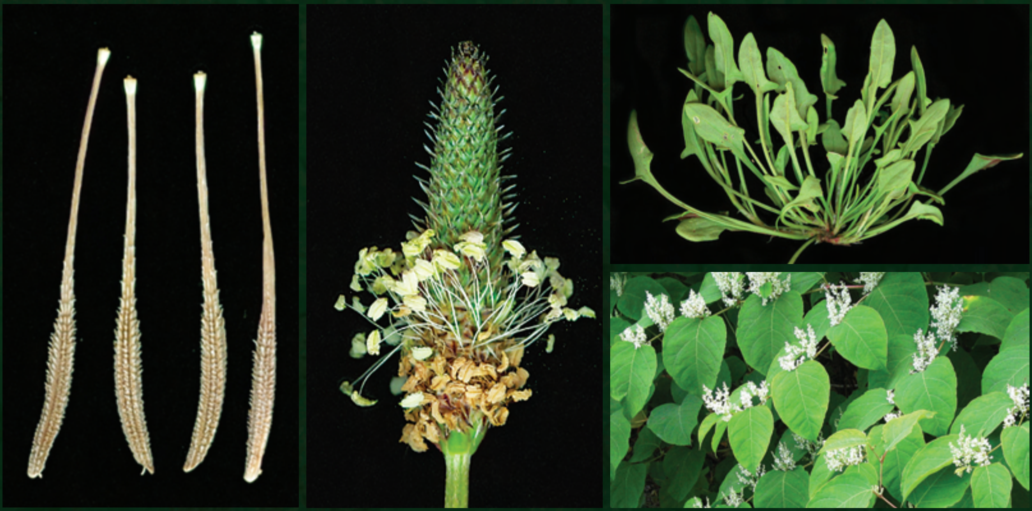
PERSISTENCE STRATEGIES OF WEEDS



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Preface

Weeds reduce crop yields, lower the quality of agricultural produce, affect livestock health, and interfere with human life in a variety of ways. A considerable amount of time, money, and other resources are spent in controlling weeds by producers as well as by the general public, yet weeds persist. Unfortunately, we have relied very heavily on the use of synthetic herbicides to control weeds for the past several decades. This has hampered research on other nonchemical options for weed management. It is now well recognized that excessive use of synthetic herbicides carries risks to both the environment and the sustainability of herbicides as a tool. Widespread resistance to herbicides has developed among weed species and for almost all major classes of herbicide chemistry.

Stemming from concerns for human health and the environment, public opposition to the use of synthetic herbicides is progressively increasing. The sustainability of our food production systems is rapidly becoming an important issue globally, and pesticide-free, organic produce is becoming increasingly popular. In order to develop novel and more holistic methods for weed management, a sound understanding of persistence strategies of weeds is necessary. This understanding will help us identify the vulnerabilities of different weeds and could lead to development of novel, safe, and effective weed management strategies by making modifications to our production systems and reduce our dependence on synthetic herbicides. However, because weeds are masters of persistence, have co-evolved with humanity, and are very much the product of how we manipulate agroecosystems and other environments, we need to look beyond short-term simplistic remedies and understand our complex relationship with weeds.

This book takes a comprehensive approach to understand the persistence of weeds and strives to fill the gap in our understanding of the underlying issues behind the problem of weed persistence and serves as a comprehensive source of information for students, researchers, and weed managers. The various topics covered in this book include an overview of weed persistence, the role of seed production, dissemination and seedbanks, variability in seed dormancy, physiology and genetics of seed dormancy, seed longevity, vegetative propagation and propagule banks, the influence of agronomic practices, allelopathy, predation, soil microbes, climate change, weed evolution, and the development of herbicide resistance. Because weeds and their management are global concerns, specialists from around the world have been selected to write chapters on these topics.

The key learning objective of this book for students and other readers is to enhance understanding of what underpins the persistence strategies of weeds. While this book is aimed to serve upper-level undergraduates and/or graduate students, it can also be used as a reference or text for courses in agroecology and organic agriculture. Weed scientists and weed management professionals working for universities and government agencies, agribusiness consultants, organic farmers, and other environmentally conscious producers will find this book a valuable source of information on persistence strategies of weeds. We also expect this book to stimulate research on development of environmentally friendly weed management options.

We thank all the chapter authors of this book for contributing informative chapters in their areas of specialization, external reviewers for their critical and constructive reviews of chapter manuscripts, and our families for their cooperation, patience, and encouragement.

