BIOLOGY AND ECOLOGY OF
AMBROSIA TRIFIDA L. SEEDLING EMERGENCE

DISSERTATION

Presented in Partial Fulfillment of the Requirements for
the Degree Doctor of Philosophy in the Graduate
School of The Ohio State University

By

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Ambrosia trifida (giant ragweed) is a North American native summer annual that has become one of the most problematic weeds in the eastern Corn Belt. Management of A. trifida has been challenging in part because of its temporal seedling emergence pattern. In agricultural fields, seedling emergence continues sporadically throughout the growing season. Studies were conducted to 1) determine characteristics of seed dormancy loss in the natural environment, 2) determine the seed dormancy mechanism associated with prolonged seedling emergence, 3) model seedling emergence in agricultural fields, and 4) elucidate the maternal effects on seed bank persistence. Seed dormancy loss in the natural environment occurred in response to cold-moist conditions and involved the sequential reduction of embryo and coat-imposed dormancy. Embryo dormancy and its interaction with soil temperature was the dormancy mechanism primarily responsible for the prolonged seedling emergence pattern of agricultural populations. Two integrated Weibull models described seedling emergence as a function of hydrothermal time in tilled and no-tillage environments and two locations in Ohio. Models indicated emergence was insensitive to periods of no rainfall and that emergence occurred during two intervals separated by a period of little emergence around May 1st. The biphasic emergence pattern was explained by diverse emergence times among the
progeny of particular maternal plants. Maternal families characterized by smaller seeds were more likely to emerge after May 1st compared to maternal families characterized by larger seeds. Furthermore, maternal families with smaller seeds were more likely to remain viable in the soil after one emergence season compared to maternal families with larger seeds. Seed bank longevity was influenced by dispersal unit maturation time and maturation effects varied between years. The most persistent fraction of the seed population originated from small-seeded individuals at a particular time during the seed maturation period.
Dedicated to my wife, Elizabeth
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PUBLICATIONS


FIELDS OF STUDY

Major field: Horticulture and Crop Science
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1.1 Introduction

A weed can be defined as a plant that “grows entirely or predominately in situations markedly disturbed by humans (without being planted deliberately)” (Baker 1974). Weeds can interfere with human intentions for a plant community or provide a service (Liebman 2001). In this dissertation, weeds are considered as detriments to crop production. From a grower’s perspective, weeds reduce profits. From a societal standpoint, weeds decrease land-use efficiency. Therefore, control of agricultural weeds is a shared need.

Conventional weed control primarily involves mechanical or chemical destruction of weeds. Concerns for long-term efficacy, human health effects and ecosystem impact of current practices drives the search for a more sustainable approach (Liebman 2001). The goal is weed management incorporated into all production decisions including rotation, cultivar selection, soil management, row spacing, planting date and density, fertilization and postharvest management. As a result of multiple control tactics, weed
populations will retreat to tolerable levels without excessive mechanical or chemical inputs (Liebman and Gallandt 1997). The success of this approach depends on knowledge of weed biology, especially attributes that render a plant difficult to control (Mohler 2001b).

1.2 *Ambrosia trifida* interference with crop production

*Ambrosia trifida* L. (Asteraceae) has been identified by growers in the central and southern regions of the U.S. as one of the most problematic weeds of corn and soybean production (Jordan 1985; Loux and Berry 1991; Webster et al. 2000; Webster et al. 2001). Currently, *A. trifida* ranks as the most troublesome crop production used in the eastern U.S. Corn Belt (Gibson et al. 2005).

A weed’s capacity for interference is estimated from field experiments composed of treatments with varied weed density in a constant crop density (Stoller et al. 1987). Grain yields are expressed relative to weed-free conditions and plotted as a function of weed density. The relationships between relative yield and weed density are summarized with nonlinear models. One such model is the rectangular hyperbola:

\[
\text{Yield loss (\%)} = \frac{Ix}{1 + \frac{Ix}{A}} \quad [1]
\]

where \(I\) accounts for the additive effect of weeds at low weed densities, \(x\) is weed density and \(A\) is the upper asymptote (Cousens 1985). The parameter \(I\) provides an estimate for yield reductions associated with the first weed per unit area (Harrison et al. 2001).
parameter $A$ indicates maximum yield reduction as weed density approaches infinity (Cousens 1985). Comparisons of published $I$ and $A$ values indicate relative competitiveness of species within a particular crop environment (Bensch et al. 2003).

Published maximum $I$ and $A$ values for full-season interference of common weeds in corn fields of central and eastern North America are shown in Table 1.1. Typically, the parameter $I$ is presented in units of percent yield reduction for the first weed per meter square. However, model parameters for *A. trifida* were determined with lower weed densities than those typically used (Harrison et al. 2001). For *A. trifida*, $I$ is in units of percent yield reduction for the first weed per 10 m$^2$. *A. trifida* model parameters $I$ and $A$ were found to be similar despite different environmental conditions (Harrison et al. 2001). For many weed species, $I$ and $A$ parameters are influenced by differences in the environment (Fischer et al. 2004; Weaver et al. 2006). Therefore, model parameters $I$ and $A$ indicate that *A. trifida* is the most consistently competitive weeds in corn tested thus far (Harrison et al. 2001).

In addition to the rectangular hyperbola [1] proposed by Cousens (1985), the relationships between weed density and crop yield can be expressed by other nonlinear models. When a variety of nonlinear models is used to summarize weed interference in a particular crop, competitiveness is assessed by comparing relative yields at a fixed weed density. Measures of weed interference in soybean from different nonlinear models are
reported in Table 1.2. Crop row spacing influences weed competitiveness and needs to be considered. Narrower rows increase competitiveness of the crop and wider rows increase the competitiveness of the weed (Hock et al. 2006). But, *A. trifida* is so competitive in soybean fields that row spacing differences may be irrelevant.
<table>
<thead>
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<td><em>Setaria spp.</em></td>
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</tr>
<tr>
<td><em>Sorghum bicolor</em></td>
<td>15</td>
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</tr>
<tr>
<td><em>Ambrosia trifida</em></td>
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Table 1.1. Rectangular hyperbola [1] parameters for full-season weed interference in corn grown in 76 cm rows. Parameters are maximum values reported. *I* represents yield reductions for the first weed per m². **A** represents potential yield reduction as weed densities approach infinity. ***For *A. trifida*, I represents yield reduction for the first weed per 10 m².
<table>
<thead>
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<td><em>Amaranthus spp.</em></td>
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<td>50</td>
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<td>60</td>
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<tr>
<td><em>Datura stramonium</em></td>
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<td>76</td>
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<td><em>Ambrosia trifida</em></td>
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<td>76</td>
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Table 1.2. Soybean yield reductions for a weed density of one plant per square meter.
1.3 *Ambrosia trifida* biology

1.3.1 Asteraceae

Composed of 1,535 genera and approximately 23,000 species, the Asteraceae is one of the largest families of flowering plants. Diagnostic of the Asteraceae is the inflorescence, which consist of a head with many, densely packed, stalkless flowers (Heywood et al. 1977). This type of inflorescence is referred to as a capitulum (plural capitula) and represents advanced inflorescence evolution (Stebbins 1974). The selective pressures of pollination have produced capitula of different forms within the Asteraceae (Leppick 1977).

