a biotype from Arkansas that is resistant to herbicide from Groups, 3, 14 and 15 (Heap 2023). As reports of resistance to modes of action used in horticultural production tend to be more regional than widespread, limiting the movement of seed on equipment or on propagules and transplants will be a key component to preserving the effectiveness of these modes of action.

Where present, Palmer amaranth is a troublesome and economically detrimental weed of annual horticultural production systems (Garvey et al. 2013; McGowen et al. 2018; Norsworthy et al. 2008). For example, at a density of one plant per meter^{-1} of row, yield losses from competition with Palmer amaranth have been reported to reach 28% in peanuts (*Arachis*

hypogaea L.) and up to 50% in terms of marketable sweet potato (Burke et al. 2007; Meyers et al. 2010). As with row crop production systems, cover crops have been investigated as a tool for managing herbicide-resistant biotypes of Palmer amaranth (Dobrow Jr et al. 2011). More generally, recent research has focused on winter cover crops and their combination with herbicide programs for the control of problematic summer annual weed species (Price and Norsworthy 2013; Webster et al. 2013). Results from Malik et al. (2008) suggest that a combination of herbicides along with overwintering radish (Raphanus *raphanistrum* L.) and cereal rye were required to optimize sweet corn yield and ensure an acceptable level of weed control. Living mulches are another form of cover crop that has been evaluated for weed control in horticultural production systems (Bhaskar et al. 2021; Paine and Harrison 1993; Westbrook et al. 2022). These systems are differentiated from overwintering cover crops by the fact that the living mulch is grown at the same time as the primary crops, typically between the rows. To address the threat to these high values horticultural systems that Palmer amaranth represents, it is likely that conventional approaches to weed management such as herbicides, cover crops and living mulches, will need to be integrated with newer emerging technologies, including robotics for mechanical weed management (Fennimore and Cutulle 2019) and computational neural networks for weed specific herbicide application (Bilodeau et al. 2023).

4.3 Natural or Uncropped Areas

Pre-colonial distributions of Palmer amaranth can be traced to the arid regions of the southwestern USA (Sauer 1957). While its recent range expansion across the south and midwest USA has been most frequently described in respect to arable lands (Ward et al. 2013), it has also been reported to invade agriculturally adjacent areas that are natural, uncropped, or unmanaged. Field margins, roadsides, right of ways, rail lines, or even fields that are part of the Conservation

Reserve Program (CRP), can serve as a refuge for problematic weed species like Palmer amaranth (Bagavathiannan and Norsworthy 2016; Korres et al. 2015; Mühlenbach 1979; Yu et al. 2021). For example, in their survey of roadsides along the eastern Arkansas-Mississippi Delta, Korres et al. (2015) reported the presence of Palmer Amaranth in 64% (313/459) of their randomly selected sampling sites. Unsurprisingly, the authors identified adjacent arable land use a primary factor contributing to the distribution of Palmer amaranth and other problematic weed species surveyed in this work. Roadsides and field margins serve as refugia for many weed species and can contribute to the preservation of herbicide resistance traits that may be selected against when crop rotation or alternative herbicide modes of action are used in agricultural production (Beres et al. 2018; Gage et al. 2015; Page et al. 2019b). Further work by Bagavathiannan and Norsworthy (2016) examining the roadsides of eastern Arkansas confirmed that Palmer amaranth populations with resistance to multiple herbicide modes of action are widespread in these agriculturally adjacent areas. Source populations such as these contribute to the difficulty in managing herbicide-resistant biotypes and can help to vector problematic weed species, including Palmer amaranth and waterhemp, through contaminated agricultural machinery, water born dispersal or epi- and endozoochory (Farmer et al. 2017; Norsworthy et al. 2014).

The many vectors and sources for the potential introduction of Palmer amaranth into natural, cropped, or uncropped areas were highlighted in a recent publication describing the multiple introductions and eventual eradication of Palmer amaranth from the state of Minnesota (Yu et al. 2021). The authors outlined several presumed sources for the repeated introduction of Palmer amaranth to the state, including the use of contaminated seed mixes used for plantings on CRP lands, and the spread of contaminated gravel on utility roadways, among others. The CRP,