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Foreword

Weeds have been a costly problem for farmers since the dawn of agriculture. They have evolved with the crops, the farming methods, and the new environments as crops spread across the world. To be successful, weeds had to be genetically flexible in order to adapt to changing agricultural practices. Many thousands of wild plant species have not become successful weeds in agriculture. Successful weed species have many similar traits, but changing agricultural practices impact the relative importance of different traits. In short, successful weed species prosper in the disturbed and changing environments found in agriculture. Understanding weed biology and genetics is providing insight into the traits that contribute to the persistence and spread of weeds.

This book explores the many traits that make weeds successful. To persist, reproduction and propagation are paramount. A major factor in propagation is prolific production of long-lived, dormant seeds, with properties contributing to dispersal. This is especially true in weed management systems that rely heavily on tillage. The importance of seed biology in the persistence of weeds is illustrated by the fact that nine of the sixteen chapters in this book deal with seed biology. Weed seed dormancy is a complicated and fascinating trait influenced by many genetic, environmental, and even seed morphology factors. Seed biology is also integral to topics covered in other chapters, such as that on herbicide resistance.

Vegetative propagation of weeds is dealt with in Chapter 11. This persistence mechanism is found in many weed species that also produce seeds but is the predominant or even the only means of propagation in some species. Vegetative propagation is highly effective for many highly virulent weed species (e.g. Johnsongrass and purple nutsedge). The evolution of herbicide resistance can occur without seed production (e.g. in the aquatic weed *Hydrilla*).

Weeds have been with us for thousands of years. This has given weeds time to evolve traits allowing them to persist in farming systems practiced prior to introduction of herbicides. For example, weeds that have a similar visual appearance to the crop could avoid hand weeding. The advent of synthetic herbicides in the mid-twentieth century subjected weeds to a novel and intense selection pressure. However, this relatively efficient technology has not put any significant weed species on an endangered species list to my knowledge. The interplay between changing herbicides and evolved resistance continually shifts the relative importance of different weed species in time and space. The genetic flexibility of weeds in resisting herbicides has been remarkable. I think that Darwin would have been gratified to see such rapid, profound, diverse, and widespread responses to selection pressures. This amazing display of evolution in action is covered in Chapter 7.

Plants being sessile, their evolutionary response to pathogens and herbivores (including insects) has largely been chemical, producing secondary compounds that are toxic or fight these enemies in other ways, such as attracting beneficial insects that feed on herbivore insects. Some plants clearly release secondary products (allelochemicals) that inhibit the growth of competing plant species. Chapter 14 deals with this phenomenon in weeds and provides some enlightening case studies.

The influence of climate change on weed persistence is the topic of Chapter 12. Increased atmospheric CO_2 and temperature, as well as precipitation changes, will influence all plants, including crops and weeds. The relative efficacy of different herbicides on different weed species will change, especially between C_3 and C_4 species. The robust adaptability of weeds (as covered in Chapter 15) will ensure that weeds cope with changing climate.

These are but a few of the topics considered in the broad scope of this book that provides a valuable update by international experts on the many ways in which weeds have evolved to persist in agriculture and other disturbed ecosystems. It describes what we understand about weed persistence mechanisms and identifies the questions for which answers are still incomplete. I hope that it will inspire future research to fill these knowledge gaps so that we can devise more successful means of protecting crops and the environment from weeds. I expect that the bookshelves of serious students of weed and pest biology will contain this volume, as it provides the most current and update on how weeds persist, despite intense and costly efforts to manage them.

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1

Persistence Strategies of Weeds: Introduction

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1.1 Introduction

Since time immemorial, humanity has been plagued by weeds. Today weeds infest almost every environment on earth that is managed. These environments include wilderness areas where the ideal is a "pristine habitat" free of non-native weeds, expansive rangeland habitats where weeds threaten forage quality for livestock, more intensively managed cropping systems where weeds threaten yields, and even our urban yards where weeds negatively impact "the perfect lawn," which is the goal of many home owners. In any case, by now the reader is probably asking the question every weed scientist gets asked repeatedly – "what is a weed?"