Members of the Asteraceae are organized according to morphological similarities and shared evolutionary histories (Bremer 1994). Genera are classified to (from least to most exclusive): subfamily, tribe, and subtribe. *Ambrosia trifida* belongs to subfamily Asteroideae, tribe Heliantheae and subtribe Ambrosiinae. The Asteroideae is the largest of three Asteraceae subfamilies, consisting of 1,135 genera and approximately 16,200 species (Bremer 1994). Tribe Heliantheae includes many familiar genera including: *Bidens, Coreopsis, Cosmos, Dahlia, Echinacea, Galinsoga, Helianthus, Heliopsis, Rudbeckia,* and *Zinnia* (Bremer 1994). Within the Heliantheae, species with pollen and capitula adapted to wind pollination are assigned to the subtribe Ambrosiinae (Bremer 1994). Subtribe Ambrosiinae includes two genera with agricultural weeds: *Ambrosia* and *Xanthium.*
1.3.2 Natural history

According to palynological studies, *A. trifida* has grown in riverbanks and lakeshores north of the Ohio river since the retreat of the Wisconsin glacier approximately 10,000 years ago (Bassett and Terasmae 1962). In this region, *A. trifida* proliferated approximately 200 years ago, coinciding with European settlement (Bassett and Terasmae 1962). Today *A. trifida* is found in ruderal and agricultural habitats of temperate regions in North America, South America, Europe and Asia (Bassett and Crompton 1982; Ishikawa et al. 2006).

1.3.3 Lifecycle characteristics

*A. trifida* seeds are disseminated within single-seeded dispersal units. Dispersal units range from 6 to 11 mm wide, 7 to 14 mm long and are highly polymorphic among individuals (Sako et al. 2001). The anatomy of a dispersal unit is a hardened involucral body surrounding the fruit and seed (Davis 1930). Pericarps contain phytomelanin, an extracellular secretion that confers resistance to puncture and decay (Pandey et al. 1989; Stafford et al. 1984). The pericarp encapsulates the seed which consists of a membranous seed coat and embryo. Initially, dispersal units are incapable of producing a seedling because of inhibitory influences within the embryo and embryo-covering structures (Davis 1930).

Dispersal units fall from maternal plants typically in autumn, but a portion remains on the maternal plant into winter. Incorporation of dispersal units into the soil occurs by rainfall, cryoturbation, and earthworm activity (Regnier et al. 2001). While on
the soil surface, dispersal units are susceptible to predation by mice (*Peromyscus* spp.) and ground beetles (*Harpalus pensylvanicus*) (Harrison et al. 2003). During the winter, up to 43% of dispersal units are consumed and within one year, 88% are predated (Harrison et al. 2003).

Compared to other summer annual species, *A. trifida* is among the first to emerge in early spring (Abul-Fatih and Bazzaz 1979a). Seedlings can emerge from relatively deep depths. Optimum burial depth is 2 to 5 cm but *A. trifida* seedlings can emerge from 16 cm (Abul-Fatih and Bazzaz 1979b). Dispersal units that do not produce seedlings are known to have at least two fates including: seed bank persistence (Stoller and Wax 1974; Davis et al. 2005; Harrison et al. 2007) and destruction by soil microbial activity (Chee-Sanford et al. 2006).

Seedlings quickly grow taller than coexisting species. By late May, plants can be three times taller than neighboring plants (Abul-Fatih and Bazzaz 1979a) and by season’s end, plants can extend 6 m (Bassett and Crompton 1982). Large leaves (20 – 30 cm in length) are arranged primarily near the tops of plants (Abul-Fatih and Bazzaz 1979c) and form dense canopies that reduce light available to subcanopy species (Abul-Fatih and Bazzaz 1979a).

As summer day length decreases, vegetative growth becomes reproductive. *A. trifida* is monoecious. Staminate capitula occur in racemelike clusters at the tips of stems and branches. Pistillate capitula occur in clusters at leaf axils below staminate capitula. Within an individual, stigmas are receptive to pollen prior to pollen shedding (Bassett and Crompton 1982). Pollination is anemophilous and is more successful between than
within individuals (Bassett and Crompton 1982). Individuals can flower for up to 25
days (Bazzaz and Carlson 1979). Consequently, dispersal units mature asynchronously
from late summer to autumn (Harrison et al. 2001).

During maturation, dispersal units are susceptible to predation by fruit flies
(Diptera: Tephritidae), weevils (Coleoptera: Curculionidae) and moths (Lepidoptera:
Gelechiidae) (Regnier et al. 1999; Harrison et al. 2001). Furthermore, \textit{A. trifida} produces
parthenocarpic involucres. In total, up to 62\% of a population’s dispersal units can be
damaged or hollow (Harrison et al. 2001).

1.3.4 Putative reasons for interference

Despite low fecundity, \textit{A. trifida} is a severe weed in row-crop agriculture. One
reason is that rapid and plastic vegetative growth quickly establishes plants in agricultural
fields. Plants among the crop remain competitive in part by capturing light above and
within the canopy (Webster et al. 1994). In addition to growth characteristics, resilience
to weed control measures contributes to \textit{A. trifida} success. There are \textit{A. trifida}
populations in Ohio reported to be resistant to acetolactate synthase (ALS)-inhibitors and
glyphosate (Heap 2007). In addition, decreased herbicide efficacy can result from stalk-
boring insects disrupting translocation (Ott et al. 2007).

One of the more compelling reasons for \textit{A. trifida} interference in crops is its
prolonged seedling emergence pattern. Although \textit{A. trifida} occurs throughout the U.S.
Corn Belt, weed problems are largely restricted to the eastern Corn Belt. When planted
in a common environment, eastern Corn Belt populations from agricultural fields
exhibited seedling emergence until mid-summer and western Corn Belt populations exhibited emergence only in early spring (Sprague et al. 2004). Similar to western Corn Belt populations, successional populations from the eastern Corn Belt emerged only in early spring (Sprague et al. 2004). Differences in seedling emergence patterns among successional and agricultural populations are likely due to different selection pressures (Hartnett et al. 1987). Early-season emergence is advantageous in successional environments since it reduces competition for resources. Late-season emergence is advantageous in agricultural fields due to evasion of weed control practices. Knowledge of late-season seedling emergence can improve control efforts and reduce the spread of weedy *A. trifida* populations.

1.4 Seed germination ecology

1.4.1 Primary seed dormancy

Seed germination comprises the events inside the seed that occur from imbibition to radicle elongation (Bewley 1997). Primary seed dormancy is an internal condition of the seed that develops during maturation and defines the environmental conditions in which radicle elongation occurs (Finch-Savage and Leubner-Metzger 2006). Causes for seed dormancy vary among species. Baskin and Baskin (2004) proposed a comprehensive seed dormancy classification system that organizes the multitude of dormancies into five classes: physiological, morphological, morphophysiological,
physical and combinational (physical plus physiological). Dormancy in the Asteraceae is classified as physiological, which is defined as dormant seeds with water-permeable seed coats and fully developed embryos.

