

# **Effects of Diverse Cropping Systems on Arthropod Communities and Weed Seed Predation**

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## Abstract

Projected and ongoing climate change presents challenges and opportunities for wheat-based cropping systems throughout the inland Pacific Northwest (iPNW). Producers are interested in reducing the amount of land in fallow to increase overall crop production, as well as create more sustainable cropping systems that are resilient to a projected variable climate. Examples of crop rotation diversification and intensification for wheat systems include the addition of pulse crops such as dry pea and chickpea, and multi-species cover crops into rotations. Monitoring arthropod community responses to diversification and intensification can inform producers on which alternative crops are also associated with increased biodiversity and arthropod-mediated ecosystem services, such as pollination and biological control. Biological control of weedy pests in fields is a key ecosystem service provided predominately by epigeic arthropods and small mammals. The work presented here examines epigeal arthropod community structure and weed seed predation under three diversified and intensified wheat-based cropping systems at two trial locations. Results show that epigeal activity-density and diversity were greatest in winter pea plots compared to the other crops tested. Granivore community metrics were not affected by crop or sampling date at the St. John, Washington site but at the Genesee, Idaho site, winter pea consistently had greater diversity and activity-density compared to winter wheat. Generally, activity-density and diversity were greater in the crops unique to diversified rotations, though evenness was greater in winter wheat plots than in winter pea or cover crop plots. Weed seed removal was greater in fallow plots than in plots planted to any crop. Removal rates differed among four sample dates but there was no seasonal trend or interaction between sample date and crop. In weed seed preference trials, *Anthemis cotula* was consumed at significantly lower rates than *Bromus tectorum* or *Chenopodium album*, but when physical defenses (seed coverings) were artificially breached, *A. cotula* was consumed at higher rates than *B. tectorum*. Diversified wheat cropping systems in the iPNW either reduce or remove fallow from rotation, which could lead to increased

weed abundance in seed banks, exacerbating weed management problems in these systems.

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I'd like to thank Bronte Sone, whose friendship and support helped me navigate a divorce during grad school and a pandemic. I'm forever grateful.

## Dedication

I'm dedicating this thesis to myself, for I truly didn't think I would finish it.

*"You are capable of more than you know. Choose a goal that seems right for you and strive to be the best, however hard the path. Aim high. Behave honorably. Prepare to be alone at times, and to endure failure. Persist! The world needs all you can give."*

- E. O. Wilson

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## Chapter 1 | Introduction

### Changing Climate and Agriculture in the Inland Pacific Northwest

Climate is shifting globally and maintaining current wheat production is presenting new challenges to growers worldwide. While local and regional temperatures are increasingly variable, global temperature trends indicate a steady increase (Hansen et al. 2006; Shen et al. 2022), as well as increased variability and intensity of extreme weather events (i.e. drought, flood). A global reduction in wheat production is projected as a result of warming and changes in precipitation (Asseng et al. 2011, 2015; Huzsvai et al. 2022; Karatayev et al. 2022; Neupane et al. 2022). Growers and researchers are searching for ways to mitigate increased pest and disease pressures, maintain or increase crop yield to meet rising demands, and increase the overall resiliency of wheat production systems. Currently, growers in rainfed regions often rely on fallowing – the practice of leaving farmland uncultivated for a period – to conserve water in the soil profile (Schillinger and Papendick 2008; Schillinger 2016) for the wheat crop in the following year. However, fallowing is associated with increased soil erosion (Singh et al. 2012; Sharratt et al. 2018), soil degradation (Mosier et al. 1991; Lemke et al. 1999; Nielsen et al. 2011), and the potential for increased greenhouse gas emissions (Liebig et al. 2010; Bista et al. 2017). Fallowing is also seen as a loss of farm income as there is no crop planted and growers may treat fallowed land with herbicides to suppress weed populations between growing seasons (Nielsen et al. 2011). Frequent, long-term use of this practice is not sustainable in semi-arid production systems with projected climatic shifts.

The inland Pacific Northwest (iPNW) is a region encompassing central Washington to North Idaho and Northeast Oregon. Nearly 17% of the nation's wheat is produced in the iPNW (USDA) and the region is projected to have growing seasons with higher temperatures while experiencing less rainfall compared to the previous 30 years (Karimi et al. 2018). Increased temperatures and more intense drought conditions are expected to harm wheat production in the iPNW (Sharma-Poudyal and Chen 2011; Karimi et al. 2021). Without a shift in current water

management strategies, changes in precipitation regimes and warming (Mote and Salathé 2010) are expected to increase the prevalence of fallowing (Kaur et al. 2017), which could have negative consequences for system-wide sustainability and resilience (Pi et al. 2019). A major obstacle that growers face in the iPNW is finding economically and ecologically stable crop alternatives to fallowing.

Landscapes in Transition (LIT) is a United States Department of Agriculture-funded Coordinated Agricultural Project that started in 2018, with the goal to guide ongoing land-use change in the iPNW. LIT is an interdisciplinary project with researchers working to identify the key agronomic, climatic, biological, and economic factors that affect wheat-based production systems of the region as its climate changes. The project aims to diversify wheat production systems to increase sustainability and resiliency in the regional agricultural landscape. The work presented in this thesis contributes to identifying the impacts of diversified wheat systems in the iPNW on the entomological component of agroecosystems.

### **Diversification and Intensification**

The inland Pacific Northwest is characterized by a climate gradient, resulting in variable cropping systems across the region. Agroecological classes (AECs) are derived from annual land use information from the USDA-NASS Cropland Data Layer ('USDA National Agricultural Statistics Service Cropland Data Layer' 2017) combined with bioclimatic and cultural drivers (Huggins et al. 2014), which sets AECs apart from other attempts to delineate land use (agroecological zones). There are three main AECs in the iPNW: continuous cropping, continuous cropping-fallow transition, and crop-fallow (Huggins et al. 2014). Continuous cropping zones are characterized by having less than 10% of land in fallow, receiving more than 457mm of annual precipitation, and having a rotational scheme of winter wheat-spring wheat-spring legume. The continuous cropping-fallow transition zone has 10-40% of land in fallow, 304-457mm annual precipitation, and a rotational scheme of winter wheat-spring wheat-summer fallow. Crop-fallow zones have more than 40% of land in fallow, greater than 304mm of precipitation in a year, and winter wheat-summer fallow rotations (Karimi et al. 2017). Knowledge of the crops and limitations posed by

climate and soils in each AEC allows for the development of zone-specific farming practices for the long-term stability of the entire region.

Common crop rotations in lower rainfall areas of the iPNW are two- and three-year rotations of winter wheat-fallow and spring wheat-fallow-winter wheat (Schillinger et al. 2015; Schillinger 2016), which creates a patchwork landscape of wheat monoculture and bare ground. Alternative options to fallow are needed to diversify the production landscape, as well as intensify traditional dryland systems in an ecologically and economically stable way. In many semi-arid regions, including the iPNW, this includes adding legumes such as dry pea, lentil, and chickpea into the rotation (known as a pulse crop) (Gan et al. 2015; McGee et al. 2017; Schillinger 2017, 2020), as well as incorporating cover crops to be utilized for grazing or haying (Adhikari and Menalled 2020; Kumar et al. 2020; Baraibar et al. 2021; Garland et al. 2021). Incorporating a pulse crop can benefit the wheat production system in several ways. For example, faba bean and pea have a high potential for fixing nitrogen in the soil (Williams et al. 2014) as well as increasing the yield of the subsequent cereal crop (Williams et al. 2014; Gan et al. 2015), which has been attributed to legumes using less water than wheat (Chen et al. 2006; Schillinger 2017). Decreased applications of nitrogen fertilizer have also been reported for wheat fields following a pulse crop (Miller et al. 2003). Cover crops have many similar benefits as pulse crops

but have had a slower adoption rate by growers as cover crops are typically not an economically viable alternative to fallowing (Acharya et al. 2019).

Common cropping rotations in the high rainfall areas of the iPNW are three- and four-year rotations of winter wheat-spring grain (wheat or barley)-spring legume (pea, lentil, chickpea), and winter-wheat-spring grain-winter wheat-spring legume (Kirby et al. 2017). Higher rainfall zones in the iPNW have a climate that generally supports continuous cropping, though the region's soils are vulnerable to runoff and erosion due to the steep slopes and winter precipitation. Diversification strategies include removing conventional tillage practices as well as incorporating winter legumes, spring canola, or cover crops into traditional rotations. Some producers implement rotations with two consecutive years of broadleaf crops to enhance weed management (Kirby et al. 2017). In the iPNW, the adoption of novel cropping systems is highly dependent on the regional agroecological classes (AECs) (Stöckle et al. 2018).

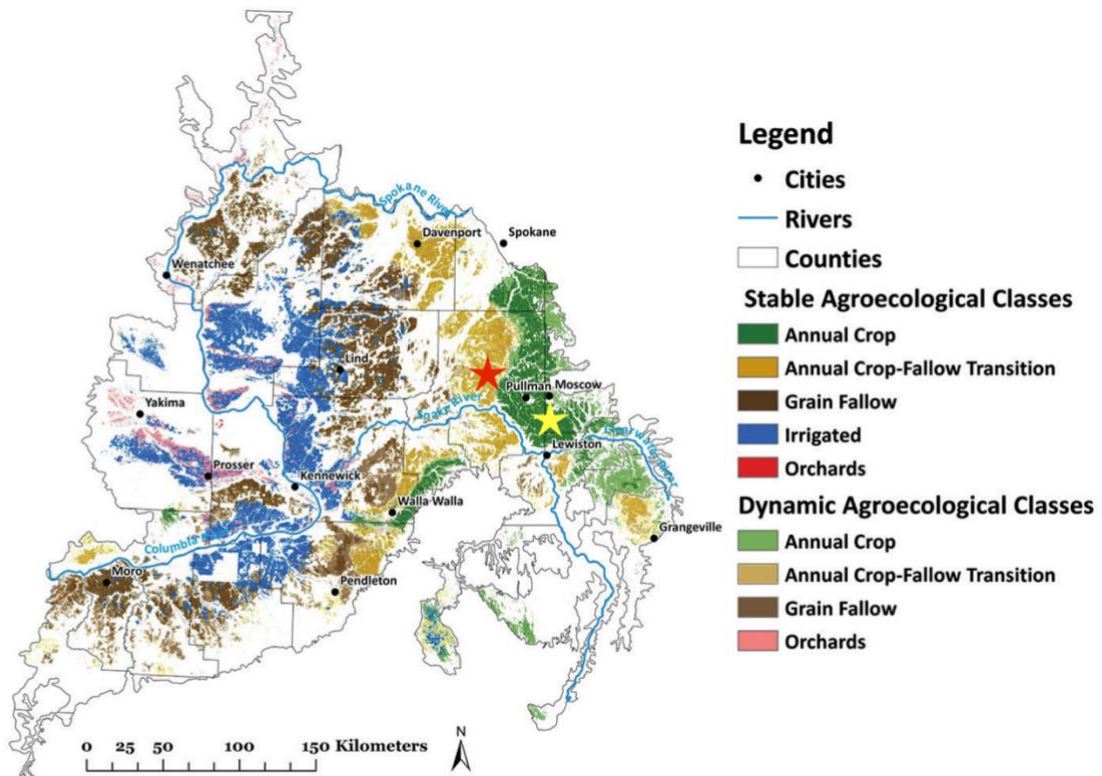


Figure 1.1 Map of agroecological classes in the inland Pacific Northwest. The two study sites used for research presented in this thesis are Genesee, Idaho (yellow star) and St. John, Washington (red star). Map from Kaur et al. 2017.

The alternatives to fallowing mentioned above simultaneously result in diversifying and intensifying iPNW wheat-based cropping systems. Agricultural intensification is characterized by higher inputs of fertilizers and pesticides (Cassman and Pingali 1995), as well as increased production per unit area (Rudel et al. 2009), while the implementation of diverse crop types contributes to ecological diversification on-farm and across the agricultural landscape. While work has been done to understand how diversification and intensification will affect crop yield (Poveda et al. 2008; Nunes et al. 2018; Tamburini et al. 2020) and on-farm diversity of weeds (Liebman et al. 2001; Sharma et al. 2021; Adeux et al. 2022), how arthropod communities respond to these changes has not been studied.

### **Diversity in Agroecosystems**

Diversity in agricultural systems is comprised of spatial and temporal components; spatial diversity refers to the diversity within the space of the farm (i.e., hedgerows, intercropping) while temporal diversity typically refers to the year-to-year diversity of cultivated crops (i.e., crop rotations, cover crops) (Hooper et al. 2005). There is evidence that asynchronous crop production at the farm and landscape levels lends to the stability of the overall production system (Egli et al. 2020). By contributing to habitat heterogeneity, spatial and temporal diversification enhances the associated biodiversity of weeds and arthropods (Altieri 1999; Benton et al. 2003; Lichtenberg et al. 2017).

Arthropods are ubiquitous in agriculture, mainly receiving attention as pests or vectors of plant pathogens that constrain production (Marzocchi and Nicoli 1991; Zhang et al. 2007; Tschumi et al. 2018; Bin Farook et al. 2019). Annually, pestiferous insects cause nearly 18% of global production losses in wheat (Oerke 2006). On the other hand, arthropods mediate several ecosystem functions and services that are critical to agricultural systems such as pollination, biological control, and nutrient cycling (Isaacs et al. 2009; Jankielsohn 2018; Raitif et al. 2019). Conserving the ecosystem services and functions provided and maintained by arthropods is essential to sustainable agroecosystem management in variable dryland climates (Schowalter 2013; Schowalter et al. 2018). Agroecosystems with greater vegetational diversity are

typically have fewer pests (Root 1973; Andow 1991; Letourneau et al. 2011). In a meta-analysis that examined the effects of diversified agroecosystems on arthropod pest and predator abundances, Letourneau et al. (2011) found that herbivore abundances and crop damage decreased and predator abundances increased in systems with increased vegetational diversity. They also found that pest-suppressive diversification strategies significantly lower crop yield (Letourneau et al. 2011), a potential drawback to diversifying production systems.

### **Ecosystem Services**

Ecosystem services are the conditions and processes within an ecosystem that sustain and maintain human life (Daily 1997). According to the Millennium Assessment (2005), ecosystem services fall under four categories: provisioning, regulating, supporting, and cultural. Provisioning services include products obtained from an ecosystem such as food, fiber, fuel, and water. Regulating services are the benefits obtained from the regulation of ecosystem processes, such as air and water quality regulation, erosion regulation, disease and pest regulation, and pollination. Supporting services include nutrient and water cycling, photosynthesis, and soil formation; these services are the foundation of the production of all other ecosystem services.

Regulating and provisioning services are of particular interest to researchers in recent years (Vihervaara et al. 2010). The provisioning services of pollination and biological control are critical ecosystem services mediated by arthropods in agricultural systems (Kremen and Chaplin-Kramer 2007; Noriega et al. 2018). While research on ecosystem services has steadily increased in recent years, services provided by arthropods are severely understudied, comprising only 6.7% of the total body of ecosystem service research (Noriega et al. 2018). Pollination and biological control are perhaps the most valued arthropod-mediated ecosystem service in agroecosystems. Losey and Vaughan (2006) estimated that native pollinators are responsible for \$3.07 billion worth of fruits and vegetables produced in the United States. Honeybees (*Apis mellifera*) have been estimated to contribute \$5.2 billion in pollination services in the United States (Southwick and Southwick 1992). Pest



control services from natural enemies, which can directly substitute for insecticides, have been estimated to contribute \$4.5 billion per year to the agricultural industry (Losey and Vaughan 2006). Climate change, agricultural intensification, and habitat fragmentation all threaten the ecosystem services provided by arthropods (Allen-Wardell et al. 1998; Kremen et al. 2012). The loss of these services in the agricultural landscape, especially at the farm level, present ecological and economic challenges for agriculture globally, as well as wheat production in the iPNW.

### *Weed Seed Predation*

Weed management in agriculture is resource-intensive, requiring considerable monetary resources and time (Holm and Johnson 2009, Pimentel et al. 2005). Herbicides are the major strategy for controlling weeds in North America but increased dependence on them has resulted in problems such as herbicide-resistant weeds (Nakka et al. 2019), environmental pollution (Guzzella et al. 2006; Lewis et al. 2009; Rosculete et al. 2019), and effects on non-target plants (Power et al. 2013; Boutin et al. 2014; Mehdizadeh et al. 2021). Management of broadleaf crops is especially challenging in wheat production systems diversified with pulse crops, as few herbicide options do not also damage the crop. Therefore, an integrated weed management approach is needed to mitigate the negative consequences of traditional weed management in diversified systems. Among options available, biological control of weeds is a potential alternative.

Weed seed predation is a regulatory service that falls under biological control of pest species. Seed predation by both vertebrates and invertebrates is well documented in agroecosystems (Westerman et al. 2003; O'Rourke et al. 2006; Kulkarni et al. 2015), indicating it is a key ecosystem service that contributes to in-field weed management. Mice and birds comprise the vertebrate granivore population in agroecosystems while Carabidae, Gryllidae, and Formicidae are the main taxa responsible for invertebrate seed predation (Carmona et al. 1999; Cromar et al. 1999; van der Laat et al. 2015; Blubaugh et al. 2016; Evans and Gleeson 2016). Post-dispersal seed predation can benefit producers by removing weed seeds from the seedbank (Bohan et al. 2011; Carbonne et al. 2020) and has the potential to

decrease on-farm costs of herbicide (Mauchline et al. 2005) and increase crop yield (Petit et al. 2017; Gaba et al. 2020). However, differential mobility, food and habitat preferences, and population dynamics may dictate how granivores respond to diversified and intensified agricultural practices (Kulkarni et al. 2015; Sarabi 2019).

### **Thesis Aims**

The overall aim of the work described here is to improve the understanding of crop diversity and management on arthropod communities and to explore the relationships between weed seed regulation, seed predator diversity, and agricultural intensification and diversification in dryland wheat production systems. The specific objectives were to (1) to characterize the epigeic arthropod communities in crops that are prevalent in two different agroecological classes in the inland Pacific Northwest and (2) to determine the post-dispersal weed seed predation rates of three common weeds wheat production system and investigate potential defenses of these weed seeds.