In 1912, Blatchley defined a weed as "a plant out of place or growing where it is not wanted." Although this seems like a pretty all-encompassing definition, there is room for many other perspectives, such that of renowned American transcendentalist and writer Ralph Waldo Emmerson, also in 1912, who referred to a weed as a "plant whose virtues have not yet been discovered" (as quoted in Zimdahl 1999). If a weed is determined to be "out of place" (regardless of any potential virtues), in practical terms the weed is often very difficult to "weed out," especially because biologically weeds have evolved tremendous persistence strategies, which greatly affect human endeavors, especially agriculture.

Agriculture is an important component of the world's economy and an important means of livelihood, especially in developing countries (Alston and Pardey 2014). However, there is a lot of risk involved in crop production, much of which comes from insect pests, weeds, and pathogens. Weeds compete with crops and cause huge economic losses, estimated at an annual yield loss of 9% to global agriculture (Oerke 2006) and in economic terms, about US$ 27 billion to US agriculture alone (Pimentel et al. 2005). Similarly, weeds are also a

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problem in non-crop systems (e.g. roadsides, waterways, etc.) and natural ecosystems (e.g. forests, landscapes) where invasions of undesirable plants can cause aesthetic and economic losses and reduce biodiversity (Neve et al. 2018). They have continued to evolve and persist, despite humankind's efforts to control them.

1.2 Persistence of Weeds

Merriam-Webster's dictionary defines the word "persist" as "to continue to exist especially past a usual, expected, or normal time" or "to go on resolutely or stubbornly in spite of opposition" ("Persist" Merriam–Webster.com Dictionary n.d.). In this book we refer to "weed persistence" as "the ability of undesirable plant species to continually evolve, survive, thrive, and reproduce under a variety of natural and anthropogenic selection pressures." Weed scientists, farmers, and land managers continue to be baffled by the persistence of these species despite a wide variety of management techniques developed to eliminate them. In this context, some questions that can be raised include the following: (i) What makes a weed so persistent? (ii) Why are the natural and human-developed selection pressures failing to eliminate them? (iii) What lessons can we learn from the strategies that they have developed to persist in the various ecosystems? (iv) How can we use this knowledge of weed persistence to minimize the damage they cause to agroecosystems and other human-managed ecosystems?

Although Baker (1965) listed the factors that enable a species to become a weed, the plants continue to persist despite our knowledge of these factors. For decades, we have tried to manage weeds with the so-called four corners of weed management, i.e. biological, chemical, cultural, and mechanical weed control, and yet weeds have persisted. Therefore, it is essential to revisit this list to discuss weed persistence.

Baker (1965) listed the following characteristics that make a plant successful as a weed: no special environmental requirements for germination, discontinuous germination, longevity of seeds, rapid seedling growth, short vegetative periods, ability to maintain seed production as long as growing conditions permit, self-compatible but not necessarily self-pollinated or apomictic, cross-pollinated types that can be pollinated by various methods, ability to produce numerous seeds even under unfavorable environments, good mechanisms for short- and long-distance dispersal, vigorous and multiple methods of vegetative reproduction in asexually reproducing species, and having good competitive mechanisms. Some very persistent weeds may have only one or two of these characteristics, whereas others may have nearly all; the point is that this set of characteristics represent key characteristics that make weeds so successful. In summary, we are dealing with plants that have very successful persistence mechanisms despite of above- and belowground natural and human-induced selection pressures and management methods (Figure 1.1). In the following text, some of these mechanisms will be discussed briefly to give an overview of the persistence strategies of weeds.

In this chapter, we discuss persistence of weeds in terms of (i) seed dormancy, germination, seedling emergence, seed production, and seed return, (ii) soil seedbank and longevity of seeds in the soil seedbank, and (iii) ability to persist against natural and human selection pressures and management methods. The other chapters in the book will describe these phenomena in detail and provide valuable insights to understand the persistence strategies of weeds.