At dispersal, radicle protrusion in seeds with physiological dormancy can occur within a narrow range of thermal and hydrological conditions. As seed dormancy is alleviated, the temperatures and moisture conditions conducive to radicle elongation expand. Dormancy alleviation requirements vary among species and are typically either cold, hydrated environments or warm, dry environments (Foley 2001). Once dormancy is sufficiently low, it is terminated by environmental factors including fluctuating temperature, light, or nitrate (Benech-Arnold et al. 2000). Radicle protrusion and seedling growth then occurs in response to temperature and moisture conditions.

The ecological significance of dormancy is to position radicle protrusion at a time and place optimal for seedling establishment. When seeds of summer annuals are dispersed in autumn, radicle protrusion can occur only at high temperatures (Benech-Arnold et al. 2000). Dormancy alleviation by cold, moist conditions during winter gradually decreases the minimum temperature at which germination can proceed. As spring arrives, soils gradually warm and radicle protrusion can occur once soil temperatures and germination permissive temperatures overlap. Similarly, when seeds of winter annuals are dispersed in early summer, radicle protrusion can only occur at low temperatures (Benech-Arnold et al. 2000). Dormancy alleviation by warm, dry
conditions increases the maximum temperature at which germination can proceed. With the onset of fall, soils cool and radicle protrusion can occur once soil temperatures and germination permissive temperatures overlap.

Dormancy terminating factors optimize the spatial environment for seedling growth. Radicle protrusion at deep depths can be fatal due to exhaustion of cotyledon or endosperm resources. As seed burial depth increases, the light and fluctuating temperature requirements necessary for dormancy termination become diminished, preventing radicle protrusion (Ghersa et al. 1997). Seedling emergence in the vicinity of a more established plant can be fatal as well. A more established plant subjects a nearby seed to an altered light environment, dampened temperature fluctuations and a zone of reduced soil nitrate (Hillhorst and Karssen 2000). Therefore, dormancy terminating factors may be the most abundant in vegetation gaps, thus promoting seedling establishment.

1.4.2 Seed dormancy mechanisms

Dormancy mechanisms are identified according to the location of the germination constraint (Bewley 1997; Foley 2001). Coat-imposed dormancy mechanisms inhibit radicle elongation through the embryo-covering structures. Seeds with coat-imposed dormancy mechanisms contain embryos that germinate upon removal of covering structures. Embryo dormancy mechanisms inhibit radicle elongation internally, and seeds with embryo dormancy mechanisms contain embryos that do not elongate when
covering structures are removed. Furthermore, a seed can have a combination of embryo and coat-imposed dormancy mechanisms (Ellery and Chapman 2000; Flintham 2000; Garvin and Meyer 2003).

1.4.2.1 Embryo dormancy

Since embryo dormancy is a developmental response to environmental stimuli, plant hormones are considered important elements of embryo dormancy. Amen (1968) proposed that seeds simultaneously contain germination promoters (gibberellin and cytokinin) and inhibitors (abscisic acid), and that dormancy was a consequence of the balance between hormones. The hormonal balance theory was modified by Karssen and Lacka (1983), who stated abscisic acid and gibberellin were synthesized at different times and that abscisic acid induces dormancy and gibberellin terminates dormancy. It is generally accepted that both hypotheses explain embryo dormancy (Finch-Savage and Leubner-Metzger 2006). Abscisic acid preserves dormancy and, in response to dormancy alleviation, abscisic acid biosynthesis decreases over time. Gibberellin promotes radicle elongation and its biosynthesis is induced by dormancy terminating factors. At any time the probability of radicle protrusion relates to the ratio of abscisic acid to gibberellin. High abscisic acid-to-gibberellin ratios inhibit radicle elongation. Low abscisic acid-to-gibberellin ratios promote radicle elongation.
Depending upon the species, abscisic acid can be produced within the embryo (Le Page-Degivry et al. 1997) or supplied to the embryo by the embryo-covering structures (Garello and Le Page-Degivry 1999). Hormonal deficient mutants and exogenous inhibitors of hormone synthesis indicate the importance of abscisic acid produced within the embryo in embryo dormancy.

While on the maternal plant, induction of primary seed dormancy requires the synthesis of abscisic acid within the embryo (Karssen et al. 1983). Application of fluridone, an inhibitor of abscisic acid synthesis, prior to a natural increase of endogenous abscisic acid prevents *Helianthus annuus* embryo dormancy (Le Page-Degivry and Garello 1992). In addition to the presence of endogenous abscisic acid, embryos must be sensitive to the hormone for the induction of primary dormancy (Walker-Simmons 1987). During the final stages of seed maturation, abscisic acid levels decrease but there is no consistent relationship between the degree of primary dormancy and abscisic acid content at dispersal (Foley 2001). In other words, embryonic abscisic acid during seed maturation induces primary dormancy but residual abscisic acid is not the primary mechanism of dormancy maintenance.

A *de novo* synthesis of abscisic acid within the embryo post-imbibition preserves the dormant state. This is supported by the observation that when subjected to dormancy termination, dormant embryos synthesize abscisic acid and nondormant embryos reduce abscisic acid in species such as *Hordeum distichum* (Wang et al. 1995), *Helianthus annuus* (Le Page-Degivry and Garello 1992), *Fagus sylvatica* (Bianco et al. 1997), *Triticum aestivum* (Garello and Le Page-Degivry 1999), *Nicotiana plumbaginifolia*
(Grappin et al. 2000). Abscisic acid levels in dormant and nondormant *Arabidopsis thaliana* seeds contrast in a similar manner (Ali-Rachedi et al. 2004) and gene expression profiles of *Arabidopsis thaliana* (accession Cvi) indicate that ABA-responsive elements are over-represented in dormant seeds compared to nondormant seeds (Cadman et al. 2006). Associated with dormancy alleviation is a decrease the capacity for abscisic acid synthesis (Bianco et al. 1997; Foley 2001).

The physiological role of abscisic acid in seed dormancy maintenance is not fully understood. Abscisic acid has been proposed to antagonize gibberellin induced germination processes (Rock 2000). Exogenous abscisic acid prevents gibberellin induced mobilization of starch reserves in cereals (Finkelstein et al. 2002). However, starch degradation is a post-germination event. Furthermore, inhibition of reserve mobilization may not be a universal abscisic acid response. Lipid mobilization during *Arabidopsis thaliana* germination was not inhibited by abscisic acid (Pritchard et al. 2002). Abscisic acid limits cell expansion by prevention of cell wall loosening (Schopfer and Claudia 1985) and may maintain dormancy by inhibiting radicle cell expansion.

Following the decline of abscisic acid and prior to radicle emergence, gibberellins are synthesized and induce genes for cell elongation in the embryo axis of *Arabidopsis thaliana* (Ogawa et al. 2003). Newly synthesized gibberellins are essential for germination since gibberellin synthesis inhibitors prevents germination of quiescent seeds (Foley 2001). Furthermore, gibberellin deficient *Arabidopsis thaliana* and *Lycopersicon euculentum* mutants do not germinate without exogenous gibberellin (Koornneef and van der Veen 1980; Groot and Karssen 1987). Environmental signals that terminate
dormancy, such as light, induce gibberellin synthesis (Derkx and Karssen 1993). Furthermore, the promotional effects of dormancy terminating environments are nullified by gibberellin synthesis inhibitors (Derkx and Karssen 1993). Associated with dormancy alleviation is an increased the capacity for gibberellin production in seeds of *Avena fatua* (Metzger 1983) as well as an increased sensitivity to gibberellin (Karssen and Lacka 1986; Foley 2001).