## **Chapter 2 | Arthropod abundance, diversity, and evenness depend on crop and sampling date in diversified wheat production systems**

### **Abstract**

Projected and ongoing climate change presents challenges and opportunities for wheat-based cropping systems throughout the inland Pacific Northwest (iPNW). Producers are interested in reducing the amount of land in fallow to increase overall crop production, as well as create more sustainable production systems that are resilient to projected climate change. Examples of crop diversification and intensification for wheat systems include the addition of pulse crops such as dry pea and chickpea, and multi-species cover crops into rotations. Monitoring arthropod community responses to diversification and intensification can inform producers on which alternative crops are also associated with increased biodiversity and arthropod-mediated ecosystem services (i.e., biological control, pollination). The goal of this chapter is to determine the arthropod community composition and function associated with traditional and diversified alternative crops in iPNW wheat-based cropping systems. Arthropods were sampled using pitfall traps in six crop treatments in a large-plot field trial during the 2018 and 2019 growing seasons in Genesee, Idaho and St. John, Washington; these arthropods were identified to family and binned into granivorous or predator functional groups. Epigeal activity-density and diversity were greatest in winter pea plots across sites compared to the other crops tested. Granivore community metrics were not affected by crop or sampling date at the St. John site but at the Genesee site, winter pea consistently had greater diversity and activity-density compared to winter wheat. Predator activity-density was greater in spring wheat plots in Genesee and fallow plots in St. John, though across sites predator communities were more even in winter wheat plots compared to winter pea or cover crop plots. Generally, activity-density and diversity were greater in the crops within diversified rotations, though evenness was greater in winter wheat plots.

## Introduction

Dryland cropping systems are found in regions with average annual precipitation of less than 600mm and where no irrigation is used (Schillinger et al. 2015). Land devoted to dryland cropping in the western United States is 4,380,000 ha and around 76% of that land is situated in the inland Pacific Northwest (iPNW) (Schillinger et al. 2015), a region that stretches from eastern and central Washington, to northeastern Oregon, and the Idaho Panhandle. In the iPNW, current cropping systems typically consist of a two-year rotation of winter wheat and summer fallow or wheat-legume rotations (Schillinger and Papendick 2008). Growing concerns among producers and researchers for fallow-based production include degraded soil health and declining productivity, as fallowing is associated with increased soil erosion (Singh et al. 2012; Sharratt et al. 2018), soil degradation (Mosier et al. 1991; Lemke et al. 1999; Nielsen et al. 2011), and the potential for increased greenhouse gas emissions (Liebig et al. 2010; Bista et al. 2017).

Researchers and producers have experimented with a variety of alternative crops such as pea, sunflower, canola, and flax; however, an alternative crop has not yet been found that competes agronomically or economically with the winter wheat-summer fallow rotation (Schillinger and Papendick 2008). Research has shown that the addition of legumes or oilseeds into rotations have multiple short- and long-term benefits, such as improved weed management, improved soil structure, and reduced greenhouse gas emissions (N<sub>2</sub>O emissions) (Awale et al. 2017; Burke et al. 2017; Karimi et al. 2021). Winter pea and canola are potential candidates for alternative crops (Schillinger 2020), as it is well-documented for wheat yields to be higher following pea compared to following wheat (Miller et al. 2003; Williams et al. 2014). Canola is a non-host crop for multiple soil pathogens (Smith et al. 2004), although it is unclear how canola affects wheat yield in the subsequent growing season (Schillinger and Paulitz 2018).

The LIT project builds on REACCH by working with stakeholders at multiple points in the wheat-based supply chain to diversify the wheat-fallow cropping system. The main alternative crops of interest in this project include winter pea and cover crops. In this project, cover crops are defined as a crop comprised of multiple species

that are harvested with the intention of haying for livestock. Cover crops have the potential to enhance on-farm ecosystem services by promoting spatial and temporal diversity (Reiss and Drinkwater 2022).

Biodiversity in agroecosystems is increasingly being recognized as a major determinant of ecosystem functioning (Hooper et al. 2005). Diversity can refer to genetic variations within a species to the distribution of species within a biome (Wilson 1988). Diversity in agriculture can also be thought of in terms of spatial (within-field, field-level, and landscape-level) and temporal scales (within and outside of a growing season). There are several mechanisms through which biodiversity positively affects ecosystem services (Hooper et al. 2005). Through the sampling effect (the greater likelihood of finding species with a strong impact on ecosystem function in highly diversified communities (Huston 1997; Wardle 1999)), diverse communities are more likely to have assemblages containing multiple species that contribute to an ecosystem service, an attribute of a resilient system. Diverse communities may also include combinations of species that complement and facilitate each other in resource use (Ives et al. 2005). These mechanisms contribute to the evidence that biodiversity supports ecosystem services such as pollination and pest suppression through supporting ecosystem functioning (Dainese et al. 2019). It is established that species richness increases the supply of some ecosystem services (Costanza et al. 2007; Obrist and Duelli 2010; García and Martínez 2012) but the effect of species richness on the stability of those services has yet to be established. Community evenness, and more specifically predator community evenness, is at least as important as richness. In some cases, predator community evenness was a better determinant of biological control services than was predator richness (Crowder et al. 2010, 2012). Crowder et al. (2010) experimentally manipulated predator and pathogen evenness in enclosures in potato fields to monitor effects on plant growth and potato beetle mortality and found that predator and pathogen evenness increased plant biomass and yield, as well as increased potato beetle mortality. The results suggest that high abundance, richness, and evenness are all essential components of biologically diverse communities. Arthropods in the study presented in this thesis were caught with pitfall traps,

meaning that catches more accurately reflect the interaction of the activity and the density (referred to as activity-density) of each taxon rather than actual abundances (Saska et al. 2013).

The diversity of functionally equivalent species (functional diversity) is hypothesized to stabilize ecosystem functioning and the provision of ecosystem services (Hooper et al. 2005). The portfolio concept in ecology posits that the combination of diverse species' responses to environmental variation along with redundancy in species resource use will conserve ecosystem services when species are lost or cannot contribute (Schindler et al. 2015). For example, in the event of an extreme weather event that inhibits one or more predatory species, community diversity expressed in an overlap of climatic niches ensures that at least one predator species will feed on the pest. More diverse communities can be comprised of predator species that use different modes of attack on pests, attack at different times, or in different spaces; ultimately maximizing pest mortality (Ives et al. 2005; Snyder 2019). Although there is mounting evidence for the benefits of biodiversity to ecosystem services, there is still a lack of information supporting the importance of biodiversity to the stability of ecosystem services in agroecosystems.

The main goal of this chapter was to characterize the epigeic arthropod communities in current and projected dryland wheat production systems in the iPNW within two multi-year replicated field trials and to determine the taxonomic and functional composition of those communities. Hypotheses tested include: (H<sub>1</sub>) granivorous and predaceous arthropod communities are dissimilar among crops; (H<sub>2</sub>) activity-density, diversity, and evenness (community metrics) of arthropod communities differ among crops; (H<sub>3</sub>) metrics of arthropod communities differ among sampling dates. Both H<sub>2</sub> and H<sub>3</sub> are composite hypotheses.

## Methods

### Site Description

Three three-year, wheat-based rotations were established in replicated field plots in St. John, Washington (47.121055, -117.539027) and Genesee, Idaho (46.514564, -116.823590) as part of the LIT project to evaluate alternative and business-as-usual (BAU) rotations. Field plots (9.7m x 22.8m) were established in the fall of 2017. Rotations had staggered starts, such that each crop of each rotation was present in a block, yielding nine plots (Figure 2.1A). This was replicated five times for a total of 45 plots (3 rotations x 3 crops within rotation x 5 replications) at each site so that all three crops in each rotation were present within a season (Figure 2.1B). Rotational treatments differed slightly between the St. John, WA and Genesee ID

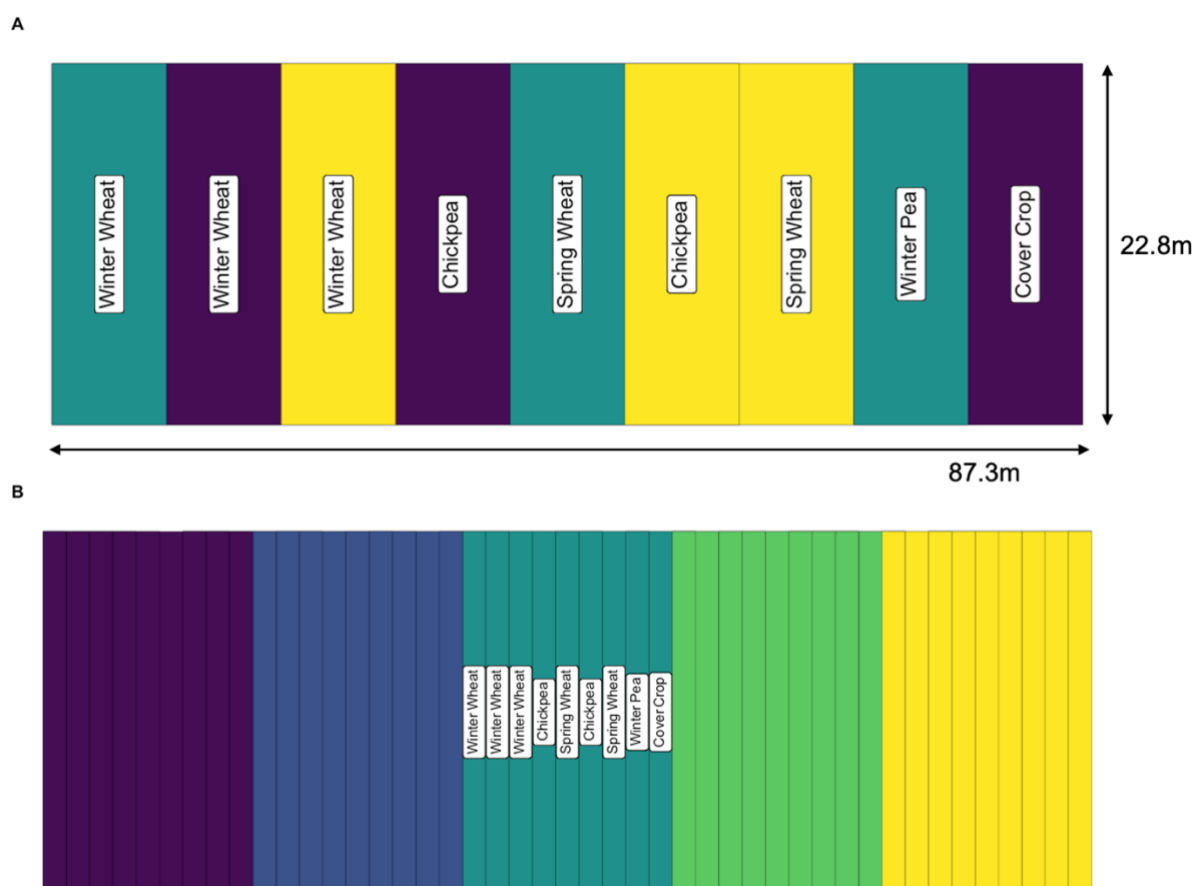


Figure 2.1 Experimental design for field plots. Three replications of three rotations (WP-WW-SW (green); CC-WW-CP (purple); and CP-WW-SW (yellow)) were present at both sites (A). This was replicated five times at each study site (B) for a total of 45 plots at each site.

study sites to accommodate the unique agroecological class within which the site was located. These agroecological classes are derived from the land classification from the USDA-NASS Cropland Data Layer combined with bioclimatic and socio-economic drivers (Huggins et al. 2017). Climate in the iPNW is generally Mediterranean-like with cold, wet winters and hot, dry summers (Schillinger et al. 2006). Annual precipitation ranges from 460mm in St. John, WA to 600mm in Genesee, ID. Crop varieties at both sites are Jasper winter wheat, WB9518 spring wheat, and Windham winter pea. The chickpea variety planted at Genesee was Billybeans. Different plant species comprised the cover crop mixtures at either site. St. John: oat, barley, pea, sunflower, and turnip. Genesee: oat, pea, crimson clover, radish, and turnip.

The St. John site is in the Annual Crop/Fallow Transition agroecological class (Huggins et al. 2014, 2015). The soil at this site was predominately mesic Cumulic haploxerolls (Soil Survey Staff 2021a). The rotational treatments were a BAU: fallow-winter wheat-spring wheat rotation, and two alternatives: winter pea-winter wheat-spring wheat, and cover crop-winter wheat-spring wheat. For the 2017-2018 growing year, winter crops were planted on 3 Oct. 2017 and spring crops were planted on 30 Mar. 2018. For the 2018-2019 growing year, winter crops were planted on 25 Sep. 2018 and spring crops were planted on 24 April 2019.

The Genesee site is in the continuous cropping agroecological class (Huggins et al. 2014, 2015). The soil at this site was mesic Pachic Ultic Haploxerolls and mesic Typic Argixerolls (Soil Survey Staff 2021b). The rotations were a business-as-usual: chickpea-winter wheat-spring wheat rotation, and two alternatives: winter pea-winter wheat-spring wheat, and chickpea-winter wheat-cover crop. For the 2017-2018 growing year, winter crops were planted on 5 Oct. 2017 and spring crops were planted on 27 April 2018. For the 2018-2019 growing year, winter crops were planted on 4 Oct. 2018 and spring crops were planted on 2 May 2019.

#### *Pitfall Traps*

Pitfall traps were two 470 ml plastic cups (Dart Container, Inc.) nested and buried in the soil so that the lip of the inner cup was flush with the soil surface. The



outer cup was used to stabilize the hole so that the inner cup could be easily removed for sample collection and refilling of the trap. Propylene glycol (Colonial Chemical Solutions, Inc.) was used as a preservative and a surfactant in the pitfall trap – 100 ml of a 30% propylene glycol solution was replaced in each trap at weekly intervals. Two pitfall traps were placed within each plot, two meters from the center of the plot (Figure 2.2). This trap design follows the recommendations of Brown and Matthews (2016). Traps were left open continuously, with sampling taking place in the morning once every seven days at each site throughout the growing seasons of 2018 and 2019. Traps were removed from plots at the time of crop harvest.

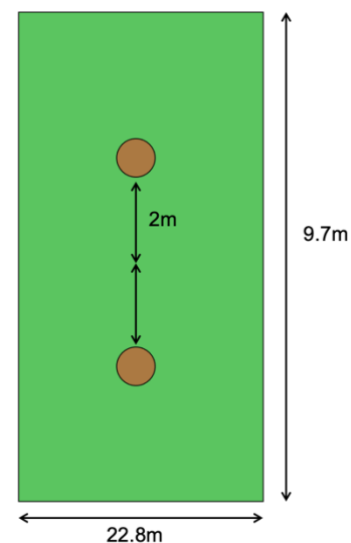


Figure 2.2 Pitfall trap placement within each plot.

Pitfall trap catches were stored in 70% ethanol solution. Individuals that are considered to be predominately epigeal were identified to Family, following Borror and DeLong's Study of Insects 7<sup>th</sup> edition (Triplehorn et al. 2005). Individuals belonging to Mollusca, Acari, Thysanoptera, and Collembola were identified to order. Ground beetles (Coleoptera: Carabidae) were identified to Genus. Taxa were assigned to functional groups based on primary habitat (foliar, epigeic) and mode of feeding (predator, granivore), meaning that some taxa are included in more than one community subset. These assignments were based on life history information in Triplehorn et al. (2005).

### *Statistical Analysis*

All statistical analyses were done in RStudio open-source software R version 4.0.2 (R Core Team 2020). Samples with a 'zero community' – no individuals captured in a trap during a sampling period – were removed from the dataset before ordinal community analyses were conducted. Due to the potential usefulness of bycatch in the pitfall traps (Hatten et al. 2013; Hung et al. 2015; McCravy 2018), analyses were done with five sets of community data: all taxa present in pitfalls, epigeic taxa, foliar taxa, granivorous taxa, and predatory taxa. For all communities,

data were analyzed separately by site and year. This is due to the uneven rotational treatments at each site, as well as only having two levels for both site and year variables.

Hypotheses were tested using a repeated-measures analysis of variance (ANOVA). Fixed effects were crop, sampling date, and their interaction. Random effects were plot, nested within replication. Activity-density was transformed to  $\log(x + 1)$  to increase the normality based on residuals. When significant effects of crop were detected, pairwise comparisons were made using the 'emmeans' package with alpha levels adjusted for multiple comparisons using the Bonferroni correction (Lenth et al. 2022). Due to uneven sampling effort across the growing season, data were only analyzed for the intervals that all crops or fallow were present at the site, meaning that samples taken after the first crop was harvested are not analyzed here. Sampling dates for St. John were 26 April-19 July 2018 and 10 May-12 July 2019; sampling dates for Genesee were 25 May-20 July 2018 and 15 May-20 July 2019. Cover crop plots were excluded from Genesee for the 2019 analysis because there are only three sampling dates for those plots in that year due to complications of pitfall traps drying out during high heat periods and yielding no arthropod catches.

Diversity indices used to compare arthropod communities include Simpson's diversity, Simpson's evenness, and species abundance or activity-density. The Simpson's diversity index was calculated as  $D = 1/(\sum p_i^2)$ , where  $p_i$  is the proportion of individuals of a species  $i$  among the total individuals collected (Magurran 2004). The Simpson's evenness index was calculated as  $E_{1/D} = (1/D)/S$ , where  $S$  is the number of taxa collected (Magurran 2004).

The activity-density of the epigeic, granivorous, and predator communities during the whole sampling period were compared among the crop treatments using nonmetric multidimensional scaling (NMDS). NMDS was used because it attempts to represent pairwise dissimilarity between objects using a dissimilarity matrix in low-dimensional space and does not make assumptions about linear relationships of the data. NMDS was conducted using the 'vegan' package (Dixon 2003; Oksanen et al. 2013). The metaMDS function was used to create NMDS ordination plots with Bray-Curtis distances. Stress ( $s$ ), non-metric fit ( $r^2$ ), and PERMANOVA ( $p$ ), statistics

measuring goodness-of-fit of the NMDS ordination distances to the data dissimilarity, were also computed (Oksanen et al. 2013). Again, sites and years were analyzed separately.

## Results

Cumulatively at both sites, pitfall traps collected 45,129 total individuals (Table 2.1), of which 11,300 individuals are predaceous. A total of 35,831 foliar-dwelling individuals were collected. There were 9,298 epigeic individuals collected and of those, 2,034 individuals are granivorous (Table 2.1). The most abundant family collected was Aphididae (Hemiptera). Among the foliar, epigeic, granivorous, and predaceous taxa, Lycosidae (Araneae), Aphididae, and Carabidae (Coleoptera) were the most abundant, respectively.