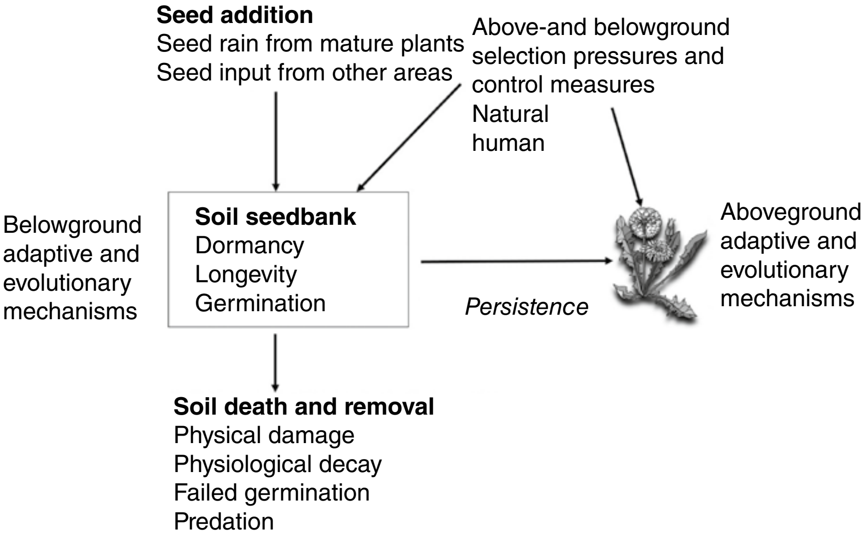

Figure 1.1 Cycle of above- and below-ground natural and human selection and management pressures, continued adaptation, evolution, and persistence of weeds that reproduce by seeds in agroecosystems and other human-managed ecosystems.

1.2.1 Seed Dormancy, Germination, Seedling Emergence, Seed Production, and Seed Return

Seed dormancy has been defined generally as the failure of a seed to germinate despite favorable conditions (Bewley and Black 1994; Benech-Arnold et al. 2000). There are two main types of seed dormancy – primary and secondary (induced) (e.g. Karssen 1982; Bewley and Black 1994). Many weed seeds are known to possess the ability to remain dormant, but viable, in the soil for extended periods of time. For example, the classic, pioneer experiment of W.J. Beal who studied seed dormancy and viability of buried weed seeds in Michigan has been cited in numerous publications (e.g. Kivilaan and Bandurski 1981; Baskin and Baskin 1985; Burnside et al. 1996; Telewski and Zeevart 2002). These and other studies have demonstrated that seeds of some weeds can retain viability and remain dormant for up to more than 100 years. Therefore, seed dormancy can be considered as a primary factor contributing to weed persistence, and knowledge of and a sound understanding of this phenomenon is of prime importance for weed management.

Once dormancy is broken, seeds germinate (emergence of radicle) when the necessary environmental conditions for water, temperature, oxygen, and, in some species, light are met. The range of favorable environmental conditions to stimulate germination depends on the plant genotype (Baskin and Baskin 2001). Seed germination occurs when these factors are present at or above the minimum threshold but below the species-specific maximum levels (Bewley and Black 1994; Baskin and Baskin 2001).

Unlike crop seeds that have a narrower range of optimum conditions for germination, studies have shown that weed seeds can adapt and germinate under a wide range of environmental conditions (e.g. Grundy et al. 2000; Steinmaus et al. 2000; Leon et al. 2004). Whitney and Gabler (2008) suggested that many invasive plant species do not have specialized germination requirements and are highly flexible, making it possible for them to adapt to a wide range of environments. Even under projected climate change scenarios, weed seed persistence is an area of concern. Walck et al. (2011) emphasized the importance of conducting research on seed ecology because they believed that seeds of weedy species could evolve relatively quickly to keep pace with climate change. Furthermore, germination of a few weed seeds and seed production from the resulting plants can add thousands of seeds to the soil seedbank, ensuring the persistence of the weeds.

Since germination is a process primarily driven by a combination of temperature and moisture, researchers have modeled weed seed germination based on the combination of these two factors, i.e. hydrothermal time (e.g. Gummerson 1986; Roman et al. 2000; Bradford 2002). Although these models have enhanced the knowledge of the parameters of weed seed germination, how to use this information from a management standpoint and reduce persistence of weeds in our ecosystems remains a challenge. Nevertheless, modeling is an important component of understanding and predicting population dynamics of weeds and therefore for our understanding of weed persistence. Borgy et al. (2015) emphasized that prediction of population dynamics of annual plants is challenged by soil seedbanks that are difficult to see and presented a time series model to assess weed population dynamics based on data from growing plants and the soil seedbank.

Seed vigor, good seed bed preparation, and proper soil conditions for seedling emergence have been cited as primary needs of seedling establishment of agricultural crops for optimum yields (Finch-Savage and Bassel 2016). However, in the case of weeds, they can emerge and complete their life cycle in less than optimum soil conditions compared with crops. A few weed seedlings that emerge and establish can produce thousands of seeds that go back to the seedbank. Weed seedlings can emerge from the harshest of soil or other substrates, complete their life cycle, and produce seeds (Figure 1.2).