administered by the USA Department of Agriculture–Farm Service Agency, incentivizes landowners to establish perennial cover in place of agricultural production on marginal agricultural lands (Drum et al. 2015). While these agriculturally adjacent CRP lands provide valuable ecosystems services, such as reducing erosion and providing habitat for migratory birds, they can also act as source populations for invasive weeds. In fact, a recent study of migratory waterfowl demonstrated that Palmer amaranth was consumed by various migratory waterfowl and that it retained ~25% viability having passed through the digestive track of mallard ducks (*Anas platyrhynchos* L.) (Farmer et al. 2017). These authors reported that viable Palmer amaranth seed were recovered over 40 h after ingestion, resulting in a potential distribution radius of 2,964 km (given an average flight speed of 78 km h^{-1} and maximum sustained duration of 38h). Given the tendency for waterfowl to visit both cropped and uncropped areas during their migration, the dispersal of problematic weed species like waterhemp and Palmer amaranth via endozoochory is likely to add to the many vectors contributing to the observed range expansion in these species.

5.0 Appropriateness – Did the Mitigation Work?

Like the assessment step, appropriateness is typically achieved through monitoring activities using targeted survey approaches. While in Canada there is a history of monitoring towards biovigilance of Prairies pests [reviewed in McCallum et al. (2021)], these surveys provide a larger scale, coarse spatial resolution targeting well established weeds. This may not be compatible to the scale needed for assessing either the extent of initial invasion or the appropriateness of mitigation measures for invasive weeds. When managing herbicide-resistant weeds, it is important to scout 3 to 4 weeks following post-emergence, foliar-applied chemistry

and 3 to 4 weeks following crop emergence of pre-emergence, soil-applied chemistry. If control cannot be achieved, more aggressive mitigation strategies will need to be followed to ensure plants are eliminated. The use of burning was successfully employed in Minnesota and their appropriateness-level monitoring occurred for three years following detection (Yu et al. 2021).

Conclusions. Palmer amaranth and waterhemp invasion and spread into Canadian agro-ecosystems will affect long-term system sustainability due to their propensity for reproduction and spread, potential for yield reductions, and evolution of herbicide resistance. Here, we describe a biovigilance framework approach to anticipate their invasion, understand what factors affect their invasion and persistence, recommend an awareness campaign for broad-scale detection, monitoring, mitigation, and appropriateness assessment for mitigation efforts. One limitation to this approach will be the broad area of land requiring monitoring given the multiple pathways which Palmer amaranth and waterhemp can invade: through seed pathways, animal feed pathways, contamination of equipment, and spread through waterfowl and other animals. Early extension activities to involve the public in early detection efforts was critical to success in Minnesota (Yu et al. 2021). These efforts may be supported by drone-based remote sensing operations, but this will require additional research. Genetic testing capabilities should expand to support the seed industry to ensure rapid detection of contaminants of these invasive amaranths. The evolution of multiple herbicide-resistant biotypes for both Palmer amaranth and waterhemp is concerning so control of detections should be executed rapidly to prevent establishing a seedbank and providing selection pressure on herbicides in Canadian agro-ecosystems.

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Table 1. Species naturalized and detected from herbarium collections made in Canada. Canadian species ranges derived from specimens examined and verified for species identification by Costea and Tardif (2003) plus the recently recorded instance of *A. palmeri*. Common names follow Darbyshire et al. (2000) or the Flora of North America (eFloras 2008) and reports of herbicide resistance worldwide are summarized from the International Survey of Herbicide-Resistant Weeds (Heap 2023).

Species	**Common name**	**Canadian Distribution**	**Herbicide Resistance[1]**	**Status**
A. albus L.	Tumble pigweed	BC, AB, SK, MB, ON, QC, NS, NB, PEI	Group 5	Weedy and second most common species in Canada.
A. blitoides S. Wats.	Prostrate pigweed	BC, AB, SK, MB, ON, QC	Groups 2 and 5	Native.
A. blitum S. Wats. subsp. *blitum*	Purple amaranth	ON, QC		Adventive. *Amaranthus blitum* is listed as invasive with a world wide distribution including USA, Europe, Asia, Africa and Australia. Holm et al. (1991) listed it as a serious or principal weed in eight countries.
A. blitum subsp. *emarginatus* (Moq. ex Uline & Bray) Carretero, Munoz Garm. & Pedro		BC, QC		Naturalized.
A. californicus (Moq) S. Wats.	California pigweed	AB, SK, MB, ON, QC		Naturalized.
A. caudatus L.	Love-Lies-Bleeding	SK, ON		Crop/ornamental escapee.
A. cruentus L.	Red amaranth	ON	Group 5	Ornamental escapee.
A. hybridus L. subsp. *hybridus*	Smooth pigweed	ON	Group 2, 4, 5, 6, 9, 14	Weedy. *Amaranthus hybridus* is listed as a serious or principal weed in 14 countries around the world (Holm et al. 1991).
A. hybridus subsp. *quitensis* (Kunth) Costea & Carretero		ON		Weedy.
A. hypochondriacus L.	Prince's-Feather	BC, AB, ON, QC		Crop/ornamental escapee.