Tests were conducted to evaluate (H<sub>1</sub>) granivorous and predaceous arthropod communities are dissimilar among crops; (H<sub>2</sub>) activity-density, diversity, and evenness (community metrics) of arthropod communities differ among crops; (H<sub>3</sub>) metrics of arthropod communities differ among sampling dates

Low stress solutions were found for NMDS ordinations for granivorous and predaceous communities at St. John and Genesee in both years (Figure 2.3, Figure 2.4) and distances within ordinations were highly correlated to pitfall trap data dissimilarity (Table 2.2). Although the community separation was not visibly striking, PERMANOVA results indicate significant separation of granivorous communities between crops in Genesee both years ( $p = 0.001$  for 2018 and  $p = 0.003$  for 2019), but not at St. John (Table 2.2A) and significant separation of predator communities between crops at both sites and years ( $p = 0.012$  for St. John 2018,  $p = 0.001$  for St. John 2019 and Genesee both years) (Table 2.2B).

### *Crop x Date Interaction*

The crop x date interaction had variable effects on community metrics at both sites. The interaction of crop and date significantly affected activity-density of foliar and predator communities at both sites in both years (Table 2.3, Table 2.6), though

not on activity-density of epigeic or granivore communities (Table 2.4, Table 2.5). Foliar community diversity was significantly affected by the crop-date interaction at Genesee in 2018 and at St. John in 2019 (Table 2.3). Foliar community evenness was also significantly affected by the crop-date interaction at Genesee in 2018 and at St. John in 2019 (Table 2.3). Epigeic community evenness was significantly affected by the crop-date interaction at St. John (Table 2.4). Arthropod abundance and diversity loosely followed crop stand maturity – abundance and diversity were lower in the beginning of the season and during crop senescence and were greater in the two weeks leading up to peak maturity. The different crop stands mature at different times during the growing season, greatly contributing to the crop x date interaction.

### *Crop*

Overall, crop had an effect on nearly all community metrics at Genesee (except for predator evenness) but only affected foliar and predator community metrics at St. John. Activity-density and diversity of foliar and predator communities were significantly affected by crop at St. John (Table 2.3, Table 2.6), but not activity-density of epigeic and granivore communities (Table 2.4, Table 2.5). Crop significantly affected epigeic and predator evenness at St. John (Table 2.4, Table 2.6). Crop generally did not affect epigeic or granivorous communities at St. John, with the exception of epigeic evenness. Crop significantly affected activity-density, diversity, and evenness of all communities tested at Genesee (Table 2.3, Table 2.4, Table 2.5), except for predator diversity (Table 2.6).

### *Date*

The effect of date was more prevalent at St. John than at Genesee. Date significantly affected activity-density of all communities tested at St. John (Table 2.3, Table 2.4, Table 2.5, Table 2.6) but only on foliar and predator communities at Genesee (Table 2.3, Table 2.6). Diversity was similarly affected by date, with diversity of all communities tested at St. John significantly affected by sampling date (Table 2.3, Table 2.4, Table 2.5, Table 2.6). Date had effects only on the foliar

community diversity evenness at Genesee in both years (Table 2.3) and on the predator community diversity and evenness at Genesee in 2019 (Table 2.6).

Evenness of all communities tested at St. John was affected by date (Table 2.3, Table 2.4, Table 2.5, Table 2.6).

Table 2.1 Table of taxa collected, their abundances, and the community dataset they were included in for statistical analysis.

<b>Arthropod Taxa</b>	<b>Abundance</b>	<b>Foliar</b>	<b>Epigeic</b>	<b>Granivore</b>	<b>Predator</b>
Acrididae	275		x		
Alydidae	22	x			
Anthicidae	184	x			
Anthocoridae	68	x			x
Aphididae	11404	x			
Berytidae	43	x			x
Buprestidae	53	x			
Caliscelidae	1	x			
Cantharidae	38	x			
Carabidae	865		x	x	x
Chilopoda	7		x		x
Cercopidae	207	x			
Chrysomelidae	665	x			
Chrysopidae	1	x			x
Cicadellidae	968	x			
Coccinellidae	1165	x			x
Coreidae	8	x			
Cryptophagidae	173	x			
Curculionidae	1801	x			
Dermestidae	500		x		
Dictynidae	344		x		x
Elateridae	251		x		
Forficulidae	265		x		
Formicidae	726		x	x	x
Geocoridae	2095	x			x
Gryllidae	443		x	x	
Histeridae	70		x		
Latridiidae	789		x		
Linyphiidae	787		x		x
Lycosidae	2511		x		x
Lygaeidae	1286	x			
Meloidae	548	x			
Melyridae	371	x			x
Membracidae	1	x			
Miridae	289	x			
Molusca	20		x		
Mordellidae	126	x			
Nabidae	307	x			x

Arthropod Taxa	Abundance	Foliar	Epigeic	Granivore	Predator
Opiliones	119		x		x
Pentatomidae	78	x			
Reduviidae	8	x			
Rhaphidophoridae	78		x		
Rhopalidae	12	x			
Rhyparochromidae	375	x			
Salticidae	194	x			x
Scarabaeidae	61	x			
Scaptiidae	584	x			
Scutelleridae	2	x			
Silphidae	474		x		
Staphylinidae	639		x		x
Tenebrionidae	135		x		
Tettigoniidae	4	x			
Thomisidae	1058	x			x
Thysanoptera	11631	x			

Table 2.2 NMDS goodness-of-fit values for the granivore community (A) and predator community (B).  $k$  is the number of dimensions for each NMDS,  $S$  (stress value) is a goodness-of-fit value based on the sum of squared differences between ordination-based distances and the distances predicted by the regression,  $r^2$  is a non-metric fit between ordination distances and the observed dissimilarities, and  $p$  is the  $p$ -value for the PERMANOVA, which tests if the centroids of the distance matrices differ between groups.

A	Site	Year	k	s	$r^2$	$p$
	St. John	2018	2	0.09	1	.938
		2019	2	0.09	0.99	.225
Genesee	2018	2	0.01	1	.001	
		2019	3	0.01	1	.003
B	Site	Year	k	s	$r^2$	$p$
	St. John	2018	4	0.14	0.97	.012
		2019	3	0.14	0.98	.001
Genesee	2018	3	0.11	0.99	.001	
		2019	4	0.12	0.98	.001

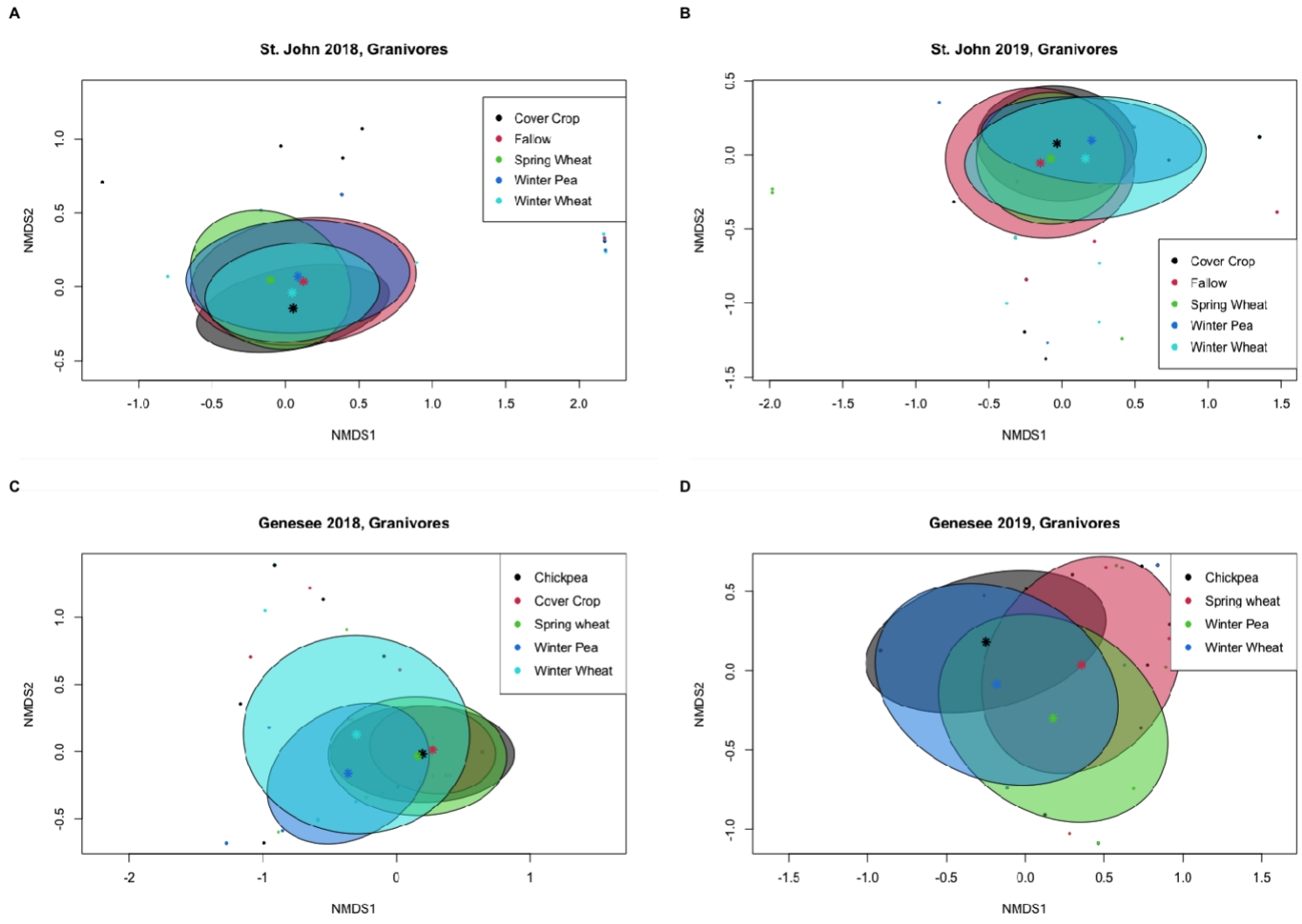


Figure 2.3 NMDS ordination for the granivore communities at both sites in both years. Centroid points represent mean community composition for each crop.



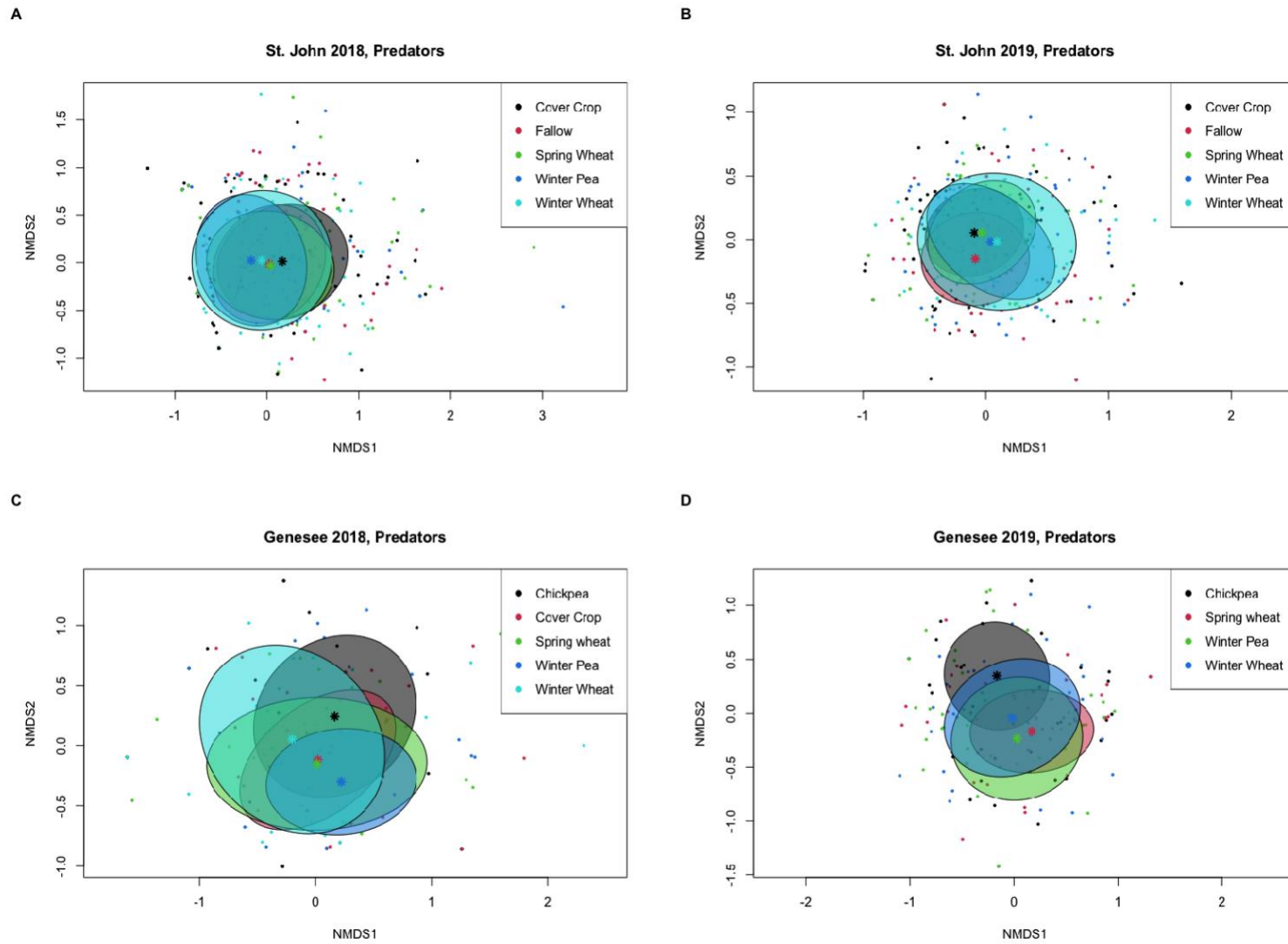


Figure 2.4 NMDS ordination for the predator communities at both sites and both years. Centroid points represent mean community composition for each crop.

Table 2.1 ANOVA table for foliar community metrics for both sites and years.

	St. John						Genesee					
	2018			2019			2018			2019		
	<i>F</i>	<i>df</i>	<i>P</i>	<i>F</i>	<i>df</i>	<i>P</i>	<i>F</i>	<i>df</i>	<i>P</i>	<i>F</i>	<i>df</i>	<i>P</i>
<b>Activity-density</b>												
Crop	14.427	4, 38	<0.0001	26.898	4, 36	<0.0001	9.0930	4, 36	<0.0001	32.975	3, 32	<0.0001
Date	139.117	1, 360	<0.0001	92.566	1, 262	<0.0001	36.921	1, 106	<0.0001	5.118	1, 115	0.0250
Crop*Date	0.979	4, 360	<0.0001	7.420	4, 262	<0.0001	2.942	4, 106	0.023	4.674	3, 115	0.0030
<b>Simpson's Diversity</b>												
Crop	10.657	4, 38	<0.0001	4.294	4, 36	0.006	1.082	4, 36	0.3796	6.571	3, 32	0.001
Date	25.806	1, 360	<0.0001	60.217	1, 262	<0.0001	15.017	1, 106	0.0002	32.746	1, 115	<0.0001
Crop*Date	2.294	4, 360	0.0580	6.994	4, 262	<0.0001	6.046	4, 106	0.0002	1.726	3, 115	0.1640
<b>Simpson's Evenness</b>												
Crop	8.907	4, 38	<0.0001	2.593	4, 36	0.0527	5.979	4, 36	0.0009	0.929	3, 32	0.437
Date	35.916	1, 360	<0.0001	50.504	1, 262	<0.0001	26.569	1, 106	<0.0001	27.436	1, 115	<0.0001
Crop*Date	0.810	4, 360	0.5180	2.581	4, 262	0.0370	1.669	4, 106	0.0370	0.545	3, 115	0.6510

Table 2.2 ANOVA table for epigeic community metrics for both sites and years.

	St. John						Genesee					
	2018			2019			2018			2019		
	<i>F</i>	<i>df</i>	<i>P</i>	<i>F</i>	<i>df</i>	<i>P</i>	<i>F</i>	<i>df</i>	<i>P</i>	<i>F</i>	<i>df</i>	<i>P</i>
<b>Activity-density</b>												
Crop	1.672	4, 38	0.177	1.704	4, 36	0.170	6.977	4, 36	<b>0.003</b>	1.218	3, 32	0.318
Date	2.675	1, 360	0.103	9.901	1, 262	<b>0.001</b>	0.340	1, 106	0.561	1.693	1, 115	0.196
Crop*Date	1.982	4, 360	0.098	3.076	4, 262	<b>0.017</b>	1.003	4, 106	0.411	1.806	3, 115	0.151
<b>Simpson's Diversity</b>												
Crop	0.732	4, 38	0.576	3.311	4, 36	<b>0.020</b>	2.968	4, 36	<b>0.032</b>	5.536	3, 32	<b>0.003</b>
Date	13.456	1, 360	<b>0.0003</b>	1.477	1, 262	0.225	1.894	1, 106	0.172	0.33	1, 115	0.566
Crop*Date	2.041	4, 360	0.089	0.143	4, 262	0.965	0.41	4, 106	0.800	1.402	3, 115	0.247
<b>Simpson's Evenness</b>												
Crop	0.783	4, 38	0.543	2.633	4, 36	<b>0.050</b>	3.731	4, 36	<b>0.012</b>	2.222	3, 32	0.104
Date	4.217	1, 360	<b>0.041</b>	6.070	1, 262	<b>0.014</b>	1.072	1, 106	0.303	1.354	1, 115	0.247
Crop*Date	2.628	4, 360	<b>0.035</b>	2.13	4, 262	<b>0.078</b>	0.425	4, 106	0.789	2.031	3, 115	0.115

Table 2.3 ANOVA table for granivore community metrics for both sites and years.