Other hormones such as brassinosteroids and ethylene promote germination (Kępczyński and Kępczynski 1997; Steber and McCourt 2001). *Ambrosia artemisiifolia* germination is promoted by ethylene (Brennan et al. 1978). Ethylene and brassinosteroids act in parallel or downstream of gibberellin regulated germination (Karssen et al. 1989; Leubner-Metzger 2002; Ogawa et al. 2003). These findings do not diminish the role of gibberellin but indicate the complexity of seed germination and the possibility for multiple controls.

1.4.2.b Coat-imposed dormancy

Coat-imposed dormancy is influenced by the structure, composition and permeability of the embryo-covering structures (Debeaujon et al. 2000). The basis of coat-imposed dormancy differs among species and can include: 1) physical restriction of embryo growth, 2) interference with embryo gas exchange, 3) limited loss of inhibitors from the embryo, and 4) supply of growth inhibitors to the embryo (Bewley 1997). Coat-imposed dormancy causes are not mutually exclusive. For instance, interference with embryo gas exchange can prevent degradation of embryo-based inhibitors (Barthe et al. 2000). Furthermore, coat-imposed dormancy depends on the character of the embryo so
that the expression of coat-imposed dormancy results from an interaction between the embryo and embryo-covering structure. As an example, physical restriction of embryo growth is a consequence of embryo growth potential and the restraining force of the embryo-covering structures (Khan 1996).

1.4.3 Maternal phenotype

The combined effects of the maternal plant genotype and environment influence seed dormancy (Roach and Wulff 1987). A seed population includes cohorts from different maternal genotypes growing in unique environments; and as a result, variation in dormancy (Andersson and Milberg 1998; Meyer and Allen 1999b; Cruz et al. 2003; Schütz and Rave 2003) and seedling emergence (Herrera 2000) can be detected among maternal plant cohorts. Several species with dormancy imposed by water-impermeable seed-coats exhibit differences among maternal cohorts (Norman et al. 2002; Lacerda et al. 2004). Seed-coats and other embryo-covering structures are of maternal origin, and therefore differences among cohorts can be expected for species with a coat-imposed dormancy.

Seed dormancy and seedling emergence characteristics vary among species and are strongly influenced by the environment, but they are generally considered to have a genetic basis (Foley 2001). Assuming an element of genetic control, phenotypic variation in seed dormancy is necessary for evolution in response to changes in the seedling emergence environment (Norman et al. 2002).
In addition to seed germination behavior, seed size differs among maternal plants (Byers et al. 1997; Telenius and Torstensson 1999; Simons and Johnston 2000; Susko and Lovett-Doust 2000; Halpern 2005). Seed size variation among maternal plants is considered to have a genetic basis (Harper et al. 1970). Species level variation in seed size influences seed behavior in the field (Moles and Westoby 2004). In some floras, smaller-seeded species persist in the seed bank thereby spreading emergence over time whereas larger-seeded species exhaust seed bank reserves within a relatively short time (Thompson et al. 1993; Funes et al. 1999). Differences in seed bank persistence and seed size among coexisting species have been attributed to an evolutionary tradeoff between seed size and seed bank persistence (Venable and Brown 1988). Both seed traits represent adaptations to heterogeneous establishment environments, wherein seed bank persistence is a response to temporal heterogeneity and seed size is a response to spatial heterogeneity. Since seed bank persistence and seed size represent adaptations to variable emergence environments, selection for one coincides with weaker selection for the other (Venable and Brown 1988). The association between seed size and seed bank persistence among individuals within a population has not been explored.

1.4.4 Maturation environment

Environmental conditions of the maternal plant during the final period of seed maturation affect seed dormancy (Roach and Wulff 1987; Baskin and Baskin 1998; Gutterman 2000). Influential maternal factors affecting seed dormancy include day length, light quality and mineral nutrition. In addition, the thermal and hydrology of the
maternal plant affects seed dormancy. Generalizations regarding the effects of these factors are difficult to make due to species-specific responses. But, several researchers have found that seeds produced in higher temperatures or under water stress have reduced dormancy compared to seeds produced at lower temperatures, and favorable moisture (Alexander and Wulff 1985; Meyer and Allen 1999a; El-Keblawy and Al-Ansari 2000; Allen and Meyer 2002).

Within a plant population, the maturation of individual seeds is rarely synchronous. Presumably due in part to changes in the environment, dormancy differs among seed maturation times (Lacey and Pace 1983; Roach 1986; Baskin and Baskin 1995; Cardina and Sparrow 1997; El-Keblawy and Al-Rawai 2006). Periodic collections from wild populations indicate a fifteen day maturation interval alters seed dormancy characteristics of *Abutilon theophrasti* (Cardina and Sparrow 1997), a thirteen day collection interval affects seedling emergence of *Geranium carolinianum* (Roach 1986).

The degree to which seed germination behavior is influenced by the maternal plant environment varies among genotypes (Sawhney and Naylor 1979; Alexander and Wulff 1985; Meyer and Allen 1999a). Variation in sensitivity to the maturation environment among individual plants suggests the potential for evolution by natural selection (Schmitt et al. 1992). Maturation environment effects on seed germination are adaptive forms of transgenerational phenotypic plasticity if the maturation environment factor that elicits the response provides information about the environment that the progeny will encounter (Donohue and Schmitt 1998; Mousseau and Fox 1998). For example, spectral composition (in particular red to far red ratios) can indicate the
competitive environment offspring may experience and accordingly, seed germination behavior is influenced by changes in the light spectrum during maturation (Donohue and Schmitt 1998).

1.5 Seedling emergence models

Real-time knowledge of weed seedling emergence patterns can facilitate optimal scheduling of weed control practices (Forcella 1998). For species that exhibit physiological seed dormancy (Baskin and Baskin 2004), cumulative percent seedling emergence can be predicted as a function of time (reviewed in Forcella et al. 2000; Grundy and Mead 2000). Seedling emergence is a consequence of three successive processes: seed dormancy alleviation, radicle elongation (dormancy termination), and pre-emergence seedling elongation. Each component of the seedling emergence process proceeds in response to the soil environment at different rates. Seedling emergence models account for the components of emergence by one of two ways: 1) components are separated and modeled independently (mechanistic models), 2) components are combined and observed seedling emergence is modeled (empirical models). The developmental procedures for mechanistic and empirical models differ, and there are benefits and drawbacks associated with each approach.
1.5.1 Mechanistic models

Mechanistic seedling emergence development initiates by measuring rates of dormancy alleviation, dormancy termination and seedling growth over a range of controlled conditions. Then the soil environment at a site of interest is monitored. Based on rates determined under controlled conditions; rates of dormancy alleviation, dormancy termination and seedling emergence are projected for the site. Projected rates are integrated and to provide the probability of emergence at a particular time (Benech-Arnold and Sánchez 1995; Vleeshouwers 1997; Vleeshouwers and Kropff 2000; Batlla and Benech-Arnold 2003).