A. powellii subsp. *bouchonii* (Thell.) Costea & Carretero	Powell amaranth (Green pigweed)	BC, ON, QC	Group 2,4, and 5	Weedy.
A. powellii S. Wats. *Subsp.* Powellii		BC, AB, SK, MB, ON, QC, NS, PEI		Weedy.
A. retroflexus L.	Redroot pigweed	BC, AB, SK, MB, ON, QC, NS, NB, PEI	Groups 2, 5, 6, and 14	Most common species in Canada. Holm et al. (1991) lists this species as serious or principal in thirty-two widely distributed countries.
A. spinosus L.	Spiny amaranth	MB, ON	Groups 2 and 9	Adventive. Invasive western USA, Asia, Australia, and Africa. Listed as serious or principal weed for twenty-two countries (Holm et al. 1991).
A. tricolor	Joseph's coat	ON		Ornamental/vegetable escapee.
A. tuberculatus var. *tuberculatus* (Moq.) Sauer	Waterhemp; Tall waterhemp; Common waterhemp	ON, QC	Groups 2, 4, 5, 9, 14, and 27	Native. With A. *tuberculatus* var. *rudis* is a major weed of row crops (Steckel 2007).
A. tuberculatus var. *rudis* (Sauer) Costea & Tardif		BC, ON		Weedy and invasive.
A. viridis L.	Slender amaranth	QC	Groups 2 and 5	Adventive. Invasive and very widely distributed: southern and western USA, southern Europe, Sweden, Finland, Asia, Australia, and Africa.
A. palmeri S. Wats.	Palmer's pigweed	MB	Groups 2, 3, 4, 5, 9, 14, and 27	Adventive? Native to southwestern USA but a major agricultural weed in the USA (Steckel 2007) and scattered countries including: Sweden, Norway, Finland, Denmark, Spain, France, Italy, Greece, Cyprus, Turkey, Egypt, Ethiopia, China.

[1] Herbicide Resistance types identified by Group numbers assigned by HRAC/WSSA.

Table 2. *Amaranthus* species with potential for dispersal or invasion into Canada based on current distribution or invasiveness based on Kew's Plants of the World Online (POWO) (2024) and the Invasive Species Compendium (Center for Agriculture and Biosciences International (CABI) 2022). Common names are listed from the Flora of North America (eFloras 2008) or Global Biodiversity Information Facility (GBIF) (2022). Distributions should be viewed with caution as underlying records have not been reviewed by a taxonomic expert, so names are likely erroneously applied in some cases, and because under collection will mean the current ranges of these species are underrepresented.

Species	**Common name**	**Adjacent States**	**CABI List**	**Considerations**
A. arenicola Johnst.	Sand amaranth	MY, MN, WI, PA	Yes	Aggressively expanding within the USA from native USA range.
A. capensis Thell.	Cape pigweed	None	Yes	Native to South Africa this species has been introduced to Germany.
A. cannabinus (L.) Sauer	Salt-marsh water hemp	NY, PA	No	Dioecious. Native to the USA.
A. crispis (Lesp. & Thévenau) A.Braun ex J.M.Coult. & S.Wats.	Crisp-leaved amaranth	NY	Yes	Native range in South America with introductions in the eastern USA (New Jersey, New York, North Carolina, and Virginia), southern Europe (France east to Romania and Bulgaria) and southwestern Australia.
A. deflexus L.	Large-fruit amaranth	NY, PA	Yes	Species with native range in South America now listed as introduced to the eastern and western USA, much of Europe east into Asia (Portugal to Great Britain east to Kazakhstan and Pakistan as well as Sweden, Norway, Finland and), northwestern Africa, Japan, New Zealand, and Trinidad-Tobago.
A. dinteri Schinz.	Dinter's amaranth[1]	None	No.	Native to southern Africa and introduced to Great Britain, Germany, Sweden, and Switzerland.
A. muricatus (Moq.) Hieron.	Muricate amaranth	None	Yes	Native to South America and listed as introduced to northwestern and southern Africa, southwestern Europe (Portugal to Italy), southeastern Australia and Alabama (USA).
A. polygonoides L.	Smartweed amaranth	None	Yes	Native to Central America with introductions sporadically across the globe: Finland, Belgium, Netherlands, Germany, Spain, Italy, India, China, and Trinidad-Tobago.