	St. John						Genesee					
	2018			2019			2018			2019		
	<i>F</i>	<i>df</i>	<i>P</i>	<i>F</i>	<i>df</i>	<i>P</i>	<i>F</i>	<i>df</i>	<i>P</i>	<i>F</i>	<i>df</i>	<i>P</i>
<b>Activity-density</b>												
Crop	0.288	4, 38	0.883	0.683	4, 36	0.608	11.428	4, 36	<b>&lt;0.0001</b>	3.398	3, 32	<b>0.030</b>
Date	10.297	1, 360	<b>0.001</b>	18.225	1, 262	<b>&lt;0.0001</b>	1.691	1, 106	0.197	0.418	1, 115	0.520
Crop*Date	0.433	4, 360	0.784	0.655	4, 262	0.624	2.350	4, 106	0.063	1.431	3, 115	0.243
<b>Simpson's Diversity</b>												
Crop	0.578	4, 38	0.680	0.690	4, 36	0.603	3.456	4, 36	<b>0.018</b>	5.586	3, 32	<b>0.003</b>
Date	5.222	1, 360	<b>0.024</b>	9.323	1, 262	<b>0.002</b>	2.558	1, 106	0.114	0.402	1, 115	0.528
Crop*Date	0.298	4, 360	0.878	0.581	4, 262	0.677	1.759	4, 106	0.147	0.214	3, 115	0.886
<b>Simpson's Evenness</b>												
Crop	0.527	4, 38	0.716	0.502	4, 36	0.733	5.293	4, 36	<b>0.002</b>	3.476	3, 32	<b>0.027</b>
Date	6.392	1, 360	<b>0.013</b>	11.940	1, 262	<b>0.0008</b>	3.226	1, 106	0.077	0.119	1, 115	0.731
Crop*Date	0.318	4, 360	0.084	0.526	4, 262	0.716	2.117	4, 106	0.088	0.510	3, 115	0.676

Table 2.4 ANOVA table for predator community metrics for both sites and years.

	St. John						Genesee					
	2018			2019			2018			2019		
	<i>F</i>	<i>df</i>	<i>P</i>	<i>F</i>	<i>df</i>	<i>P</i>	<i>F</i>	<i>df</i>	<i>P</i>	<i>F</i>	<i>df</i>	<i>P</i>
<b>Activity-density</b>												
Crop	5.69	4, 38	<b>0.001</b>	4.455	4, 36	<b>0.005</b>	10.271	4, 36	<b>&lt;0.0001</b>	4.979	3, 32	<b>&lt;0.0001</b>
Date	4.241	1, 360	<b>0.040</b>	0.480	1, 262	0.488	17.936	1, 106	<b>&lt;0.0001</b>	17.510	1, 115	<b>&lt;0.0001</b>
Crop*Date	2.937	4, 360	<b>0.020</b>	1.764	4, 262	0.136	4.410	4, 106	<b>0.002</b>	6.943	3, 115	<b>&lt;0.0001</b>
<b>Simpson's Diversity</b>												
Crop	5.382	4, 38	<b>0.001</b>	4.901	4, 36	<b>0.002</b>	2.506	4, 36	0.059	1.056	3, 32	0.381
Date	37.934	1, 360	<b>&lt;0.0001</b>	10.489	1, 262	<b>0.001</b>	1.321	1, 106	0.252	4.326	1, 115	<b>0.039</b>
Crop*Date	1.949	4, 360	0.101	0.442	4, 262	0.778	1.401	4, 106	0.238	1.115	3, 115	0.345
<b>Simpson's Evenness</b>												
Crop	3.818	4, 38	<b>0.010</b>	5.43	4, 36	<b>0.001</b>	2.892	4, 36	<b>0.035</b>	1.948	3, 32	0.141
Date	15.807	1, 360	<b>0.0001</b>	7.732	1, 262	<b>0.005</b>	3.061	1, 106	0.082	8.424	1, 115	<b>0.004</b>
Crop*Date	1.239	4, 360	0.293	0.695	4, 262	0.595	2.219	4, 106	0.071	0.729	3, 115	0.536

Table 2.5 Foliar community metric means for both sites and years. Letters denote significance differences within crop among site and year.

Site	Year	Crop	Activity-Density	Diversity	Evenness
<b>St. John</b>	2018	Cover Crop	15.55±2.56b	2.77±0.19bc	0.18±0.03
		Fallow	15.58±3.06b	3.10±0.22c	0.14±0.02
		Spring Wheat	20.20±2.73b	2.28±0.09ab	0.31±0.03
		Winter Pea	13.70±5.10ab	2.13±0.14ab	0.32±0.05
		Winter Wheat	7.52±1.02a	1.96±0.08a	0.46±0.03
	2019	Cover Crop	20.92±3.57bc	3.79±0.35b	0.11±0.03
		Fallow	13.13±1.34ab	2.76±0.21a	0.15±0.03
		Spring Wheat	11.38±1.15a	3.23±0.12ab	0.11±0.01
		Winter Pea	31.30±4.23b	2.61±0.23a	0.15±0.03
		Winter Wheat	8.78±0.70a	3.08±0.15b	0.18±0.02
<b>Genesee</b>	2018	Chickpea	11.80±1.99ab	2.14±0.21	0.41±0.06ab
		Cover Crop	18.00±7.34ab	2.26±0.25	0.21±0.05a
		Spring Wheat	27.30±5.21b	2.10±0.16	0.28±0.05a
		Winter Pea	55.81±28.38b	1.82±0.15	0.19±0.02a
		Winter Wheat	8.29±1.85a	1.83±0.15	0.51±0.06b
	2019	Chickpea	14.13±2.09ab	2.48±0.16b	0.19±0.04
		Cover Crop			
		Spring Wheat	33.33±7.49b	2.36±0.15b	0.19±0.04
		Winter Pea	77.00±8.22c	1.42±0.06a	0.17±0.03
		Winter Wheat	12.49±1.49a	2.43±0.15b	0.25±0.04

Table 2.6 Epigeic community metric means for both sites and years. Letters denote significance differences within crop among site and year.

Site	Year	Crop	Activity-Density	Diversity	Evenness
St. John	2018	Cover Crop	4.65±0.56	1.86±0.14	0.51±0.06
		Fallow	4.48±0.48	1.74±0.13	0.54±0.06
		Spring Wheat	5.26±0.36	2.02±0.10	0.46±0.03
		Winter Pea	4.05±0.60	1.61±0.12	0.60±0.06
		Winter Wheat	3.91±0.28	1.80±0.08	0.52±0.03
	2019	Cover Crop	4.90±0.48	2.67±0.18ab	0.25±0.05ab
		Fallow	4.39±0.63	2.18±0.15ab	0.32±0.05ab
		Spring Wheat	5.08±0.30	2.69±0.12b	0.26±0.03a
		Winter Pea	4.92±0.50	2.42±0.18ab	0.29±0.05ab
		Winter Wheat	3.90±0.38	1.97±0.10a	0.46±0.04b
Genesee	2018	Chickpea	2.94±0.42ab	1.68±0.14ab	0.58±0.07b
		Cover Crop	7.24±2.02bc	1.82±0.19ab	0.47±0.10ab
		Spring Wheat	6.50±0.83c	1.71±0.12ab	0.49±0.06ab
		Winter Pea	7.47±1.18c	1.98±0.17b	0.33±0.09a
		Winter Wheat	2.17±0.21a	1.39±0.08a	0.71±0.05b
	2019	Chickpea	5.55±1.11	1.77±0.12a	0.46±0.06ab
		Cover Crop			
		Spring Wheat	7.44±0.80	2.79±0.21b	0.25±0.05b
		Winter Pea	8.10±2.12	2.67±0.28b	0.26±0.07ab
		Winter Wheat	6.49±0.68	2.32±0.13ab	0.26±0.04a

Table 2.7 Granivore community metric means for both sites and years. Letters denote significance differences within crop among site and year.

Site	Year	Crop	Activity-Density	Diversity	Evenness
<b>St. John</b>	2018	Cover Crop	1.23±0.17	1.14±0.09	0.89±0.08
		Fallow	1.42±0.23	1.00±0.00	1.00±0.00
		Spring Wheat	1.54±0.15	1.05±0.03	0.95±0.03
		Winter Pea	1.46±0.18	1.08±0.08	0.94±0.06
		Winter Wheat	1.43±0.11	1.08±0.04	0.94±0.03
	2019	Cover Crop	1.68±0.23	1.14±0.08	0.88±0.06
		Fallow	2.30±0.55	1.08±0.05	0.91±0.05
		Spring Wheat	2.02±0.17	1.19±0.05	0.85±0.04
		Winter Pea	1.47±0.16	1.09±0.07	0.92±0.05
		Winter Wheat	1.90±0.30	1.11±0.05	0.91±0.04
<b>Genesee</b>	2018	Chickpea	2.39±0.33ab	1.28±0.10ab	0.81±0.07b
		Cover Crop	5.62±1.43bc	1.34±0.13ab	0.66±0.11ab
		Spring Wheat	5.80±0.83c	1.21±0.06ab	0.75±0.06ab
		Winter Pea	6.29±1.07c	1.55±0.10b	0.44±0.08a
		Winter Wheat	1.90±0.27a	1.14±0.06a	0.88±0.05b
	2019	Chickpea	5.48±1.45b	1.16±0.05ab	0.80±0.06ab
		Cover Crop			
		Spring Wheat	2.87±0.34ab	1.38±0.08b	0.66±0.07b
		Winter Pea	2.45±0.43ab	1.49±0.20b	0.65±0.12ab
		Winter Wheat	2.19±0.38a	1.07±0.04a	0.92±0.04a



Table 2.8 Predator community metric means for both sites and years. Letters denote significance differences within crop among site and year.

Site	Year	Crop	Activity-Density	Diversity	Evenness
St. John	2018	Cover Crop	6.25±0.81ab	2.29±0.16ab	0.34±0.05ab
		Fallow	6.00±0.56b	2.24±0.15ab	0.35±0.06ab
		Spring Wheat	6.21±0.40b	2.35±0.11b	0.36±0.03a
		Winter Pea	4.16±0.59a	1.79±0.11a	0.45±0.05ab
		Winter Wheat	4.20±0.27a	1.87±0.08a	0.50±0.03b
	2019	Cover Crop	8.72±0.87b	3.43±0.24b	0.18±0.05ab
		Fallow	8.71±0.97b	3.32±0.23b	0.17±0.04ab
		Spring Wheat	8.15±0.42b	3.32±0.11b	0.13±0.02a
		Winter Pea	8.13±0.72b	3.00±0.20ab	0.16±0.03ab
		Winter Wheat	5.57±0.38a	2.53±0.12a	0.31±0.04b
Genesee	2018	Chickpea	2.95±0.42a	2.05±0.17	0.45±0.06ab
		Cover Crop	4.87±0.87ab	2.44±0.31	0.35±0.11ab
		Spring Wheat	6.68±1.06b	1.96±0.14	0.42±0.06ab
		Winter Pea	6.67±1.25b	2.28±0.25	0.24±0.06a
		Winter Wheat	2.54±0.26a	1.71±0.12	0.59±0.06b
	2019	Chickpea	8.22±1.04ab	2.34±0.14	0.25±0.04
		Cover Crop			
		Spring Wheat	10.79±1.83b	2.68±0.20	0.20±0.04
		Winter Pea	6.65±1.17ab	2.51±0.20	0.25±0.07
		Winter Wheat	5.35±0.53a	2.31±0.15	0.34±0.05

## Discussion

The objective of this study was to measure the effects of crop diversity in wheat-based production systems on the composition of epigeic arthropods. Over two years at two sites in the iPNW, there were significant differences in community metrics in different functional subsets of arthropods among crop and sampling date some of which were consistent with H<sub>2</sub> and H<sub>3</sub>. Ordinations of granivorous and predaceous communities showed significant differences in composition among crops, consistent with H<sub>1</sub>.

Regarding the first hypothesis, that granivorous and predaceous communities are dissimilar among crops, ordinations and PERMANOVA suggest that both of these communities are significantly dissimilar among crops across sites (Figure 2.3, Figure 2.4, Table 2.2). Bray-Curtis dissimilarity was used for NMDS ordinations, which incorporate arthropod species richness and evenness values for each crop type. The NMDS performed here includes all the sampling dates for the growing season of each year. The dissimilarity of both communities between crops could be due to differences in resource availability between crops, such as food or shelter. Abiotic factors such as temperature and relative humidity within and beneath the crop canopy can also affect the activity-density of arthropods (Prather et al. 2020), which is what was used to calculate the Bray-Curtis values.

The second hypothesis, arthropod community metrics differ among crops, received varying support. Crop had significant effects on community metrics of foliar and predator communities, but generally not on epigeic or granivorous community metrics. Significance of crop, particularly on diversity, varied by site and year. Epigeic diversity was significantly affected by crop, but activity-density and evenness were not. However, granivore community metrics were significantly affected by crop at Genesee. Activity-density of all four arthropod communities was typically lowest in winter wheat plots (Table 2.7, Table 2.8, Table 2.9, Table 2.10). Activity-density was generally greatest in winter pea (Table 2.7, Table 2.8, Table 2.9, Table 2.10), though predator activity-density was greatest in fallow at St. John and spring wheat at Genesee (Table 2.10).

Crop effects on diversity measures are highly dependent on arthropod community, site, and year. For example, at St. John in 2018, foliar diversity was lowest in winter wheat and greatest in fallow but in 2019 at the same site, foliar diversity was lowest in winter pea and greatest in cover crop (Table 2.7). Managing fallow plots was difficult during this project, which could contribute to the greater diversity in fallow. Foliar arthropod diversity at Genesee in 2019 was lowest in winter pea and greatest in chickpea (Table 2.7). Epigeic diversity was generally lowest in winter wheat, though which crops harbored more diverse epigeal communities depended on site and year. Epigeic diversity at St. John in 2019 was greatest in spring wheat (Table 2.8), and greatest in winter pea and cover crop at Genesee in 2018 and 2019, respectively (Table 2.8). Granivore diversity was lowest in winter wheat and greatest in winter pea (Table 2.9). Arthropod predator diversity between crops also depended on year, with the lowest diversity found in winter pea and winter wheat plots in 2018 and 2019 and the greatest diversity in spring wheat and fallow plots, 2018 and 2019, respectively (Table 2.10).

Farm management could have impacted the abundance and diversity of sampled arthropods. The plots in this study were conventionally managed for whichever crop was planted, with reduced tillage. For example, the winter pea plots were treated with Asana XL (Valent) insecticide on 30 May 2018, 7 June 2018, and 27 June 2018 and with Mustang Maxx (FMC) on 10 June 2019 and 29 June 2019 to control *Bruchus pisorum* L. (pea weevil), which could have negatively influenced all arthropod communities in winter pea plots, not just the targeted pest.

The third hypothesis, metrics of arthropod communities differ among sampling dates, received full or partial support, depending on site and arthropod community. Sampling date had significant effects on activity-density, diversity, and evenness of all four communities investigated at St. John (Table 2.3, Table 2.4, Table 2.5, Table 2.6). Foliar arthropod activity-density, diversity, and evenness were affected by date at Genesee, and predator community metrics were affected by sampling date at Genesee only in 2019 (Table 2.3, Table 2.6). Contrasts were not performed with sampling dates as the focus of this thesis and the LIT project is concerned with differences between crops or crop rotations.

The effect of sampling date on community metrics can be due to changes in ambient temperatures and relative humidity under the crop canopy (Lessard et al. 2011; Prather and Kaspari 2019; Prather et al. 2020), which depends on the stage of plant development, contributing to the interaction of date and crop. There may also be a temporal component to food and shelter resources for the taxa in these communities (Boyer et al. 2003; M. Crutsinger et al. 2008; Mello et al. 2022). For example, Crutsinger et al. (2008) found differences in arthropod activity-density and species richness among sampling dates in a *Solidago* common garden experiment.

Pitfall sampling occurred through the growing season of each crop, and in fallow plots until the last crop was harvested. Life-history traits of ubiquitous arthropods would influence trappable populations of arthropod species. For example, Carabid beetles are either spring-breeders or fall-breeders (Honek et al. 2006; Kulkarni et al. 2016), with spring-breeders being more active May-June.

The interaction between crop and sampling date generally affected community metrics of foliar taxa, indicating that foliar communities may be more sensitive to the crop maturing throughout the growing season compared to other communities that were tested. This makes sense due to the crop-specific pests that colonize fields (Clement et al. 1990, 2010; Clement 2006). For example, the pea aphid (*Acyrtosiphon pisum* Harris) tends to have low density in pea fields earlier in the growing season (May-June), with a population boom occurring early- to mid-June, and then declining in early- to mid-July, loosely following the maturity and senescence of peas (Clement et al. 2010).

When all taxa were considered, effects were similar to those detected with the foliar communities, due to foliar taxa comprising the majority of arthropods trapped (Table 2.1). An ANOVA was still conducted to test the effects of the crop, date, and their interaction (Appendix A) but is not discussed here.

The community metrics tested here varied between sampling sites and years. However, foliar and predator communities were generally affected by crop. Epigeic and granivorous communities were affected by crop only at Genesee. All communities tested were affected by sampling date at St. John, with only foliar and predator communities affected by date at Genesee. Foliar and predator communities

may be more generalizable across agroecological classes (AECs) and epigeic and granivorous communities may be more site-specific or AEC-specific in their activity-density, diversity, and evenness measurements.

### *Implications*

Increasing diversity in rotation schemes is generally beneficial to arthropod communities (Bullock 1992; Smith et al. 2008; Davis et al. 2012). Results presented here indicate that epigeic and granivorous communities are not affected by altering the crop planted in iPNW production systems (Table 2.4, Table 2.5). On the other hand, the foliar communities may be more sensitive to crop changes (Table 2.3), which may increase the need for crop-specific pest control.

Increased vegetational diversity has been shown to have positive effects on arthropod abundance (Letourneau et al. 2011). However, cover crop plots did not have significantly greater activity-density or diversity for epigeic, foliar, granivorous, or predatory communities compared with the single-species crop plots (Table 2.7, Table 2.8, Table 2.9, Table 2.10). Augmenting a wheat production system with pulse crops and cover crops has agronomic and ecological benefits to the farm (Gan et al. 2015; Schillinger 2020) and surrounding landscape (Landis et al. 2000) and increasing the species of crop cover across the landscape may provide more suitable resources for beneficial arthropods (Altieri 1999; Landis et al. 2000). Though in this study there were no significant differences in activity-density or diversity of foliar, epigeic, or predator communities between fallow and cover crop plots at St. John (Table 2.5, Table 2.6, Table 2.7, Table 2.8). This could be due poor establishment of cover crops or that fallow was difficult to maintain. Reducing fallow and the disturbances that come with it, such as tillage, may be more beneficial to the epigeic and granivorous arthropod communities (Cromar et al. 1999), though ecosystem services mediated by these communities, such as seed predation, may depreciate (Chapter 3).