Weeds are capable of producing huge number of seeds. For example, species such as Palmer amaranth (*Amaranthus palmeri*) and horseweed (*Erigeron canadensis*), which are considered to be among the worst agricultural weeds in North America (Weed Science Society of America [WSSA] 2017), can produce up to 600 000 seeds (Keeley et al. 1987) and 200 000 (Weaver 2001) to 800 000 (Shrestha et al. 2010) seeds per plant, respectively. Often, late-season weed control is ignored as the weeds do not cause crop yield loss. However, these late-emerging weeds could deposit thousands of seeds to the soil seedbank. Bagavathiannan and Norsworthy (2012) emphasized that these late-season weeds should not be ignored and suggested the development of thresholds for these weeds using bioeconomic models. Long et al. (2015) emphasized the importance of information on environmental effects on the loss of weed seeds from the soil seedbank, either by germination or death, and proposed a model to predict the length of seed persistence in a range of environments. The ability to germinate, emerge, grow, and produce viable reproductive structures under a wide range of environmental conditions is important for weed persistence. The use of simulation models to predict seedbank and weed population dynamics are therefore needed.

1.2.2 Seed Longevity, Emergence Patterns, and Soil Seedbanks

Since weed seeds and vegetative propagules in soil banks are important for persistence of weeds, they should be the focus of any management strategy for effective weed control

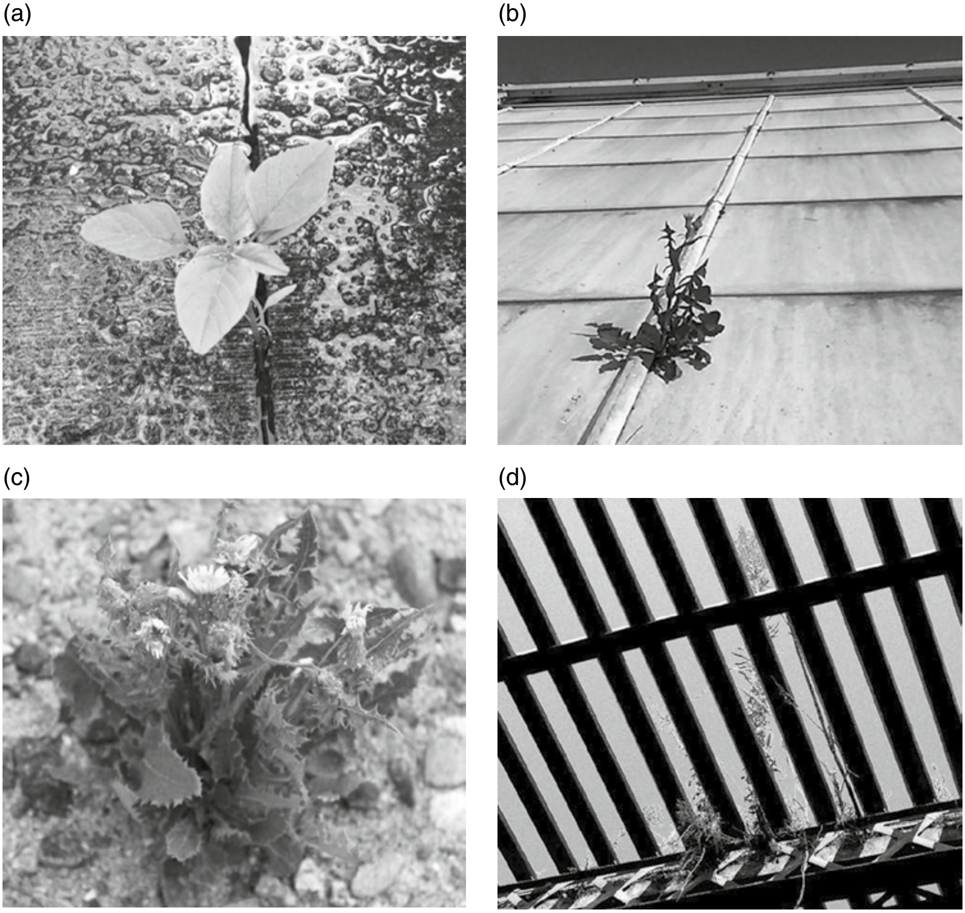

Figure 1.2 Various species of weeds growing, flowering, and producing seeds under soil-less and adverse plant-growing conditions: (a) an *Amaranthus* sp. plant growing through a crack on a sidewalk, (b) an annual sowthistle (*Sonchus oleraceus*) plant growing on the roof of a greenhouse, (c) an annual sowthistle (*Sonchus oleraceus*) plant growing on a gravel road, and (d) a horseweed (*Erigeron canadensis*) plant growing on the roof of a metal lathe house.