A. pumilus Raf.	Seabeach amaranth	NY, PA	No	Native to the USA.
A. standleyanus Parodi ex Covas	Indehiscent pigweed	None	Yes	Native to Bolivia and Argentina and considered introduced in eastern Europe from Morocco west to Italy and then north to Finland, Libya, South Africa, and China.
A. thunbergii Moq. in de Candolle	Thunberg's pigweed	None	Yes	Native to southern Africa and Eritrea this species has been introduced to Germany and South Carolina (USA) and is listed by CABI as invasive. Listed as a principal weed in three countries by Holm et al. (1991).

[1] In the absence of a common name on eFloras (2008) or the Global Biodiversity Information Facility (GBIF) (2022), this name is based on the species epithet that honours German botanist Kurt Dinter.

Table 3. Hybrid species identified in herbarium material or generated experimentally with relevance to Canadian species. Note that parental direction often unclear and, therefore, the order of the taxa does not imply cross direction. These results should be viewed with varying degrees of skepticism based on the evidence presented to confirm hybridity as not all work has included morphological, cytogenetic, and molecular evidence to support a hybrid origin. Further we note that hybridization, while necessary for introgression, is only the first step in that process.

Parent 1	**Parent 2**	**Considerations**	**Key Reference(s)**
A. albus	*A. blitoides*	*A.* X *budensis*: Inferred from Canadian specimens.	Grant 1959; Costea and Tardif 2003
A. arenicola	*A. greggii* S. Wats.	Inferred from specimens.	Sauer 1957
A. australis	*A. caudatus*	Experimentally produced.	Murray 1940
A. australis	*A. powellii*	Experimentally produced.	Murray 1940
A. caudatus	*A. cruentus*	Experimentally produced.	Greizerstein and Poggio 1995
A. caudatus	*A. hypochondriacus*	Experimentally produced.	Greizerstein and Poggio 1995
A. cruentus	*A. powellii*	Experimentally produced.	Pandey 1999
A. deflexus	*A. viridis*	*A.* X *mauritii*; Inferred from specimens.	Iamonico 2015
A. hybridus	*A. australis*	Experimentally produced.	Murray 1940
A. hybridus	*A. caudatus*	Experimentally produced.	Murray 1940
A. hybridus	*A. powellii*	Experimentally produced. Canadian records.	Murray 1940; Costea and Tardif 2003
A. hybridus subsp. h*ybridus*	*A. caudatus*	Experimentally produced.	Greizerstein and Poggio 1995
A. hybridus subsp. h*ybridus*	*A. hypochondriacus*	Experimentally produced.	Greizerstein and Poggio 1995
A. hybridus subsp. h*ybridus*	*A. spinosus*	Experimentally produced.	Greizerstein and Poggio 1995
A. hybridus subsp. *quitensis*	*A. caudatus*	Experimentally produced.	Greizerstein and Poggio 1995
A. hybridus subsp. *quitensis*	*A. cruentus*	Experimentally produced.	Greizerstein and Poggio 1995
A. hybridus subsp. *quitensis*	*A. hypochondriacus*	Experimentally produced.	Greizerstein and Poggio 1995
A. palmeri	*A. achanthochiton* Sauer	Inferred from specimens.	Sauer 1957
A. palmeri	*A. arenicola*	Inferred from specimens.	Sauer 1957
A. palmeri	*A. hybridus*	Experimentally produced.	Gaines et al. 2012
A. palmeri	*A. tuberculatus*	Experimentally produced.	Gaines et al. 2012