Results typically varied by site, indicating that the agroecological class may be an important factor in arthropod community structure, and possibly function, within crop fields. For example, granivore community metrics were idiosyncratic across

study sites. Community metrics of granivores were affected by date at St. John and by crop at Genesee (Table 2.5). The study site in St. John has a mean average temperature (MAT) of 9.1°C and mean average precipitation (MAP) of 1.04mm and Genesee site has a MAT of 16.32°C and MAP of 1.24mm. typically experiences lower annual precipitation and slightly warmer temperatures in the summer (Huggins et al. 2014).

### *Limitations*

While diversifying rotational schemes is the driving force behind this project, and others associated with the Landscapes in Transition project, this study was limited to two years of data collection – one year short of the full rotational treatments. Conclusions cannot be drawn about the rotations, only the differences between crops. Though, some preliminary legacy effect investigation was conducted (Appendix A). General trends indicate that arthropod activity-density is greater in winter wheat plots preceded by winter pea compared to fallow (Figure A1.A, Figure A2.A, Figure A3.A). Diversity and evenness trends were less consistent between previous crops in winter wheat.

The plots for this study were 9.7m x 22.8m, which is a relatively small patch for some of the arthropods sampled (i.e., Lycosidae and Carabidae). The small plot size could introduce sampling bias due to some arthropods being more active.

This study relies entirely on pitfall trapping, which has limitations such as catches being dependent on body mass of individuals, ambient temperature, and the number of traps per sampling area (Saska et al. 2013; Engel et al. 2017). The main limitation of pitfall trapping is that catch rates reflect the interaction of the activity and the density of each taxon, referred to as activity-density (Saska et al. 2013). So, conclusions about community structure based on pitfall trap data must be made cautiously. Despite these limitations, pitfall traps are commonly used to survey epigeal communities (Jansen and Metz 1979; Southwood and Henderson 2000) because they are low cost, easily maintained, and do not interfere with producer activities in the field.

## Chapter 3 | Weed seed predation depends on crop and weed species in diversified wheat production systems

### Abstract

Climate models predict summer drought conditions to worsen in semi-arid regions. Given these predictions, progressive wheat producers are seeking to implement more resilient, diversified systems. Among the challenges to doing so is increased pressure from annual weeds which are more difficult to control when broadleaf crops and cover crops increase in the rotational schemes. The goals of this chapter are to determine the removal rates of three weed pest species in five different crops in the inland Pacific Northwest, USA (iPNW), and to determine the weed seed preferences of a common granivore in agricultural systems. Seed removal rates were assessed using bait stations within each crop for two months during 2019. Exclusion cages were used to separate the effects of vertebrate and invertebrate seed predators. Weed seeds were removed from bait stations with and without exclusion cages at similar rates, implicating invertebrates as important seed predators in this study. Weed seed removal was greater in fallow plots than in plots planted to any crop. Removal rates differed among four sample dates but there was no seasonal trend or interaction between sample date and crop. The effect of crop species and fallow on seed removal rates could have several potential drivers such as microhabitat under the crop canopy or the availability of competing food sources. Weed seed preference trials were conducted in a lab setting with live-captured *Amara* spp. (Coleoptera: Carabidae). Results from the seed preference trials indicate that *Anthemis cotula* may be defended against seed predators. In the first experiment, *A. cotula* was consumed at significantly lower rates than *Bromus tectorum* or *Chenopodium album*, though when physical defenses were removed, *A. cotula* was consumed at higher rates than *B. tectorum*. Diversified wheat cropping systems in the iPNW either reduce or remove fallow from rotation, which could have implications for weed seed banks after adoption and subsequent control of annual weeds that could constrain the system.

## Introduction

Weed seed predation by invertebrates is well-documented in agroecosystems (O'Rourke et al. 2006; Bohan et al. 2011; Kulkarni et al. 2015), indicating it is a key ecosystem service that contributes to weed management. It has been estimated that there is a 25% yield loss for winter wheat in the United States and a 33% yield loss in spring wheat due to weeds (Flessner et al. 2021). Flessner et al. (2021) report that this is a potential loss of \$2.19 billion and \$1.14 billion for winter wheat and spring wheat, respectively. Although vertebrate seed predators have been shown to remove more weed seeds than invertebrates in agricultural systems (Westerman et al. 2003), invertebrate seed predators have the ability to effectively remove seeds from a field (White et al. 2007; Blubaugh and Kaplan 2015). Seed predators in agroecosystems can decrease seed density by 50% (Davis et al. 2011), potentially leading to a reduction in weed populations. High activity-density of Carabidae (Coleoptera) has been found to correlate negatively with seedbank abundance, indicating that seed predators can regulate the weed seedbank and alter weed community dynamics (Bohan et al. 2011).

Producers in the inland Pacific Northwest (iPNW) are increasingly interested in adopting novel more resilient cropping systems (Kaur et al. 2017; McGee et al. 2017; Pan et al. 2017) and are expected to adopt novel, resilient cropping systems to mitigate the negative impacts of projected climate variability (Stöckle et al. 2018). This includes ongoing and projected regional warming, accompanied by shifts in the seasonality of precipitation (Mote and Salathé 2010; Abatzoglou et al. 2014). Current practices in dryland agriculture in many parts of the world, including the drier parts of the iPNW, commonly include a fallow period in the rotation to conserve water in the soil profile (Schillinger and Papendick 2008; Schillinger 2016). Without a shift in current water management strategies, anticipated climate change in the iPNW could lead to an increase in reliance on fallow (Karimi et al. 2017; Kaur et al. 2017), which could have negative consequences for sustainability (Nielsen et al. 2011; Singh et al. 2012; Sharratt et al. 2018). Alternatives are needed to diversify and intensify these traditional dryland systems in an ecologically and economically sound way. In many semi-arid regions, including the iPNW, this includes adding legumes into the rotation



(Angadi et al. 2011; Cutforth et al. 2013; Schillinger 2017, 2020), as well as incorporating cover crops to be utilized for grazing or haying (Andrade et al. 2017; Adhikari and Menalled 2020; Kumar et al. 2020; Baraibar et al. 2021; Garland et al. 2021).

In-field diversification and other alternative management strategies can affect the removal rates of weed seeds and the relative importance of vertebrate and invertebrate granivores in the system (Shelton and Edwards 1983; Menalled et al. 2007; Lami et al. 2020). One of the potential risks of cropping system modifications includes increased vulnerability to weeds (Peairs et al. 2005; Adhikari and Menalled 2018), although this remains largely understudied in dryland cropping systems (Maaz et al. 2017; Schillinger 2017).

Weeds are deleterious and cause significant yield loss in wheat production systems in the United States (Rydrych and Muzik 1968; Flessner et al. 2021). In iPNW cereal-based systems, numerous weeds (PNW Invasive Plant Council 2022) can negatively affect crop growth and production. Broadleaf weeds present a challenge to diversifying annual cropping systems due to the difficulty of selecting appropriate herbicides (Young et al. 2000; Yenish 2007). *Bromus tectorum* L. (downy brome, cheatgrass) is one of the most challenging grass weeds for producers in the iPNW (Schillinger et al. 2015). For example, *B. tectorum* directly competes with wheat and when not managed properly (Figure 3.1A) significantly decreases wheat yield (Rydrych 1974; Lenssen et al. 2013). There is a range of dormancy period with *B. tectorum* seeds (Figure 3.1D) in the soil (Hauvermale and Sanad 2019), though the average is two to three years (Thorne et al. 2007). *Chenopodium album* L. (common lambsquarters) is a globally persistent agricultural weed (Holm et al. 1977) that is particularly difficult to manage in pulse crops due to limited herbicide availability (Figure 3.1C) (Yenish and Eaton 2002). *Chenopodium album* is palatable to both invertebrate seed predators and small mammals (Lundgren and Rosentrater 2007) and is abundant in the seedbank in many regions, including the iPNW (Clements et al. 1996; Teasdale et al. 2004; Burke et al. 2017), and the study site (Figure 3.1F). Seeds of *C. album* (Figure 3.1C) can be viable in the seedbank for up to 39 years (Toole and Brown 1946; Lewis 1973). *Anthemis cotula* L. (Mayweed

chamomile) is a globally invasive broadleaf weed that poses ecological and economic challenges with increasing concerns surrounding herbicide resistance in cereal and pulse crop fields (Lyon et al. 2017; Adhikari et al. 2020). *Anthemis cotula* can be difficult to control and poses a barrier to adopting diversified rotations in wheat-based cropping systems due to its abundance and high phenotypic variability (Adhikari et al. 2021). It is particularly aggressive at the field site used in this study (Figure 3.1B) and comprised the majority of weed seeds found in the seedbank at the study site (Figure C0.2A).

The goal of this study was to compare the removal rates of *B. tectorum*, *C. album*, and *A. cotula* in field and laboratory conditions. Field conditions include five different crops in a long-term experimental strip trial in St. John, Washington, and laboratory bioassays were conducted to determine weed seed preference of *Amara* spp. beetles (Coleoptera: Carabidae). We hypothesized that (H<sub>F1</sub>) seed removal across and within weed species depends on crop; (H<sub>F2</sub>) removal rates are dependent on weed species; (H<sub>F3</sub>) removal rates of seeds differ throughout the growing season; and (H<sub>F4</sub>) removal rates differ between exposure to vertebrate or invertebrate predators. Based on different removal rates of each weed species detected in the field, we compared their removal rates in choice and no-choice laboratory bioassays with representative seed predators. We hypothesized that (H<sub>L1</sub>) feeding on seeds by *Amara* spp. (Coleoptera: Carabidae) depends on species of seed; (H<sub>L2</sub>) seeds of *A. cotula* are chemically defended from predation; and (H<sub>L3</sub>) seeds of *A. cotula*, *B. tectorum*, and *C. album* are physically defended from predation.

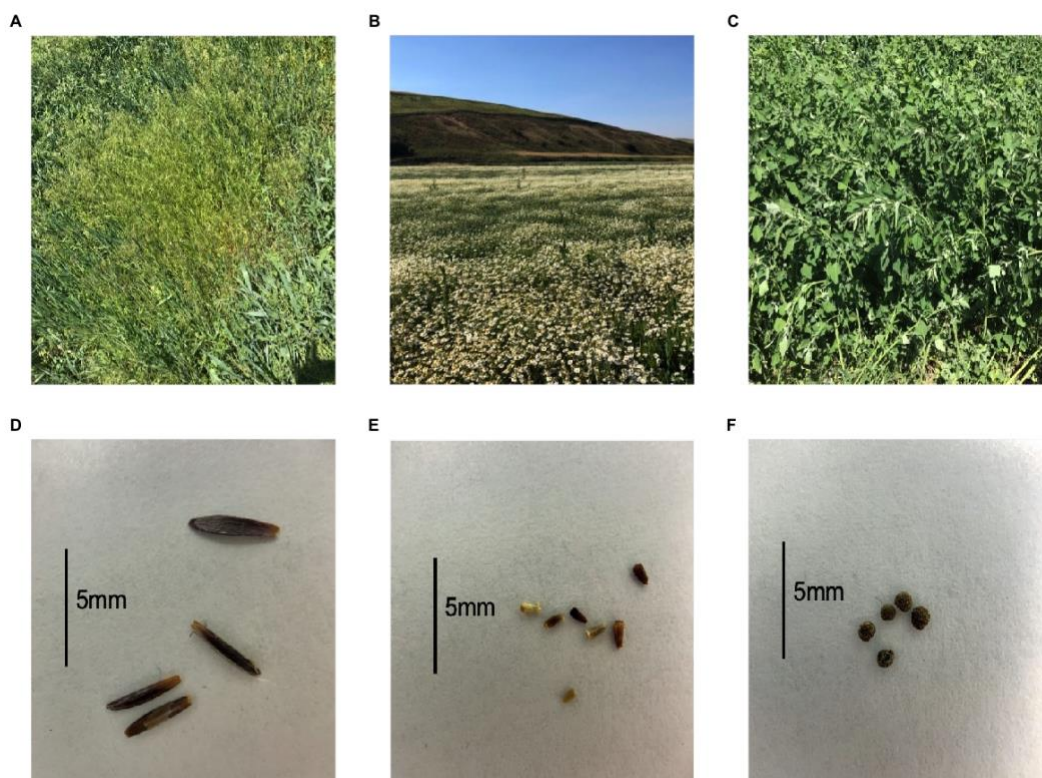


Figure 3.1 Weeds of interest in this chapter, with their seeds. *Bromus tectorum* (A,D), *Anthemis cotula* (B,E), and *Chenopodium album* (C,F).

## Methods

### *Site Description*

Three three-year, wheat-based rotations were established in a replicated field plot study in St. John, Washington as part of a USDA-NIFA-funded project to evaluate alternative and business as usual rotations. The site is within the transitional AEC in the region (Kaur et al. 2017). The soil at this site was predominately mesic Cumulic haploxerolls (Soil Survey Staff 2021a). Climate in the iPNW is generally Mediterranean-like with cold, wet winters and hot, dry summers (Schillinger et al. 2006). Mean annual precipitation is 1.04mm in St. John.

Field plots were planted in a randomized complete block design with five blocks and three rotations. Each three-year rotation was planted into each of its three crops, yielding nine plots per block and a total  $N = 45$  (Figure 3.2). Due to space constraints in the field, block 5 was situated slightly adjacent to the other four blocks, separated by a creek running through the farm. The rotations were a business-as-usual rotation: fallow-winter wheat-spring wheat, and two diversified rotations: winter pea-winter wheat-spring wheat, and cover crop-winter wheat-spring wheat. Weed seed removal rates were assessed during the second year of the trial (May – Aug 2019). Plots (9.7m x 22.8m) were established beginning in fall 2017. The number of plots in each crop treatment differed because wheat was included in all three rotations, but other crops and fallow were not. Each year there were 15 plots each of

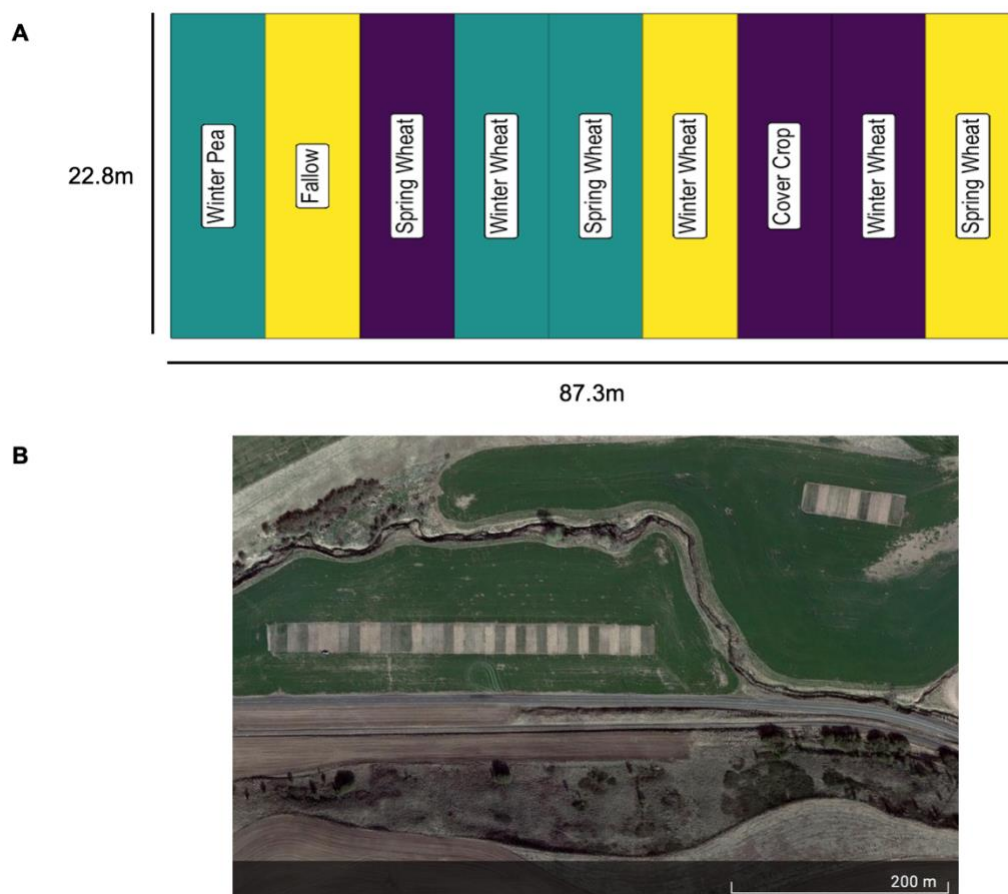


Figure 3.2 Experimental design. Three cropping rotations were established (F-WW-SW (yellow), WP-WW-SW (green), CC-WW-SW (purple)) (A). This block was replicated five times in the field, with one of the blocks situated adjacent to the rest of the trial (B).

winter wheat and spring wheat, and five plots each of winter pea, cover crop, and fallow.

Winter wheat and winter pea crops were planted on 25 Sep. 2018. Spring wheat and cover crop plots were planted on 25 April 2019. Crop varieties are Jasper winter wheat, WB9518 spring wheat, and Windham winter pea. The cover crop mix included barley (22.4 kg/ha), oat (22.4 kg/ha), pea (44.8 kg/ha), sunflower (1.1 kg/ha), and turnip (1.4 kg/ha). Fallow plots were treated with glyphosate and 2,4-D on 19 April, 11 June, and 19 July 2018, at 3.2 liters/hectare. Winter wheat herbicide treatments were Anthem Flex (FMC Corp.) at .32 l/ha on 28 Sep 2018, Brox-2EC (Albaugh Inc.) at 2.3 l/ha on 1 April 2019, and Huskie (Bayer CropScience LP) at 1.1 l/ha, MCPA-Amine (Albaugh Inc.) at 1.2 l/ha, and Affinity BS (FMC Corp.) at .7 ml/ha on 21 June 2019. Spring wheat herbicide treatments include glyphosate and 2,4-D at 2.3 l/ha on 19 April 2019 and Bronate (Bayer CropScience LP) at 1.8 l/ha and Axial Star (Syngenta) at 1.2 l/ha on 11 June 2019. Winter pea herbicide treatments include Anthem Flex (FMC Corp.) at .32 l/ha, Diurex at 3.7 l/ha, and Spartan (FMC Corp.) at .6 l/ha on 28 Sep 2018, Tricor (United Phosphorous Inc.) at 0.2 ml/ha on 1 April 2019, Assure II (AMVAC Chemical Corp.) at 0.6 l/ha on 21 June 2019, and Gramoxone SL (Syngenta) at 2.3 l/ha on 22 July and 29 July 2019. Winter pea insecticide treatments include Mustang Max (FMC Corps.) at .3 l/ha and Digion 400 (Wilbur-Ellis Company Inc.) at 0.4 l/ha on 11 June and 1 July 2019. Harvest dates were 12 July, 2 Aug., 20 Aug., and 27 Aug. for cover crop, winter pea, winter wheat, and spring wheat, respectively.