Since mechanistic seedling emergence models are founded on the ecophysiological basis for seedling emergence, they can accurately forecast seedling emergence in a variety of environments, provided the population response to the environment is the same as the population used for model development (Forcella et al. 2000; Grundy 2003). Furthermore, by projecting dormancy alleviation, mechanistic models indicate when seedling emergence might occur if dormancy is terminated. This information is useful for scheduling agricultural operations that disturb the soil and terminate dormancy (Grundy 2003). But, the extensive development procedure for mechanistic seedling emergence models is a drawback. All seedling emergence models are limited by the peculiarities of the seed population used for development (Forcella et al. 2000). Diversity among populations (Brainard et al. 2006) and changes over time
(Kremer and Lotz 1998) require seedling emergence models to be calibrated and updated. With such an elaborate procedure for development, mechanistic model modification is difficult.

1.5.2 Empirical models

Empirical seedling emergence models project seedling emergence based on observations of emergence during previous years. Empirical emergence models are classified according to how time is measured: calendar time (Stoller and Wax 1973; Ogg and Dawson 1984; Egley and Williams 1991; Buhler and Owen 1997; Hartzler et al. 1999), thermal time (Donald 2000; Myers et al. 2004; Hacault and Van Acker 2006), and hydrothermal time (Roman et al. 2000; Ekeleme et al. 2005; Leguizamón et al. 2005; Masin et al. 2005). Since seedling emergence is driven primarily by soil temperature and moisture (Grundy and Mead 2000), calendar time models are inaccurate during years characterized by atypical weather. Thermal time and hydrothermal time incorporate the soil environment and account for abnormal years.

Thermal time measures a calendar day as a growing degree day (GDD):

\[
\text{GDD} = \left(\frac{T_{\text{max}} + T_{\text{min}}}{2}\right) - T_b
\]

where \( T_{\text{max}} \) = daily maximum temperature, \( T_{\text{min}} \) = daily minimum temperature, and \( T_b \) = is the temperature below which seedling emergence will not occur. Growing degree days accumulate to provide thermal time. The base temperature \( (T_b) \) for seedling emergence is
determined either by controlled experiments (Leguizamón et al. 2005) or by iterating a set of temperatures in Equation 2 until there is maximal fit between thermal time and seedling emergence (Ekeleme et al. 2004).

Similar to thermal time, hydrothermal time measures a calendar day as a hydrothermal day (HTD):

\[
HTD = n \times GDD
\]

where \( n = 0 \) when \( \Psi_{si} \leq \Psi_b \), \( n = 1 \) when \( \Psi_{si} > \Psi_b \), \( GDD = \) growing degree day ([2]), \( \Psi_b \) is the water potential below which seedling emergence will not occur, and \( \Psi_{si} \) is the average daily water potential (Roman et al. 2000). Hydrothermal days accumulate to provide hydrothermal time. The base water potential for seedling emergence (\( \Psi_b \)) is determined according to procedures described for the base temperature (\( T_b \)).

Compared to mechanistic seedling emergence models, the development procedures for empirical seedling emergence models are simpler. This approach eases corrections for inherently different emergence patterns (Leblanc et al. 2004). But, since empirical emergence model projections are based on observed emergence, the dormancy status of the seed population cannot be forecasted.

1.5.3. Measurement of the soil environment

Direct observations of soil temperatures and water potentials frequently enough to capture soil microclimates over prolonged periods are impractical. A more feasible approach projects soil environments from weather data and knowledge of soil physical properties (Flerchinger and Saxton 1989). Soil environment models characterize soil
temperature and hydrology in vertical, one-dimensional soil profiles by integrating equations of soil physical processes (Flerchinger and Saxton 1989). The soil surface is the boundary in which radiant energy and moisture enter the soil system.

Soil surface temperature is largely due to incident solar radiation (Spokas and Forcella 2006). The amount and absorption of solar radiation at the soil surface depends on geographic location, time of year and cloud cover (Jury and Horton 2004; Spokas and Forcella 2006). The soil surface either stores radiant energy as heat or passes energy through the soil profile (Campbell 1977). Soil environment models section the soil profile into discrete nodes. Energy transfer through the soil profile is described by sequential node movement. Capacity for energy storage (heat capacity) and transmittance (thermal conductivity) is related to soil moisture and soil physical properties such as soil texture, bulk density and organic matter (Jury and Horton 2004).

Precipitation supplies the soil profile with water. Gravity-driven, downward water flux is controlled by soil matric potential and hydraulic conductivity, both characteristic of soil texture, bulk density and organic matter (Jury and Horton 2004). Upward water movement results from evaporation at the soil surface, which is influenced by atmospheric conditions and soil hydraulic conductivity (Jury and Horton 2004). As indicated above, seed germination and emergence is determined by soil water potential, which is determined from soil water content and soil texture. Initiation of soil environment models require geographic location, time of year, soil physical properties and estimates of initial soil moisture. From this point, models function with daily minimum and maximum temperature, and precipitation records.
1.6. Motivation for research

Late-season emergence contributes to *A. trifida* management difficulties and is a unique feature of agricultural populations in the eastern U.S. Corn Belt (Sprague et al. 2004). With this research project, I wanted to understand the causes of late-season emergence. My approach to this research was to study *A. trifida* emergence biology and ecology with consideration for applied aspects of potential findings.

Because of the importance of seed dormancy in seedling emergence timing (Benech-Arnold et al. 2000), I determined how seed dormancy contributes to late-season emergence. Prior to researching the influence of seed dormancy on seedling emergence timing, I clarified inconsistent and peculiar findings in the literature regarding dormancy alleviation and dormancy termination conditions (Stoller and Wax 1974; Ballard et al. 1996). Furthermore, Davis (1930) indicated *A. trifida* seed dormancy loss in controlled conditions involved the loss of embryo and coat-imposed dormancy. I wanted to understand how these dormancy mechanisms operate in natural conditions.

Once dormancy alleviation and termination conditions were identified and dormancy loss in natural conditions was better understood, I determined which dormancy mechanism, embryo or coat-imposed, primarily contributes to seedling emergence timing. Based on the precedent set by previous researchers who compared weedy and natural populations (Harris et al. 1998), I compared embryo and dispersal unit dormancy loss between *A. trifida* populations from agricultural and ruderal habitats.
Early results confirmed *A. trifida* seed dormancy can be classified as physiological (Baskin and Baskin 2004). Seedling emergence patterns of weeds that exhibit physiological seed dormancy have been modeled based on hydrothermal time (Forcella 1998). Therefore, I created a hydrothermal time model to project *A. trifida* seedling emergence in agricultural fields.

Finally, I wanted to better understand the influence of the maternal plant on seedling emergence. *A. trifida* dispersal units exhibit high degrees of genetic polymorphism (Sako et al. 2001) and Venable and Brown (1988) proposed smaller dispersal units are expected to exhibit delayed emergence due to a coevolutionary syndrome between seed size and seed bank persistence. Furthermore, *A. trifida* dispersal units mature asynchronously in a changing environment (Harrison et al. 2001) that can influence seed dormancy (Gutterman 2000). An experiment was conducted to test the hypothesis of Venable and Brown (1988) among *A. trifida* individuals and to test the hypothesis seed maturation time influences seedling emergence timing.
CHAPTER 2

PRIMARY SEED DORMANCY IN AMBROSIA TRIFIDA

2.1 Introduction

*Ambrosia trifida* (Asteraceae) is a summer annual, cropland weed in the eastern two-thirds of North America (Bassett and Crompton 1982). Unlike typical annual weeds which produce seeds capable of great longevity in the soil (Baker 1974), *A. trifida* seeds are relatively short-lived (Davis et al. 2005; Harrison et al. 2007). *A. trifida* populations remain in agricultural fields because of well-timed seedling emergence (Sprague et al. 2004) which occurs following a reduction in primary seed dormancy (Davis 1930). Knowledge of *A. trifida* primary seed dormancy loss in an ecological context will clarify a critical portion of this weed’s life cycle.