A. palmeri	*A. tuberculatus* var. *rudis*	Inferred and experimentally produced. Herbicide resistance transfer.	Sauer 1957; Wetzel et al. 1999; Trucco et al. 2007; Oliveira et al. 2018
A. palmeri	*A. spinosus*	Herbicide resistance transfer.	Gaines et al. 2012; Nandula et al. 2014; Molin et al. 2016
A. palmeri	*A. watsoni Standl.*	Inferred from specimens.	Sauer 1957
A. retroflexus	*A. hybridus*	*A.* X *ozanonii* Canadian records and experimentally produced. Invasive in other countries.	Costea and Tardif 2003; Murray 1940
A. retroflexus	*A. cruentus*	*A.* X *galli* Inferred and experimentally produced.	Iamonico 2015; Pandey 1999
A. retroflexus	*A. powellii*	*A.* X *soporoniesis* Inferred from Canadian specimens.	Costea and Tardif 2003
A. retroflexus	*A. spinosus*	Experimentally produced.	Murray 1940
A. spinosus	*A. caudatus*	Experimentally produced.	Murray 1940
A. spinosus	*A. dubius* Mart. ex Thell.	Inferred from specimens.	Grant 1959
A. tuberculatus	*A. albus*	Experimental, low	Murphy et al. 2021
A. tuberculatus	*A. hybridus*	Inferred from Canadian specimens.	Costea and Tardif 2003; Trucco et al. 2009
A. tuberculatus	*A. powellii*	Inferred from Canadian specimens.	Costea and Tardif 2003
A. tuberculatus var. *rudis*	*A. arenicola*	Inferred from specimens.	Sauer 1957
A. tuberculatus var. *rudis*	*A. australis* (A.Gray) Sauer	Experimentally produced.	Murray 1940
A. tuberculatus var. *rudis*	*A. caudatus*	Experimentally produced.	Murray 1940
A. tuberculatus var. *rudis*	*A. hybridus*	Experimentally produced. Herbicide resistance transfer.	Murray 1940; Tranel et al. 2002; Trucco et al. 2005
A. tuberculatus var. *rudis*	*A. powellii*	Experimentally produced.	Murray 1940
A. tuberculatus var. *rudis*	*A. retroflexus*	Experimentally produced.	Murray 1940
A. tuberculatus var. *rudis*	*A. tuberculatus* var. *tuberculatus*	Experimentally produced.	Murray 1940
A. tuberculatus var. *rudis*	*A. spinosus*	Experimentally produced.	Murray 1940
A. tuberculatus var. *tuberculatus*	*A. arenicola*	Inferred from specimens.	Sauer 1957

A. tuberculatus var. *tuberculatus*	*A. retroflexus*	Experimentally produced.	Murray 1940

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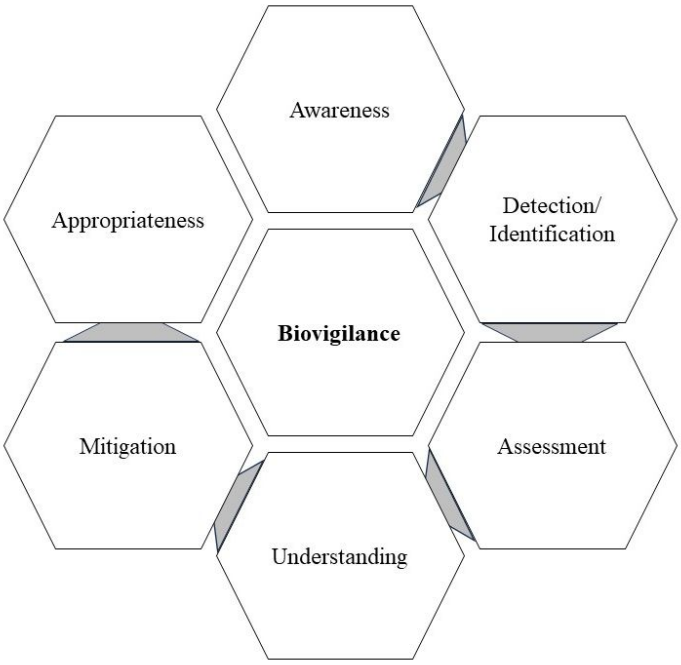
Table 4. The eighteen currently recognized taxa known to have reproductive inter-compatibility with the *Amaranthus* species most frequently cultivated for grain: *A. caudatus*, *A. cruentus* and *A. hypochondriacus*.

A. arenicola	*A. hybridus L.* subsp. *hybridus*	*A. spinosus*
A. australis (A.Gray) Sauer	*A. hybridus L.* subsp. *quitensis*	*A. torreyi* (A. Gray) Benth. Ex S. Wats.
A. cannabinus	*A. palmeri*	*A. tuberculatus* var. *rudis*
A. dubius	*A. powellii*	*A. tuberculatus var. tuberculatus*
A. floridanus (S. Wats.) Sauer	*A. retroflexus*	*A. viscidulus* Greene
A. greggii	*A. scariosus* Benth.	*A. watsoni*

Figure 1. Biovigilance research-based continuum for pest management. Figure adapted from Carisse et al. (2017).



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