#### *Sentinel Stations*

Removal rates of the seed of the three weed species, *B. tectorum*, *C. album*, and *A. cotula* were measured using sentinel seed stations. Sentinel seed stations (Figure 3.3A) (Honek et al. 2003) were constructed of Petri dish bottoms (100mm x 15mm, polystyrene, Fisher Scientific, Inc.) that were filled with sulfur-free plasticine clay (EnvironMolds, LLC). *Anthemis cotula* seeds were collected from ten farms within 95 km of the trial location in the summer of 2018. *Bromus tectorum* seeds were

collected from *B. tectorum*  
common garden

experimental plots within  
95 km of the study site.

*Chenopodium album*

seeds were collected from  
one chickpea field within

95 km of the study site.

Seeds from *C. album* and

*A. cotula* were one year

old, and seeds from *B.*

*tectorum* were c. two years old. All seeds were stored in paper envelopes at ambient lab temperature until use in this study. Twenty seeds of each of the three weed species were pressed into the clay of each station so that approximately half of each seed was exposed to potential predators. Seeds from each species occupied approximately one-third of the surface area of each seed station. Seed locations among species within the clay were randomized. Seed stations were reused for each trial. Seed stations ( $N = 90$ ) were placed flush with the soil to not impede the movement of seed feeders and to minimize seed loss due to wind. Four trials were conducted during the 2019 season. All seed stations were exposed in the field for one week and the remaining seeds were counted immediately following removal from the field. Station placement and collection occurred between the hours of 10:00 am and 12:00 pm for four one-week periods during the season: 28 June - 5 July, 19 July - 26 July, 1 Aug. - 8 Aug., and 16 Aug. - 23 Aug. 2019. Crops were harvested throughout the duration of this field experiment. All crops had emerged by the first trial date. Cover crop plots were harvested before the second trial date; winter pea plots were harvested before the third trial date; and winter wheat plots were harvested before the fourth trial date. Before each new trial, seeds that remained on stations from previous trials were removed, the stations were washed, and the clay was heated and resmoothed. Stations were retrieved from the field and seed removal was assessed in the laboratory. Partially consumed seeds were rarely observed but

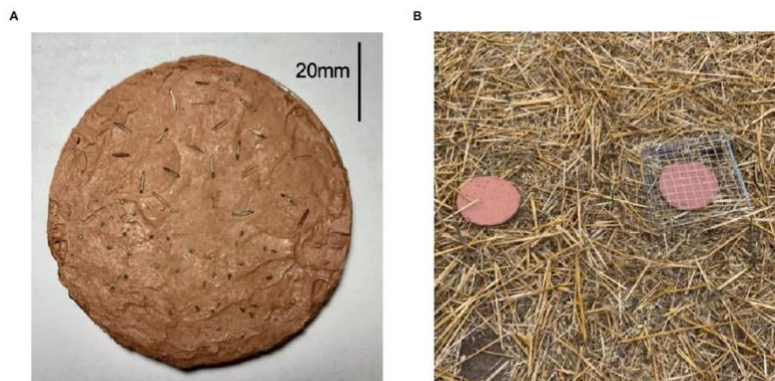


Figure 3.3 Seed stations used to determine seed predation rates. Seed trays (A) had 20 seeds of each weed species. Stations had open and closed treatments to differentiate vertebrate and invertebrate seed predation (B).

were counted as fully removed from the station because they would not mature to a viable plant.

To differentiate seed removal due to invertebrates and vertebrates, exclusion cages (13cm x 5cm boxes made from hardware cloth with 12mm x 12mm mesh size) (Figure 3.3B) were placed over half of the seed stations in each plot. Potential vertebrate seed predators in this system include birds and small mammals (Cardina et al. 1996; Cromar et al. 1999). Invertebrate seed predators present in these plots, based on pitfall samples taken throughout the season included species of Carabidae, Formicidae, and Gryllidae (Chapter 2). The most abundant granivorous Carabidae genera captured were *Harpalus*, *Amara*, and *Poecilus*.

#### *Laboratory Bioassays*

Bioassays were conducted in the fall and winter of 2020-2021. Seeds of *B. tectorum*, *C. album*, and *A. cotula* for the bioassays had the same sources described for the field experiment above. Adult carabid beetles (*Amara* spp.) were live caught in dry pitfall traps at the University of Idaho's Soil Stewards Farm (46.736729, -117.022338) between October and November 2020. *Amara* spp. were selected due to their high trapping rates at this collection site and in the St. John field site compared to other granivorous genera. Beetles were placed individually into "rest trays" consisting of 100mm Petri dishes with a 4cm<sup>2</sup> moistened paper towel to provide water and shelter between trials (an average of seven days). No food was provided to beetles while they were held in rest trays.

Experiment 1: Three-way choice trial with *A. cotula*, *C. album*, and *B. tectorum*. Trial trays were made by lining the bottom of 100mm Petri dishes with moistened filter paper and placing five seeds of each species on the filter paper. There were three treatment groups in each dish, one for each weed species. Forty beetles were placed individually in trial trays and left for 12 hours after which they were moved back to their rest trays. Each beetle underwent 17 trials from 13 Nov. 2020 to 8 Dec. 2020. The number of seeds partially and wholly consumed was recorded at the completion of each trial.

Experiment 2: Basis of avoidance of *A. cotula* seed by seed predators. Based on the results of the field trial and Experiment 1, seed of *A. cotula* was removed less than the other two species. To determine the basis of this discrimination, seeds of *A. cotula* were treated to remove potential defenses. The species is known for the strong scent of its flowers, which are unpleasant for most humans (Adhikari et al. 2020) suggesting that the seeds may be chemically defended. *Anthemis cotula* seed was treated with two chemical rinses, *n*-hexane and methanol to remove compounds of different polarity. A third treatment to disrupt physical defenses by breaking open the pericarp was performed. For each of the rinses, 20 seeds were put into a 50 mL beaker with hexanes (99.9%) or methanol (99.9%) to completely cover them (c. 25-30 mL). The suspended seeds were swirled by hand for 30 seconds and poured onto filter paper to completely dry. Disrupting the physical barrier was done by holding a seed with forceps, grasping the funiculus end of the seed, and using a razor blade to cut through the pericarp or seed coat (depending on weed species) until roughly one-third of the seed was visible within. Fifteen surviving individual *Amara* from Experiment 1 were randomly placed into four test groups of three or four individuals. Each test group was then presented with *A. cotula* seeds from one of the four treatments in a no-choice test: hexane rinse, methanol rinse, pericarp breached, or control. Trial trays for Experiment 2 were constructed as described above with 20 seeds of *A. cotula* from each treatment placed on the filter paper. Beetles were placed in trial trays for 12 hours, for four trial periods. The number of seeds partially and wholly consumed was recorded at the completion of each trial.

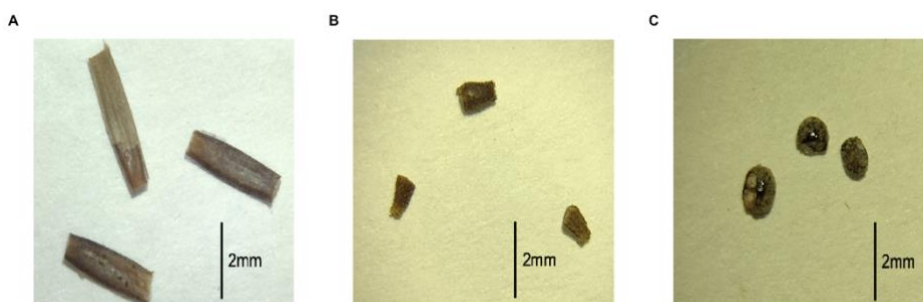


Figure 3.4 Example of 'cut' pericarp or seed coat for *B. tectorum* (A), *A. cotula* (B), and *C. album* (C). Each photo shows one seed that has had physical barriers breached, along with two intact seeds.



Experiment 3: Determine if cutting the pericarp or seedcoat affects relative predation on the three weed species by *Amara* spp. The pericarp from *A. cotula* and *C. album*, and the seedcoat from *B. tectorum* were cut using the procedure described above to expose approximately one-third of the seed (Figure 3.4). Fifteen *Amara* spp. underwent a three-way no-choice trial with five seeds from each species. Exposure time was 12 hours, for five trial periods. The number of seeds partially and wholly consumed was recorded at the completion of each of the five trials.

#### *Statistical Analysis*

For the field seed removal experiment, the response variable ‘number of seeds removed per station/20’ was arcsin(square-root(x))-transformed for analysis to satisfy assumptions of normality and homogeneity of error variances. All statistical analyses were done in RStudio open-source software R version 4.0.2 (R Core Team 2020). Tests used the `lm` function and when effects were significant, contrasts were conducted using the ‘emmeans’ package.

A 4-way Analysis of Variance (ANOVA) was performed to determine the impacts of ‘crop’ (five levels), ‘cage’ (two levels), ‘weed species’ (three levels), and ‘date’ (four levels) on seed removal (Table 3.1). A  $p$ -value  $\leq 0.05$  was considered significant. The following hypotheses were tested using contrasts: ( $H_{F1}$ ) seeds of the three species are not removed at different rates; ( $H_{F2}$ ) seed removal rates across and within species do not depend on crop; ( $H_{F3}$ ) seed removal rates by invertebrate predators do not differ from removal rates by vertebrate predators; and ( $H_{F4}$ ) seeds are not removed at different rates throughout the growing season.

For the laboratory bioassays, the response variable ‘seeds consumed per trial’ was arcsin(square-root(x))-transformed to satisfy assumptions of normality and homogeneity of error variances. Figures show untransformed data. A generalized linear model was used to fit the data to test the following hypotheses: ( $H_{L1}$ ) *Amara* spp. beetles have no preference between *A. cotula*, *B. tectorum*, or *C. album* seeds; ( $H_{L2}$ ) There are no differences in seed removal rates among species after seeds are treated with solvents to remove putative chemical defenses; and ( $H_{L3}$ ) There are no

differences in seed removal rates among species after seed coats are breached to remove putative physical defenses.

Partially and wholly consumed seeds were counted as consumed for this analysis. A  $p$ -value  $\leq 0.05$  was considered significant. Trials in which no seeds in any treatment were consumed (non-events) were removed from the dataset prior to analysis. Ten out of 42, 135 out of 217, 90 out of 437 non-events occurred in experiments 1, 2, and 3 respectively. Weed species was the only explanatory variable used in models for experiments 1 and 3, while seed defense removal treatment was the explanatory variable for experiment 2. Significance of treatment was assessed using the `anova` function from the 'car' package. Data visualizations were made with the 'ggplot2' package in R.

Table 3.1 ANOVA table for weed seed predation field trials.

<b>Factor</b>	<b>F</b>	<b>df</b>	<b>P</b>
Crop	8.19	4	< 0.001***
Species	23.1	2	< 0.001***
Cage	1.41	1	0.2356
Date	29.6	3	< 0.001***
Crop x Species	0.46	8	0.8836
Crop x Date	1.03	12	0.4097
Crop x Cage	1.48	4	0.2057
Species x Date	36.4	6	< 0.001***
Species x Cage	0.49	2	0.6124
Cage x Date	2.93	3	0.0325*
Crop x Species x Date	0.53	24	0.9672
Crop x Species x Cage	0.77	8	0.6272
Crop x Cage x Date	1.44	12	0.1420
Species x Cage x Date	0.75	6	0.6067
Crop x Species x Cage x Date	0.37	24	0.9974

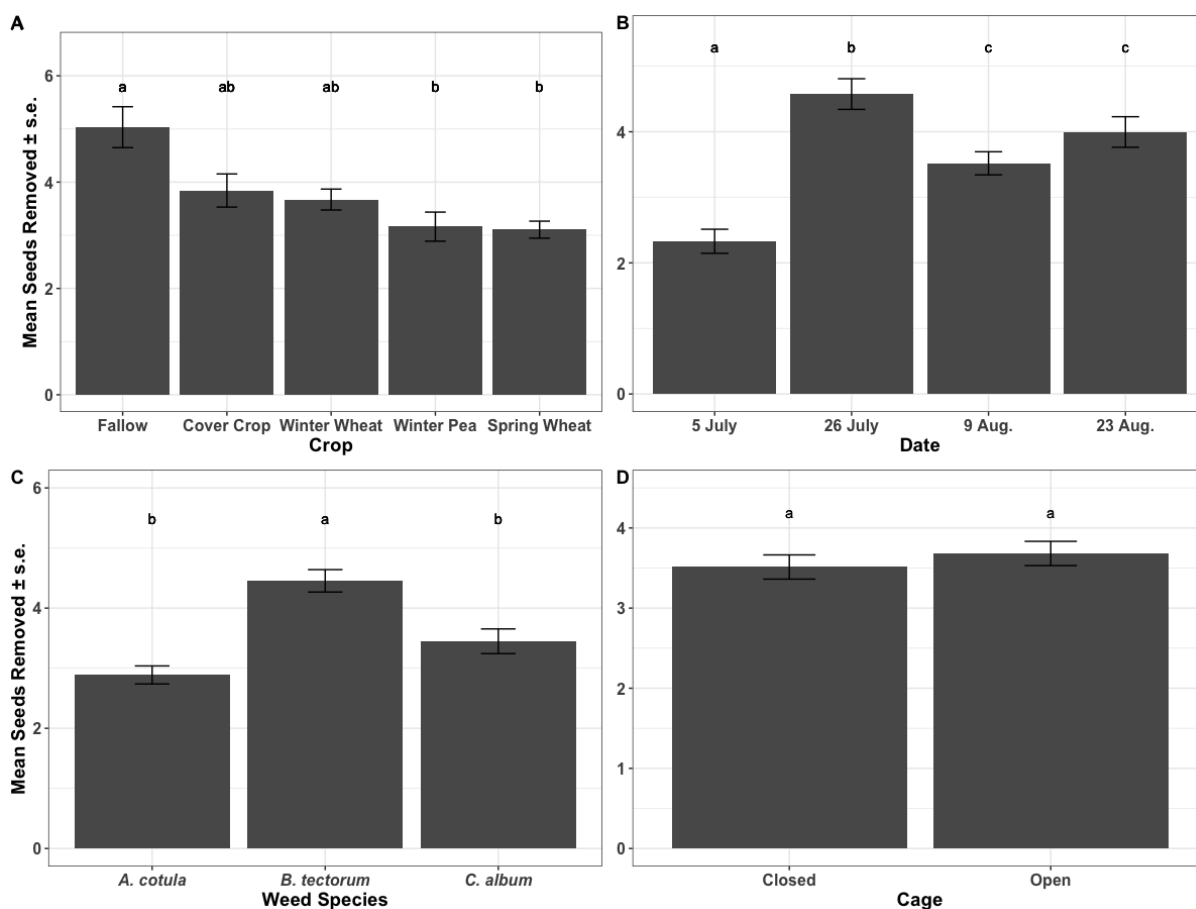


Figure 3.5 Effect of crop (A), date (B), weed species (C), and cage treatment (D) on weed seed predation from field trials. Different letters denote significant difference in means.

## Results

### Field Trials

The effects of weed species, crop, and trial date on weed seed removal rates were significant, as was the interaction between weed species and trial date (Table 3.1). Total seed removal differed among crops ( $p < 0.001$ ), with fallow plots having the greatest total seed removal compared to other crops ( $p < 0.001$ ) (Figure 3.5A). Total seed removal differed among weed species ( $p < 0.001$ ). Removal of *B. tectorum* seeds was greater than *C. album* or *A. cotula* seeds ( $p < 0.01$ ) (Figure 3.5C), but this was driven primarily by the much greater rate of removal of *B. tectorum* in the final sample date (Figure 3.6A) ( $p < 0.001$ ), accounting in part for the interaction between seed species and date ( $p < 0.001$ ). The greater removal of *A.*

*cotula* on the 26 July also contributed to the interaction (Figure 3.6A). Total seed removal was greater in later trials compared to earlier trials ( $p < 0.001$ ) (Figure 3.5B). Seed removal rates were not significantly different between caged and uncaged seed trays (Figure 3.5D).

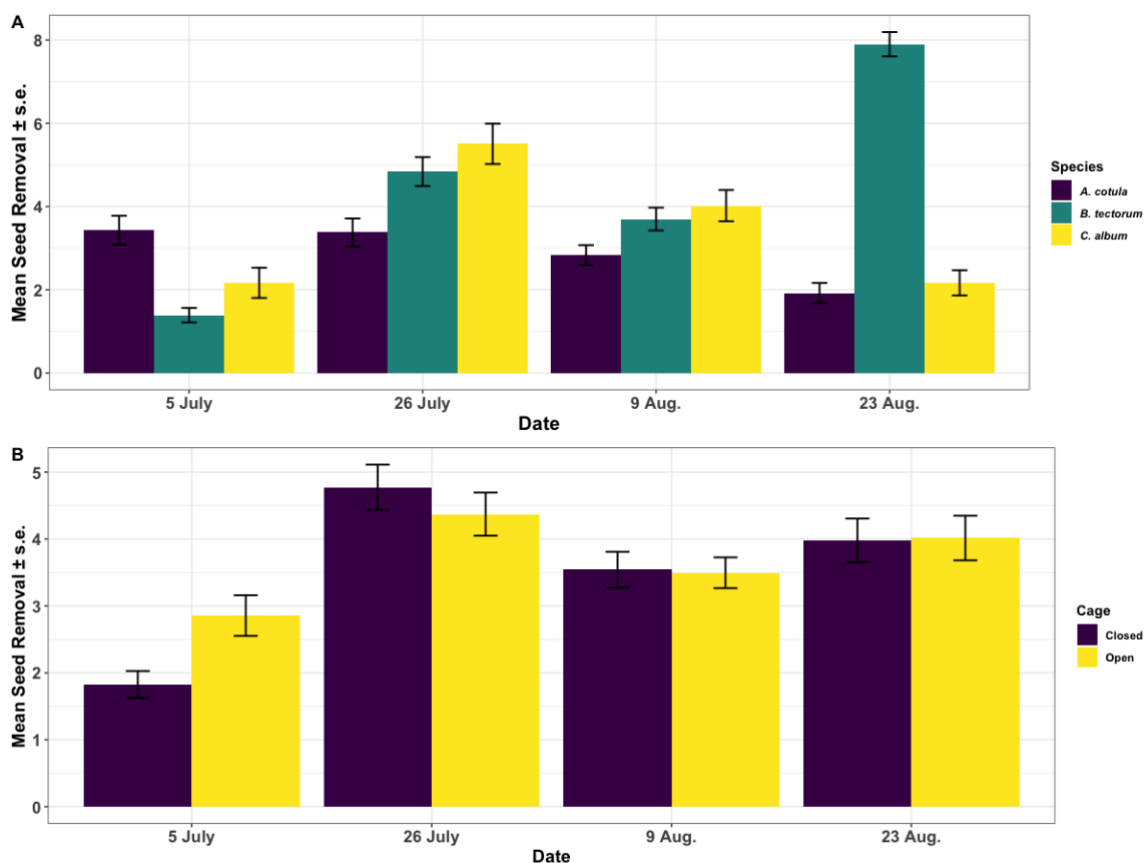


Figure 3.6 The interactions between weed species and date (A) and cage type and date (B) also had significant effects on weed seed removal.