In general, dormancy is alleviated over time by a combination of temperature and moisture conditions (Benech-Arnold et al. 2000). When dormancy is alleviated, the temperature range in which radicle elongation can occur widens. Once dormancy is sufficiently low, stimuli including fluctuating temperature, light, and nitrate terminate
dormancy (Vleeshouwers et al. 1995). The environmental conditions that influence dormancy vary over time and space and therefore, dormancy alleviation and termination requirements indicate when and where dormancy reduction occurs (Benech-Arnold and Sánchez 1995).

During the winter, *A. trifida* dispersal units can occur in either the aerial seed bank where cold dry conditions are common, or the soil seed bank where cold moist conditions are frequent. Previous researchers report inconsistent findings regarding the potential for dormancy loss in the two seed banks. Ballard et al. (1996) compared conditions for *A. trifida* dormancy alleviation and found that only cold-moist environments induced dormancy loss; warm-dry environments were not effective. But, Davis (1930) and Stoller and Wax (1974) reported dormancy reductions following prolonged, dry storage at ambient laboratory conditions. Ballard (1996) may not have detected the promotional effects of dry storage because of the duration of the study (120 days). Furthermore, the prolonged time required for dormancy alleviation in dry condition may be inconsequential if seed viability is not maintained (Murdoch and Ellis 2000).

Dormancy terminating factors such as light prevent germination at deep burial depths (Ghersa et al. 1997). *A. trifida* seedlings can emerge from up to 16 cm (Abul-Fatih and Bazzaz 1979b) and *A. trifida* dormancy termination is generally considered independent of light. But, Stoller and Wax (1974) found that a portion of *A. trifida* dispersal units responded to light. Considering the ecological significance of a light requirement for dormancy termination, the influence of light on *A. trifida* dormancy termination needs to be studied.
In addition to knowledge of dormancy alleviation and termination requirements, *A. trifida* over-wintering can be better understood by evaluating the role of dormancy mechanisms under natural conditions. In general, dormancy mechanisms are identified according to the location of the germination constraint (Bewley 1997; Foley 2001). Coat-imposed dormancy mechanisms inhibit radicle elongation through the embryo-covering structures. Seeds with coat-imposed dormancy mechanisms contain embryos that germinate upon removal of covering structures. Embryo dormancy mechanisms inhibit radicle elongation internally, and seeds with embryo dormancy mechanisms contain embryos that do not elongate when covering structures are removed. Furthermore, a seed can have a combination of embryo and coat-imposed dormancy mechanisms (Ellery and Chapman 2000; Flintham 2000; Garvin and Meyer 2003). *A. trifida* seeds are disseminated within dispersal units consisting of an embryo and a series of embryo covering structures (seed coat, pericarp, involucre) (Davis 1930). Dormancy is a consequence of the embryo (embryo dormancy) and the embryo-covering structures (coat-imposed dormancy) (Davis 1930).

Two experiments were conducted to better understand the ecology of *A. trifida* primary seed dormancy better. The objective of the first experiment was to determine the effects of dormancy alleviation and termination treatments on dispersal unit dormancy and viability. Dormancy alleviation treatments continued for an extended period of time to allow for the detection of all putative effects. The results of this experiment allowed for the identification of conditions in the natural environment conducive to dormancy reduction and dispersal unit decay. The objective of the second experiment was to
determine embryo and coat-imposed dormancy alleviation under natural conditions and to better understand the ecological significance of embryo and coat-imposed dormancy mechanisms in *A. trifida*.

### 2.2 Materials and Methods

**Experiment 1: Artificial dormancy alleviation**

**Plant material**

*A. trifida* seed-bearing inflorescences were harvested from the Ohio State University Waterman Research Farm and Laboratory in Columbus, OH (Columbus, OH 39°59’ N, 83°01’ W) on December 8, 2003. Following one week of drying in an unheated greenhouse, plant material was mechanically threshed to separate dispersal units from inflorescence structures. Chaff and hollow dispersal units were removed with forced air and dispersal units were stored in an unheated greenhouse for less than one month. Shortly after harvest, the viability of three samples of 50 dispersal units was determined by tetrazolium assay. Viability samples were averaged and are hereafter referred to as “initial viability”. Tetrazolium assays involved soaking freshly dissected embryos for 1 hr at 34 °C in a 1.0 % (v/v) aqueous solution of 2,3,5-triphenyl-tetrazolium chloride, then visually examining the embryo for red staining (Peters 2000).

**Dormancy alleviation and termination treatments**

A total of eight treatments were created by a factorial combination of four dormancy alleviation environments and two dormancy termination environments. Each treatment was replicated three times. Dormancy alleviation environments consisted of
four temperature-moisture conditions: cold-hydrated, cold-dry, warm-hydrated, and warm-dry. Cold (3 °C) and warm (20 °C) conditions were established within temperature-controlled chambers. Inside the chambers, hydrated and dry conditions were created within 0.5 L plastic pots filled with soil (fine, mixed, mesic Typic Argiaquolls) collected from the Ohio State University Waterman Research Farm and Laboratory. Preliminary experiments indicated field soil inhibited fungal attack on dispersal unit surfaces. Pots for hydrated and dry conditions were randomly arranged above a water reservoir. Constant hydration in the appropriate pots was provided by fabric wicks extending into the water reservoir. Buried in each pot was one fiberglass mesh (0.8 mm²) packet (8 X 8 cm) containing 50 A. trifida dispersal units. Packets were removed from dormancy alleviation environments following 0, 21, 42, 63, 54, 112, 154, 231, and 273 days.

Dormancy termination environments (light and dark) were created with plastic boxes (11 X 11 X 3.5 cm) lined with a moistened blotter. Packet contents were placed within plastic boxes which were then sealed with Parafilm and either wrapped in three sheets of aluminum foil or left uncovered. Boxes were placed in a germination chamber set to 20 °C, and continuous light (30 μmol m⁻² s⁻¹) from cool white fluorescent bulbs. Mesh packets destined for dark dormancy termination treatments were handled in darkness immediately following recovery from dormancy alleviation treatments.

Following 14 days of exposure to dormancy termination treatments, dispersal units were inspected and germination was counted as visible radicle protrusion. The viability of dispersal units that did not complete germination was determined by slicing
along the longitudinal axis and assessing embryo integrity with forceps. Firm, undamaged embryos indicated viable, dormant dispersal units. Following the 273-day dormancy alleviation interval, the viability of dormant dispersal units was further assessed by tetrazolium assay according to procedures described above. Viability following the 273-day dormancy alleviation interval is hereafter referred to as “final viability”.