(Kremer 1993; Dekker 1999; Walsh et al. 2018). As mentioned earlier, not all the weed seeds that are present in the soil seedbank germinate and emerge immediately or at the same time. Diverse dormancy mechanisms and modification of seed dormancy and germination by environmental cues provide weeds the ability to distribute their germination over time, which is an important factor in persistence of weeds (Baskin and Baskin 2001; Clements et al. 2004). Genotype, environmental factors during seed development and post-dispersal, and soil-borne pests and pathogens influence seed dormancy, longevity, and germination and therefore are important factors in the persistence of weed seeds in soil seedbanks (Egley and Duke 1985). Forcella et al. (1997) collected soil cores from several sites in the US corn belt and monitored weed seed germination and emergence. They found significant variability in the percentage of seedlings that emerged with time and attributed this to effects of microclimate variables. Saatkamp et al. (2011) concluded that the functional role of delayed germination and light and diurnally fluctuating temperatures are key contributors to higher soil seed persistence. Saska et al. (2020) suggested that seeds undergo changes in morphology and viability while in the seedbank. They buried seeds of several weed species in the soil, excavated them six to eight years later and assessed the changes in seed morphology and proportion of fresh seeds to determine seed persistence. They found that seed mass, volume, and proportion of persistent seeds in most species declined with increase in burial periods.

Knowledge of genetic and epigenetic factors, which regulate seed dormancy (Gu et al. 2006), is necessary to comprehend persistence strategies of weeds. A study by Pipatpongpinyo et al. (2019) reported that regulation of soil seedbank longevity was due to genes controlling seed dormancy. Davis et al. (2016) highlighted the importance of the link between inherited weed seed traits in their persistence and suggested that management practices could be tailored to specific weed species based on particular chemical or physical defenses.

Soil microbes have been reported to increase weed seed mortality in soil seedbanks (Gallandt et al. 1999; Kennedy 1999). Ullrich et al. (2011) suggested that this increased mortality could be because of seed coat being damage by soil microbes. However, their study on the effect of microbial abundance on weed seed persistence did not show a strong correlation between seed mortality and seed coat damage, suggesting that soil microorganisms may not play a major role in determining seed mortality. More research is needed to understand the magnitude of effects of soil microbes on seed longevity, viability, and germination and to exploit the potential of reducing the size of seedbanks by enhancing microbial effects.

Since seeds and vegetative propagules can survive and maintain their viability for extended periods, understanding of factors that influence their longevity is essential for understanding weed persistence and for development of effective weed management strategies. Information on seedbank persistence can help in long-term weed management and possibly weed eradication (Panetta and Timmins 2004). The persistence of weed seedbanks, therefore, is an important area of investigation for weed scientists who are working on this and various other aspects of persistence strategies of weeds, including genetics and physiology of seed dormancy and germination, seed longevity, environmental influences, ecophysiology of persistence, and effects of soil biota and allelochemical interactions, to name a few. Auld (2004) looked at the social aspects of weed seed survival in the seedbank and concluded that due to the inevitability of persistent weed populations due to seedbanks, agricultural communities must live with the inevitable presence of weeds and their effects.

Another factor that has gained some attention in terms of weed seed and seedling death is allelopathy (Arroyo et al. 2018; Weston and Duke 2003). Several studies have explored the effects of extracts from several plants, suspected to possess allelochemicals, on seeds, and seedlings of various weed species (e.g. Panasuik et al. 1986; Hoffman et al. 1996; Marles et al. 2010). Scavo et al. (2019a) reported that the crop globe artichoke (*Cynara cardunculus*) produced allelochemicals that reduced the soil seedbank of some weed species. Similarly, Vitalini et al. (2020) reported allelopathic activity of Italian ryegrass (*Lolium multiflorum*) on some weed species of rice (*Oryza sativa*) fields. However, we still need to know much more about allelopathic interactions (Scavo et al. 2019b) to be able to exploit