### Laboratory Bioassays

Total seed consumption by *Amara* spp. across trials differed among weed species with a total of 90, 67, and 14 seeds consumed of *B. tectorum*, *C. album*, and *A. cotula* respectively ( $p < 0.01$ ). *Anthemis cotula* seeds were consumed at a significantly lower rate than *B. tectorum* or *C. album* ( $p < 0.01$ ) (Figure 3.7A). Consumption of *A. cotula* seeds with treatments to remove possible defenses differed; those that had the pericarp physically broken open were consumed in greater numbers than seeds that were rinsed with either methanol or hexane and

untreated controls ( $p < 0.001$ ) (Figure 3.7B). When all three weed species with pericarp broken were tested in a three-way choice test, consumption differed among

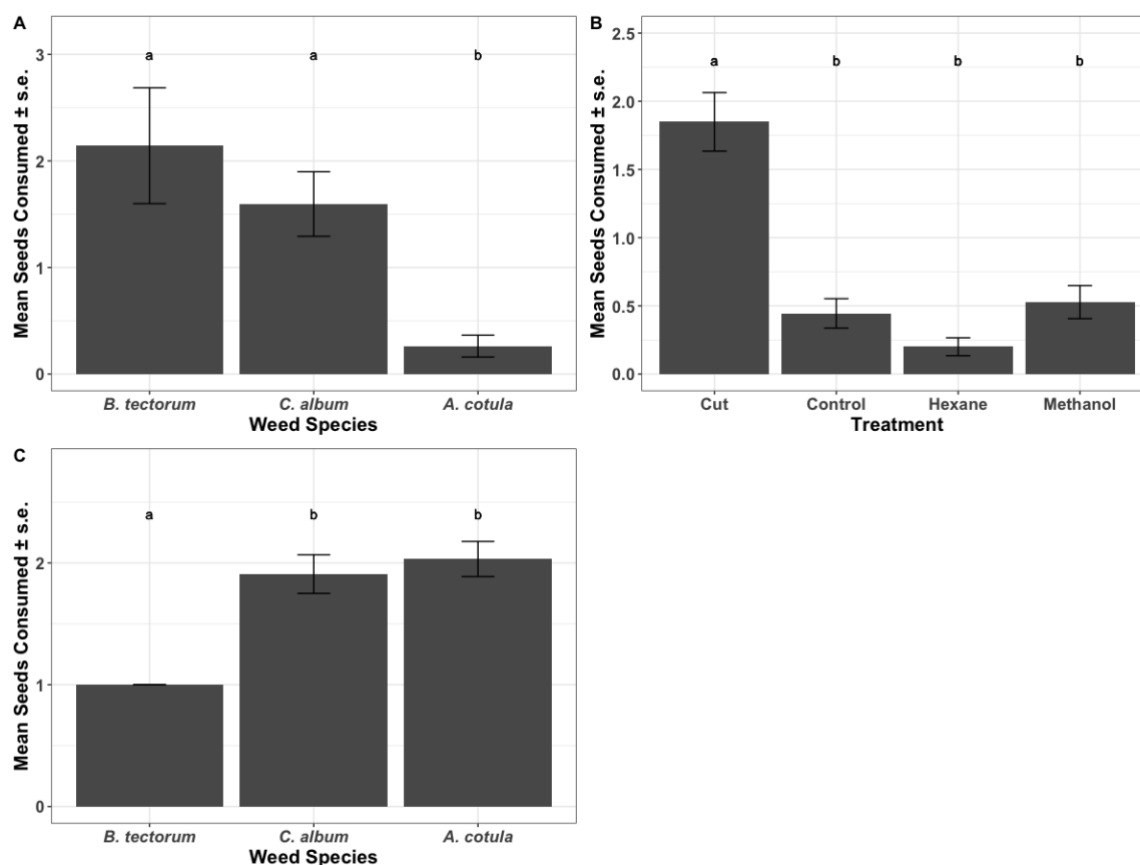


Figure 3.7 Weed seed consumption from experiments one (A), two (B), and three (C) of the seed preference bioassays.

them ( $p < 0.01$ ); consumption of *B. tectorum* was significantly less than consumption of *C. album* or *A. cotula* ( $p < 0.01$ ) (Figure 3.7C).

## Discussion

Seed removal rates of three important weed species were assessed throughout the season from a replicated field trial in the iPNW. We hypothesized that ( $H_{F1}$ ) seed removal across and within weed species depends on crop; ( $H_{F2}$ ) removal rates are dependent on weed species; ( $H_{F3}$ ) removal rates of seeds differ throughout the growing season; and ( $H_{F4}$ ) removal rates differ between exposure to invertebrate or both vertebrate and invertebrate predators.

Seed removal differed among crops, with the greatest consumption occurring for seed placed within fallow treatments. Most studies report that weed seed predation generally increases with vegetation cover. For example, weed seed predation was measured in conventionally managed soybean, with and without red clover cover, and compared to weed seed predation in fallow plots by Blubaugh et al. (2016), who found that clover cover increased the likelihood of carabid beetles feeding on *C. album* seeds by 75%, compared to bare ground. Meiss et al. (2010) compared predation rates of *Viola arvensis* (field pansy), *Alopecurus myosuroides* (black grass), and *Sinapis arvensis* (wild mustard) in alfalfa, cocksfoot, and bare ground and found that weed seed predation was significantly greater in uncut alfalfa fields compared to bare ground. Unlike these prior studies, weed seed removal was greatest from fallow, regardless of weed species. The fallow treatment in this study was unseeded and herbicide applications of glyphosate and 2,4-D (3.2 liters/hectare) took place on 3 April and 15 June to control weeds. Greater seed removal in fallow could be due to microclimate on bare ground favoring mobility and foraging by seed predators. Some studies have measured weed seed predation in fallow fields (Williams et al. 2009; Baraibar et al. 2017) but information is still lacking. Williams et al. (2009) reported 69-91% removal of *Abutilon theophrasti* (velvetleaf) and *Setaria faberi* (bristlegrass) in maize-corn rotations, though there was considerable variation in seed predation between years. Baraibar et al. (2017) examined *Lolium rigidum* (rigid ryegrass) and *Galium aparine* (catchweed bedstraw) seed predation in summer fallow fields with conventional or no-tillage and reported 62% and 49% predation, respectively. Results from Baraibar et al. (2017) suggest that leaving fields untilled may reduce inputs to the weed seed bank.

Weed seed removal rates also differed among weed species, with *A. cotula* removed less than the other species on three of four sample dates and based on an overall mean across all dates, except for the first trial period. Seeds of different species are often taken at different rates by carabids (Honek et al. 2007; White et al. 2007; Kulkarni et al. 2016) but none of these studies evaluated *A. cotula*. Differential seed removal rates can be attributed to size of the seed, size of the seed consumer, hardness of seed coat or pericarp, and nutritional content of the seed (Kulkarni et al.

2015; Sarabi 2019). *Bromus tectorum* removal rates were much greater than other species in the final trial period, which could be due to granivore community shifts within the season, the availability of alternative prey sources decreased later in the season, or the stage of crop altered conditions and the relative vulnerability of seeds in the field. There was not a change in the effect of vertebrate exclusion cages that could indicate more rodent or bird activity later in the season.

Trial date had a significant effect on seed removal rates. Overall seed removal was lowest in the first trial period, initiated on 5 July, with around 2.5 seeds/seed tray removed. There was an increase in seed removal on the second trial date, in which an average of 4.5 seeds/seed tray were removed. Seed removal was relatively consistent for the third and fourth trial dates, with 3.5 and 4 seeds/seed tray removed on 9 Aug. and 23 Aug. 2019 respectively. Lower removal rates in the first trial period could be due to all four crops being present at the study site. Throughout the season, crops were harvested at different dates, which could have affected conditions on the ground and seed removal rates. A spike in seed removal rate in cover crops occurred after their harvest on 12 July, but a similar effect was not observed after harvests of the other crops.

There was an interaction between weed species and trial date. *Anthemis cotula* removal was consistent across dates. Seeds of other species were removed at variable rates throughout the trial. *Chenopodium album* seed removal was highest during the 19-26 July 2019 trial period, and *B. tectorum* seed removal was highest during the 16-23 Aug. 2019 trial period. Shifts in relative removal rates of weed species throughout the season could reflect shifts in the seed predator community, changes in preferences of individual species within that community over the season, or both. The community of epigeic arthropods shifted throughout the season based on pitfall samples (Chapter 2).

Pitfall trapping captured more carabids than other granivorous taxa from the fallow plots throughout the season, though activity-density of granivorous taxa were comparable between fallow and spring wheat plots. Carabids are often considered important in agroecosystems, as they are generally omnivorous, feeding on small invertebrates and opportunistically feeding on seeds (Kulkarni et al. 2015; Blubaugh

et al. 2016). Numerous factors contribute to the efficacy of granivores in agroecosystems. Crops that have not reached senescence may be host to alternative prey sources to granivorous arthropods. Carabid beetles are facultative seed predators and also consume arthropod prey. Based on pitfall data, more prey taxa (aphids, thrips) were present under crops and cover crops than in fallow. The availability of these animal prey may have reduced seed consumption by predators in our study.

The basis for the differences in consumption by a key seed predator of different weed seed species was examined with laboratory bioassays. We hypothesized that (H<sub>L1</sub>) feeding on seeds by *Amara* spp. depends on the species of seed; (H<sub>L2</sub>) seeds of *A. cotula* are chemically defended from predation; and (H<sub>L3</sub>) seeds of *A. cotula*, *B. tectorum*, and *C. album* are physically defended from predation. The focal predators for these bioassays, *Amara* spp., were chosen to be representative of later season dates based on their prevalence in pitfall samples. *Amara* spp. are effective seed predators (White et al. 2007; Kulkarni et al. 2016), though their small size constrains the size and number of seeds they can consume per capita (Honek et al. 2003).

To determine the basis of lower predation rates of *A. cotula* by *Amara* spp., two laboratory bioassays were conducted focused on chemical and physical defenses. Chemical and physical characteristics differ among the three species tested. *Anthemis cotula* is known as stinking chamomile because of its offensive floral odor (Adhikari et al. 2020), and some of those odorants may be present in the seed and function as deterrents to seed predators. The small size and hardness of the seed may also contribute to low rates of *A. cotula* removal in the field. Rinsing *A. cotula* with a nonpolar solvent (hexane) or methanol to remove or disrupt chemical defenses had no effect on the consumption of these seeds in bioassay. Disrupting physical defense by cutting the pericarp, in contrast, greatly increased *A. cotula* seed consumption in bioassay. When the pericarp of all three species was cut to disrupt the physical defenses, *A. cotula* seed removal was similar to *C. album* and both greater than *B. tectorum*. The preference by *Amara* spp. for *A. cotula* seed when physical barriers are removed by cutting the pericarp could be attributed to gustatory



cues present in the seed, the nutritional quality of the seed, or both. To my knowledge, this is the first time chemical defenses of *A. cotula* have been tested in a seed predation experiment.

Low rates of *A. cotula* removal from the field trials are consistent with near rejection of *A. cotula* seeds in laboratory experiment 1, though it is possible that other seed predators are less discriminating in the field. Results from laboratory experiment 3 indicate that the seeds tested here could have physical barriers that limit granivore consumption in the field, contributing to the low consumption rates observed in the field study.

### *Implications*

Seed removal is greater in fallow compared to other crops, which could mean that the fallow period is an important phase of dryland production systems that facilitate seed predator movement in the field. This could mean complications for weed management as growers make moves towards diversified wheat cropping systems in the iPNW. In iPNW cereal systems, the widely implemented practice of fallowing seems to improve weed seed biological control

*Anthemis cotula* is a successful invasive annual weed (Adhikari et al. 2020) and the results here suggest that low rates of post-dispersal seed predation may contribute to the plant's invasive nature. The physical defenses of *A. cotula* seed against seed predation could contribute to the invasiveness of *A. cotula* (Adhikari et al. 2020). *Chenopodium album* seeds can persist in the seed bank for at least 20 years (Davis et al. 2008). Individual *A. cotula* plants can produce anywhere from 5,000 to 27,000 seeds that have the potential to be viable for 25 years in the soil (Darlington 1931; Rashid et al. 2007) but the persistence of *A. cotula* in the seed bank is unknown (Adhikari et al. 2020). Most (96-99%) of *B. tectorum* seeds germinate within the first two years of being added to the seed bank (Burnside et al. 1996; D. C. Smith et al. 2008). Blubaugh et al. (2016) found a 38% reduction in weed emergence that could be attributed to seed predators. A recent study found a reduction of the seedbank by carabids just prior to crop harvest, but found that

granivore activity-density had no significant effect on seedbank reduction (Carbonne et al. 2020).

### *Limitations*

Limitations of the study are methodological: there was a single location and season for the field study and there were three seed predator species as the focus for the laboratory bioassays. *Amara* spp. were caught in pitfall traps in crop plots in St. John, Washington, but a different population was used in the bioassays; two of the species overlapped, but one was unique to the Soil Stewards Farm. The seed predators responsible for seed removal in field trials were not determined here. Two pitfall traps placed within the plots were used to determine the activity-density of potential granivores (Chapter 2), but direct observation was not made of what species were removing seeds from the stations. *Anthemis cotula* seeds used in the bioassay were collected from flower heads and dried. In the field, seeds will be hydrated, and some may be several years old (Adhikari et al. 2020). Seeds of these species may differ in how readily they are taken after they have been in the soil environment.

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## Appendix A – Legacy Effects

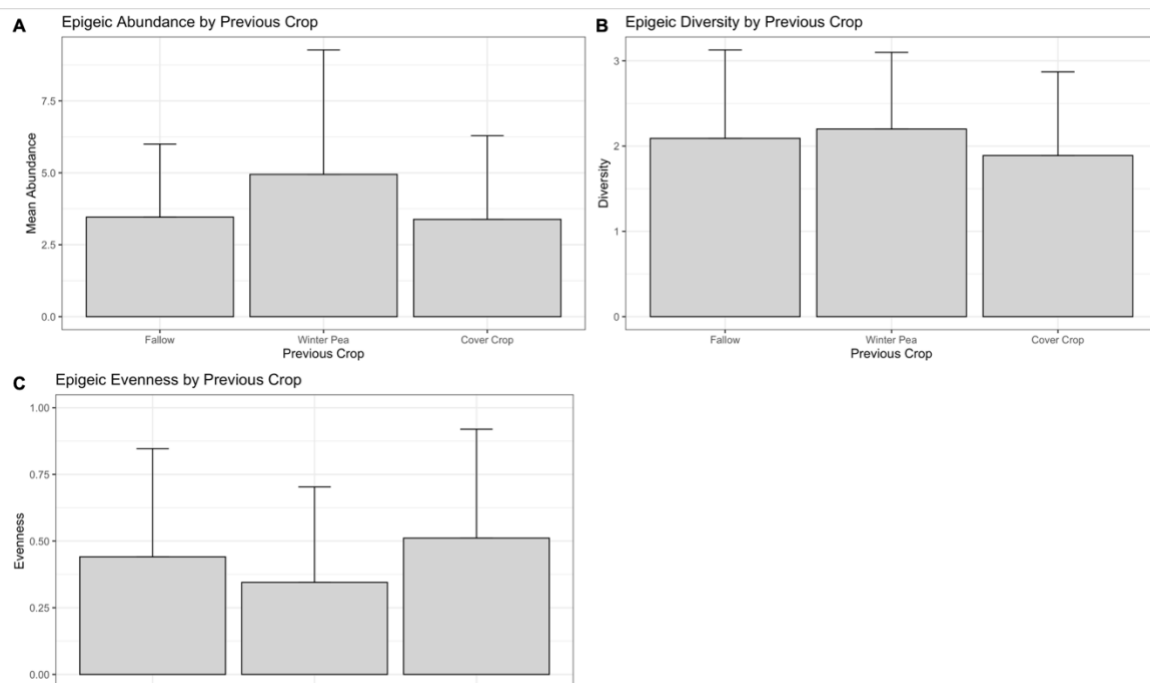


Figure A0.1 Abundance (A), diversity (B), and evenness (C) of epigeic community in winter wheat plots, based on the previous year's crop.