Data analysis

The effects of the eight treatments on dormancy were assessed by examining average percent germination over time. Treatment effects on seed viability were determined with a generalized linear mixed model. Seed viability in response to treatments over time was modeled as a binary response variate with binomial error distribution using the logit-link function (Schabenberger and Pierce 2002). An F-test was calculated on the basis of the Wald statistic and means separated with pairwise t-test (\( \alpha = 0.05 \)). Parameter estimates were back transformed with the following equation:

\[
V_a = 100 \left( \frac{e^x}{1 + e^x} \right) \tag{1}
\]

where \( x \) is the logit estimate from the model, and \( V_a \) is the approximate percent viable seeds after back transformation.
Experiment 2: Dormancy alleviation under natural conditions

Plant material

Dispersal units were harvested from the Ohio State University Waterman Research Farm and Laboratory in Columbus, OH on October 17, 2003 and October 5, 2004. Collection and processing procedures were the same as above. Dispersal units were stored dry at room temperature for approximately two months.

Dormancy alleviation

Fiberglass mesh (0.8 m²) packets (13 X 13 cm) containing 100 dispersal units each were buried 7 cm at the Waterman Research Farm on December 12, 2003 and December 17, 2004. Two data loggers (Onset Computer Corporation, Bourne, MA) were installed to record average daily soil temperature at 5 cm. In addition, dispersal units were planted in a nearby plot which was monitored for seedling emergence the following spring.

Three packets were unearthed and brought to the lab every seven to 14 days. When necessary, a portable heater was used to thaw the area directly above the desired packet. Soil heating occurred for approximately 15 minutes. Packet collection ceased once germination was detected in the field. From each packet, dispersal units were dissected to produce 15 each of the following: isolated embryos, embryos encased in pericarps (fruits), and embryos encased in pericarps and involucres (intact dispersal units). The experiment also included controls for each of the three dissection fractions, which were derived from dispersal units stored dry in the laboratory at ambient conditions.
Dormancies of the dispersal unit fractions were quantified as the percent of viable components that failed to germinate in a 14-day germination assay conducted at 20 °C; 12 hr photoperiod (30 μmol m$^{-2}$ s$^{-1}$). Germination was defined as visible elongation of the embryo axis. At the conclusion of each germination assay, dispersal units and fruits were sliced along the longitudinal axis to assess embryo viability. At each interval percent dormancy was averaged across packets and changes in dormancy over time compared with soil temperatures.

2.3 Results

Experiment 1: Artificial dormancy alleviation

The 3 °C dormancy alleviation treatment reduced dormancy of $A. trifida$ dispersal units (Figure 2.1). Dormancy alleviation at 3 °C was largely influenced by water as indicated by comparing the average final dormancies between 3 °C hydration environments: hydrated = 36 ± 4%; dry = 96 ± 1%. For dormancy alleviation at 20 °C, neither hydrated nor dry environments promoted dormancy loss.

When dormancy alleviation was effective, dormancy termination was sometimes influenced by the light environment (Figure 2.1). Following 273 days of dormancy alleviation in 3 °C-hydrated conditions, light reduced dormancy to 22 ± 6%, whereas dark dormancy termination reduced dormancy to 50 ± 4%. Furthermore, following 273 days of dormancy alleviation at 3 °C-dry, light reduced dormancy to 93 ± 2% and dark dormancy termination failed to promote dormancy loss.
All dormancy loss treatments reduced initial viability (Table 1.2). Following dormancy alleviation for 273 days, dispersal units from all treatments contained some embryos that were decayed and could not be tetrazolium assayed (Chee-Sanford et al. 2006). Intact dispersal units with highly degraded embryos were considered nonviable. Decay was most noticeable in 20 °C dormancy alleviation treatments.

Experiment 2: Dormancy alleviation in natural conditions

Prior to the completion of germination in the field, embryo and coat-imposed dormancy decreased in buried dispersal units (Figure 2.2, Figure 2.3). Initially, embryo dormancy was alleviated; then the restrictive natures of the pericarps and involucres decreased. During the time of dormancy reduction, soil temperatures fluctuated. In late-December to early-January, soil temperatures rose to approximately 10 °C. Then in mid-January, below freezing soil temperatures were recorded. The duration of subzero soils varied between years, and when it concluded, soil temperatures irregularly increased. The time at which radicle protrusion was detected in the field, soil temperatures ranged from 3 - 10 °C.

2.4 Discussion

For some summer annual species, dormancy alleviation can occur in multiple environments. For example, *Amaranthus tuberculatus* dormancy was alleviated in cold dry, cold wet, warm dry and warm wet conditions (Leon et al. 2006). Prior to this experiment, the number of environments that alleviated dormancy in *A. trifida* was not clearly understood. By conducting the dormancy alleviation treatment for 273 days, I
was able to detect dormancy alleviation in cold wet and dry conditions. This indicates that dormancy loss in the field can occur in the aerial and soil seed bank. Warm conditions did not alleviate dormancy which is consistent with previous findings for many summer annuals including *Panicum flexile* and *Heliotropium tenellum* (Baskin and Baskin 1988).

Associated with all dormancy alleviation environments was reduced seed viability. Similarly, Burgess et al. (2002) found that cold-moist environments promoted germination and decreased viability of *Uniola paniculata*. Cold-moist storage decreased viability and promoted germination while cold-dry storage only reduced viability of *Carices* spp. (Budelsky and Galatowitsch 1999). As a result of decreased seed viability, dormancy alleviation treatments that operate on prolonged time frames are of little ecological consequence. For *A. trifida*, the significance of dormancy alleviation in cold dry conditions is further reduced because constant cold temperatures never occur in the natural environment and the subsequent increased temperatures further reduce viability.

Low viability for the 20 °C-dry alleviation environment may be an artifact of the treatment design. The water reservoir within the temperature-controlled chamber may have created a humid environment which led to partial hydration of dispersal units. In general, a metabolic imbalance within partially hydrated seeds damages cells and leads to seed death (Vertucci and Farrant 1995). “Accelerated aging” (Delouche and Baskin 1973) in this experiment was unintended but indicated the potential for dispersal unit demise in humid drought. In Ohio, daily average soil temperature at 5 cm in midsummer
is approximately 25 °C. According to this experiment, summer soils are stressful environments for dispersal units and may account for the seed bank fraction that expires by means other than seedling emergence (Abul-Fatih and Bazzaz 1979b; Harrison et al. 2007).

Consistent with (Stoller and Wax 1974), this experiment indicated a light requirement for *A. trifida* dormancy termination. Light requirements for seed populations are often not uniform for all seeds within a population are responsive to light (Farmer 1978; Grime et al. 1981; Baskin and Baskin 1988; Bloom et al. 1990). But there are species such as *Diaspensia lapponica* (Densmore 1997) and *Sisymbrium officinale* (Hillhorst 1997) that absolutely require light for dormancy termination. Sources of variation for light requirements within a seed population are poorly understood. Light requirements for dormancy termination can serve to prevent radicle protrusion when seeds are deeply buried (Pons 2000). Within the soil profile, smaller *A. trifida* dispersal units are more likely to remain dormant than larger dispersal units (Harrison et al. 2007). Combined, these results suggest smaller dispersal units require light for dormancy termination, but explicit tests are needed to confirm this hypothesis.