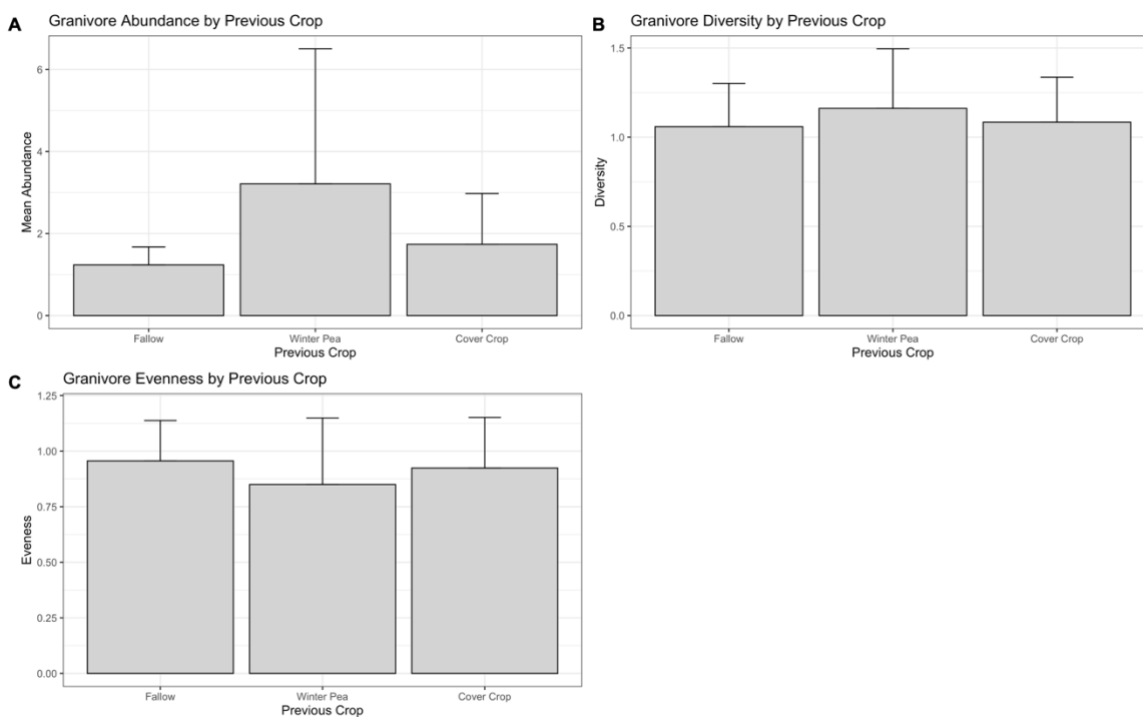


Figure A0.2 Abundance (A), diversity (B), and evenness (C) of granivorous community in winter wheat plots, based on the previous year's crop.

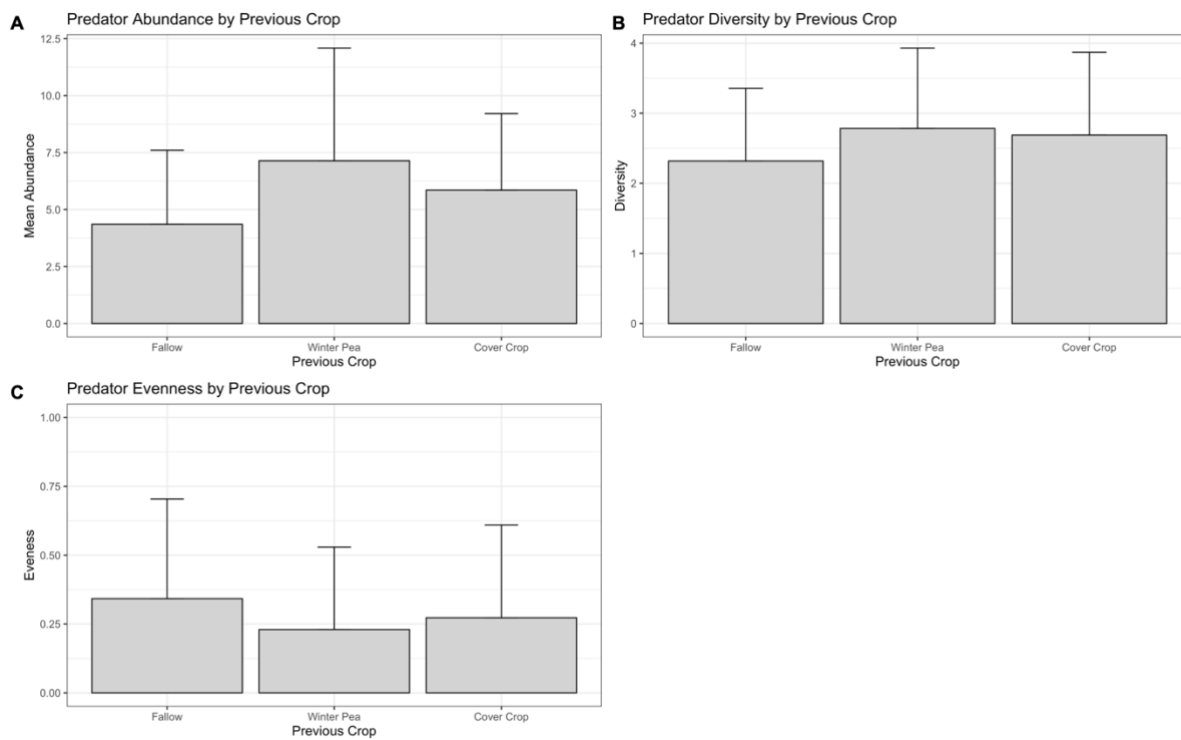


Figure A0.3. Abundance (A), diversity (B), and evenness (C) of the predator community in winter wheat plots, based on the previous year's crop.



## Appendix B – Whole Arthropod Community Analysis

Table B1. ANOVA results from whole community analysis.

	St. John						Genesee					
	2018			2019			2018			2019		
	<i>F</i>	<i>df</i>	<i>P</i>	<i>F</i>	<i>df</i>	<i>P</i>	<i>F</i>	<i>df</i>	<i>P</i>	<i>F</i>	<i>df</i>	<i>P</i>
<b>Activity-density</b>												
Crop	3.159	4, 38	<b>0.025</b>	8.682	4, 36	<b>0.0001</b>	6.526	4, 36	<b>0.0005</b>	7.586	3, 32	<b>&lt;0.0001</b>
Date	258.854	1, 360	<b>&lt;0.0001</b>	81.675	1, 262	<b>&lt;0.0001</b>	87.764	1, 106	<b>&lt;0.0001</b>	38.471	1, 115	<b>&lt;0.0001</b>
Crop*Date	4.677	4, 360	<b>0.001</b>	0.274	4, 262	0.894	2.848	4, 106	<b>0.028</b>	15.629	3, 115	<b>&lt;0.0001</b>
<b>Simpson's Diversity</b>												
Crop	2.652	4, 38	<b>0.048</b>	2.716	4, 36	<b>0.044</b>	5.551	4, 36	<b>0.001</b>	4.095	3, 32	<b>0.014</b>
Date	6.307	1, 360	<b>0.012</b>	64.089	1, 262	<b>&lt;0.0001</b>	0.043	1, 106	0.834	3.919	1, 115	<b>0.050</b>
Crop*Date	0.0598	4, 360	0.664	3.939	4, 262	<b>0.004</b>	3.505	4, 106	<b>0.010</b>	2.21	3, 115	0.091
<b>Simpson's Evenness</b>												
Crop	4.541	4, 38	<b>0.004</b>	1.817	4, 36	0.146	4.402	4, 36	<b>0.005</b>	3.111	3, 32	<b>0.039</b>
Date	66.224	1, 360	<b>&lt;0.0001</b>	74.936	1, 262	<b>&lt;0.0001</b>	6.272	1, 106	<b>0.014</b>	5.092	1, 115	<b>0.026</b>
Crop*Date	0.719	4, 360	0.579	1.221	4, 262	0.303	1.538	4, 106	0.197	4.667	3, 115	<b>0.004</b>

Table B2. Means table for whole trappable community.

Site	Year	Crop	Activity-Density	Diversity	Evenness
St. John	2018	Cover Crop	19.35±2.71	3.67±0.25	0.12±0.03
		Fallow	18.83±2.97	3.98±0.31	0.11±0.03
		Spring Wheat	24.08±2.85	3.15±0.13	0.19±0.02
		Winter Pea	16.37±5.09	2.79±0.20	0.19±0.04
		Winter Wheat	9.77±1.02	2.75±0.11	0.27±0.03
	2019	Cover Crop	25.00±3.73	5.26±0.43	0.09±0.04
		Fallow	16.92±1.58	3.96±0.29	0.06±0.01
		Spring Wheat	15.98±1.17	5.08±0.19	0.05±0.01
		Winter Pea	35.78±4.11	3.63±0.33	0.07±0.02
		Winter Wheat	11.49±0.79	4.10±0.19	0.11±0.02
Genesee	2018	Chickpea	13.57±1.98	2.88±0.27	0.23±0.04
		Cover Crop	22.53±8.40	2.99±0.32	0.18±0.07
		Spring Wheat	33.20±5.39	2.95±0.23	0.11±0.02
		Winter Pea	62.81±28.07	2.85±0.33	0.08±0.01
		Winter Wheat	8.50±1.61	2.29±0.16	0.35±0.05
	2019	Chickpea	18.23±2.19	3.25±0.20	0.13±0.03
		Cover Crop			
		Spring Wheat	39.89±7.86	3.53±0.23	0.10±0.03
		Winter Pea	85.10±9.12	1.73±0.10	0.09±0.02
		Winter Wheat	17.78±1.73	3.79±0.22	0.13±0.03

## Appendix C – Seed Bank Composition

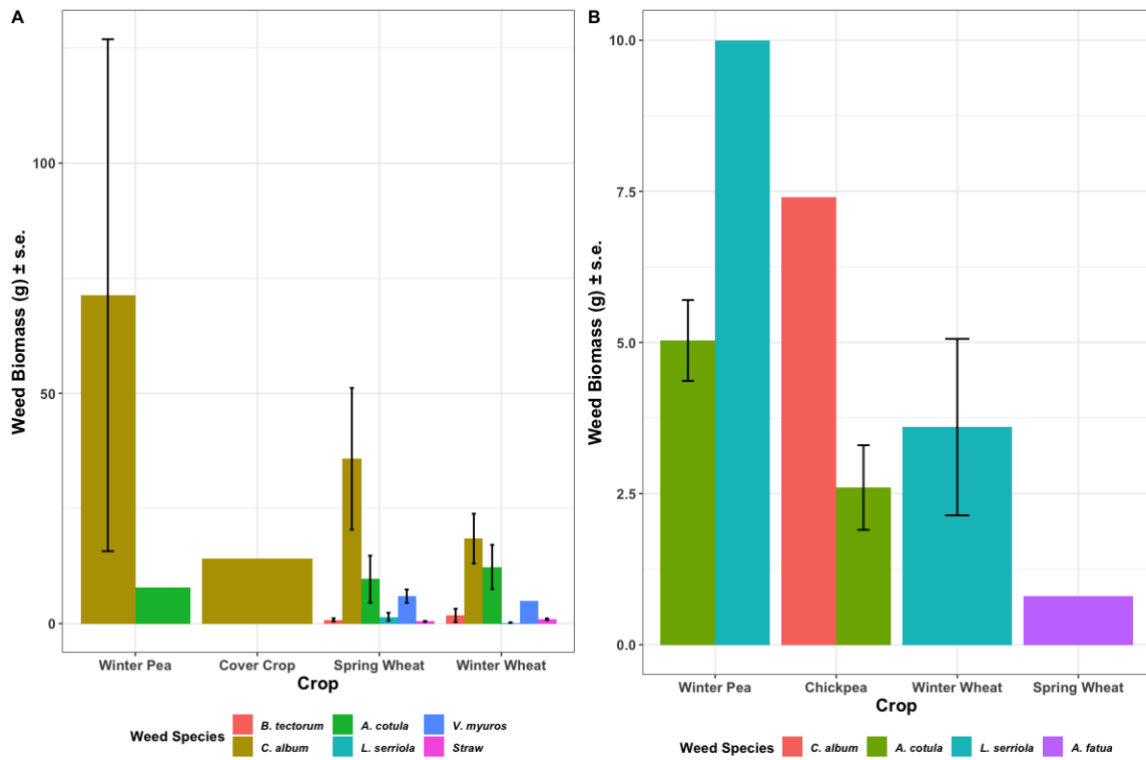


Figure C0.1 Weed biomass sampled from each crop at St. John, Washington (A) and Genesee, ID (B) in 2019.

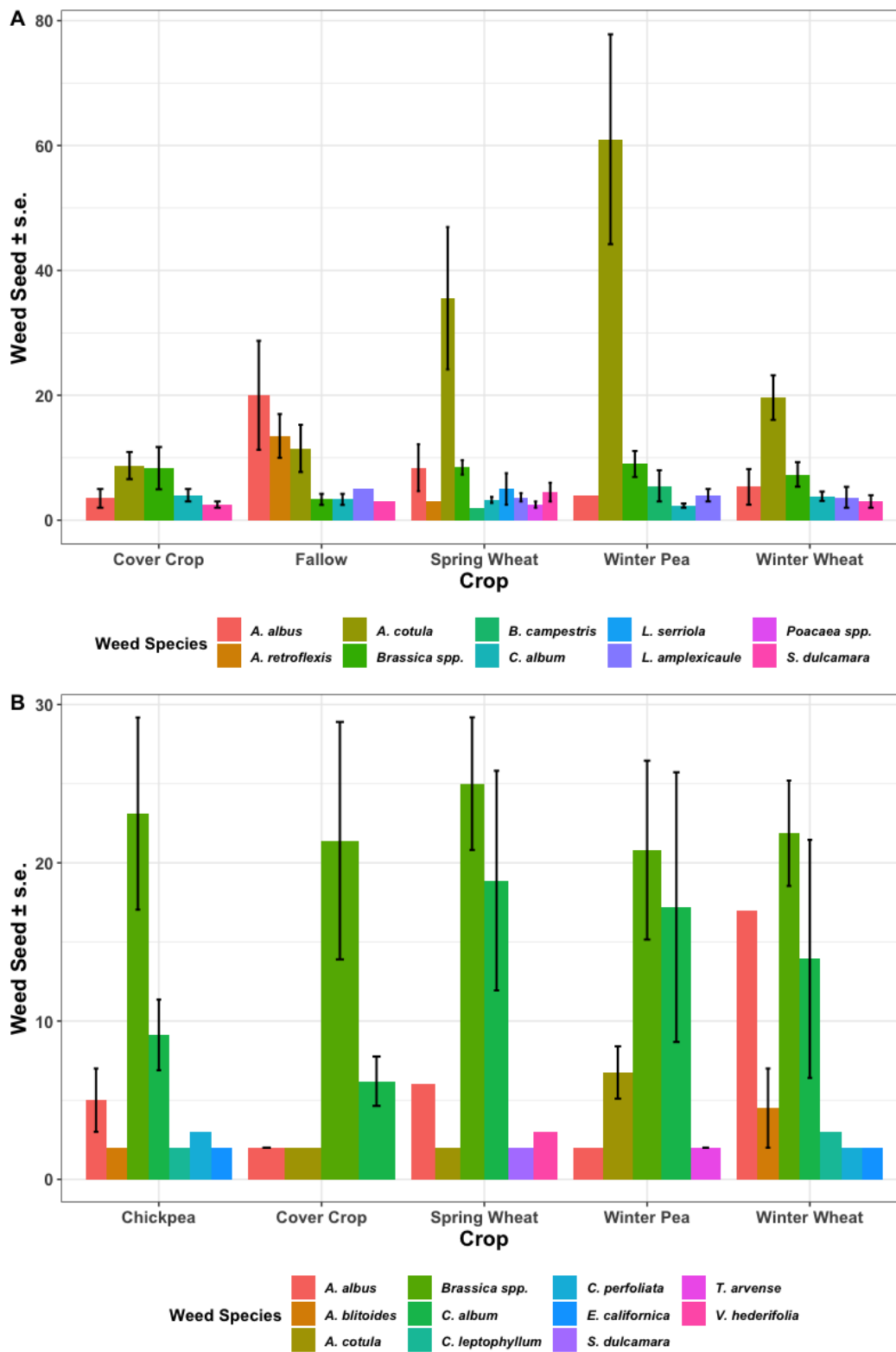


Figure C0.2 Seed bank counts by crop and species at St. John, WA (A) and Genesee, ID (B).

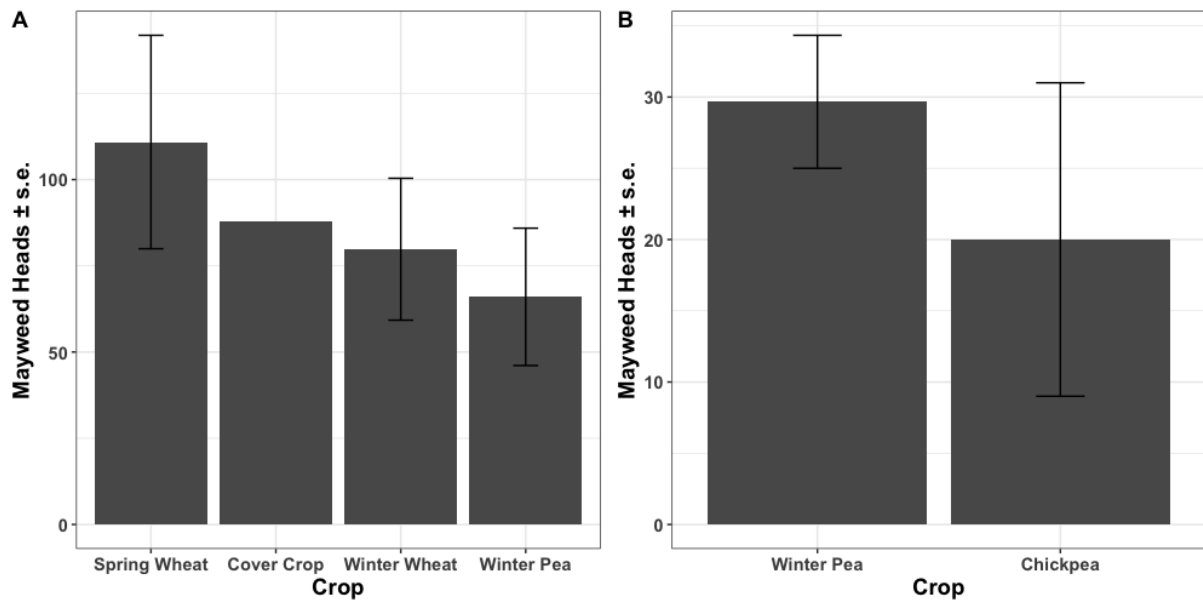


Figure C0.3 *Anthemis cotula* headcount at St. John, WA (A) and Genesee, ID (B). Flower heads were counted from the weed biomass samples.