*A. trifida* dormancy alleviation in natural conditions involved the sequential reduction of embryo- and coat-imposed dormancy. Embryo dormancy decreased steadily over the course of winter. According to our understanding of seed dormancy (Benech-Arnold et al. 2000); as embryo dormancy decreased, the temperature range in which embryo germination could have proceeded increased. Therefore, increased soil temperatures during early January potentially were within the embryo’s germination
permissive range. During this time, radicle protrusion was prevented by the embryo-covering structures.

A similar mechanism for coat-imposed dormancy has been found in seeds of *Arctotheca calendula* is a consequence of the embryo and embryo-covering structures (Ellery and Chapman 2000). *A. calendula* embryo dormancy undergoes cycles with seasons favorable and unfavorable for seedling emergence. But, at a time not conducive to seedling establishment, *A. calendula* seeds contain non-dormant embryos. During this unfavorable time, interruptions of favorable conditions occur (referred to as “false breaks”) (Ellery and Chapman 2000). Dormancy termination of *A. calendula* is prevented during false breaks by the embryo-covering structures. Test with additional species that exhibit embryo and coat-imposed dormancy (Flintham 2000; Garvin and Meyer 2003) are needed to further clarify the ecological role of coat-imposed in seeds with embryo dormancy.

The particular covering structure primarily responsible for *A. trifida* coat-imposed dormancy is not known but similarities in responses between embryos covered with the pericarp only compared to pericarp plus involucre suggest that the involucre plays a minor role in coat-imposed dormancy (Figure 2.2 and 2.3). Coat-imposed dormancy of *Xanthium strumarium*, a close relative of *A. trifida*, is due to testa (Bewley and Black 1994).
Figure 2.1. The effectiveness of eight dormancy loss treatments. Each figure presents a dormancy alleviation environment. Within figures are dormancy termination environments (open circle = light, filled circle = dark). Date points are means of three replicates with standard errors.
<table>
<thead>
<tr>
<th>Sample</th>
<th>Viability (%)</th>
<th>Note</th>
</tr>
</thead>
<tbody>
<tr>
<td>Initial</td>
<td>2.123 a</td>
<td>(89)</td>
</tr>
<tr>
<td>3 °C-Dry, Dark</td>
<td>1.562 b</td>
<td>(83)</td>
</tr>
<tr>
<td>3 °C-Hydrated, Light</td>
<td>1.386 bc</td>
<td>(80)</td>
</tr>
<tr>
<td>3 °C-Hydrated, Dark</td>
<td>1.153 bc</td>
<td>(76)</td>
</tr>
<tr>
<td>3 °C-Dry, Light</td>
<td>1.081 c</td>
<td>(75)</td>
</tr>
<tr>
<td>20 °C-Hydrated, Light</td>
<td>0.518 d</td>
<td>(63)</td>
</tr>
<tr>
<td>20 °C-Hydrated Dark</td>
<td>0.490 d</td>
<td>(62)</td>
</tr>
<tr>
<td>20 °C-Dry, Dark</td>
<td>-2.057 e</td>
<td>(11)</td>
</tr>
<tr>
<td>20 °C-Dry, Light</td>
<td>-2.442 e</td>
<td>(8)</td>
</tr>
</tbody>
</table>

Table 2.1  Parameter estimates from a generalized linear model for the effects of time and environment on probability of dispersal unit viability. Initial viability was determined at harvest and dormancy loss treatment viability was determined at experiment conclusion.

* Parameter estimates are on the logit scale. Means followed by same lower case letter are not significantly different according to pairwise t-test (α = 0.05). Values in parentheses indicate approximate mean values from back transformation with Equation [1].
Figure 2.2. **A** Dormancy loss of dispersal unit fractions during 2003 to 2004. Closed symbols represent fractions derived from dispersal units stored under natural conditions. Data points are means of three packets with standard errors. Open diamonds the pooled results from components derived from dispersal units stored in the laboratory. Radicle protrusion was detected in the field on 3/11 and seedling emergence on 3/27. **B** Daily average soil temperature at 5 cm.
Figure 2.3.  A Dormancy loss of dispersal unit fractions during 2004 to 2005. Closed symbols represent fractions derived from dispersal units stored under natural conditions. Data points are means of three packets with standard errors. Open diamonds the pooled results from components derived from dispersal units stored in the laboratory. Radicle protrusion was detected in the field on 3/19 and seedling emergence on 3/29.  B Daily average soil temperature at 5 cm.
CHAPTER 3

THE ROLE OF SEED DORMANCY IN SEEDLING EMERGENCE TIMING OF
AMBROSIA TRIFIDA

3.1 Introduction

Giant ragweed (*Ambrosia trifida*) is a North American native, summer annual that has become one of the most problematic weeds in the eastern U.S. Corn Belt (Gibson et al. 2005). It is extremely competitive in row-crop agriculture. Season-long interference of one giant ragweed plant m$^{-2}$ can reduce soybean yield by over 75% (Webster et al. 1994), and a giant ragweed density of 1.7 plants per 10 m$^{2}$ reduces corn yield by 18% (Harrison et al. 2001). Furthermore, reports of giant ragweed populations resistant to glyphosate and ALS-inhibiting herbicides create concern for future management options (Heap 2007). To improve the efficacy of current control methods, a better understanding of giant ragweed biology is required; especially the attributes that render it difficult to control.
Weedy attributes for other species have been characterized by comparisons between agricultural and ruderal/natural populations (Harris et al. 1998; Leiss and Muller-Scharer 2001; Leon et al. 2006). In addition to agricultural fields, giant ragweed is found along forest borders, creek beds, railroad embankments and in old fields (Bassett and Crompton 1982). As a consequence of natural selection, seeds collected from non-agricultural habitats exhibit seedling emergence patterns that are different from seeds collected from agricultural habitats (Hartnett et al. 1987). In a common emergence environment, non-agricultural populations initiate and conclude emergence in early spring, whereas agricultural populations initiate emergence in early spring and conclude emergence in mid-summer (Sprague et al. 2004). Each emergence pattern is advantageous to the environment of origin. In non-agricultural environments, early-season seedlings acquire resources before competing summer annual and perennial species emerge (Abul-Fatih and Bazzaz 1979a). In agricultural environments, late-season seedlings evade early-season weed control. Since late-season seedling emergence contributes to the success of giant ragweed in agricultural fields, it is important to understand the causal factors.

In general, seedling emergence timing is influenced by seed dormancy. Seed dormancy is an internal condition of the seed that defines the environmental conditions in which a seed is able to complete germination (Finch-Savage and Leubner-Metzger 2006). As seed dormancy decreases, the temperature range in which seed germination can occur expands (Vleeshouwers et al. 1995). Germination and emergence in the field occurs when germination permissive and soil temperatures overlap (Benech-Arnold et al. 2000).
Giant ragweed seeds are dormant at dispersal (Davis 1930). Dormancy is alleviated naturally in seeds buried in soil over the winter and artificially by cold, moist storage (stratification) (previous chapter). The reproductive unit of giant ragweed is an achene (pappus absent) within a hardened involucral body (Barkley et al. 1986). The collective structure is referred to as a dispersal unit. The dispersal unit positions the embryo within a series of embryo-covering structures. Previous research indicated that giant ragweed seed dormancy is a consequence of inhibitory influences within the embryo (embryo dormancy) and embryo-covering structures (coat-imposed dormancy) (Davis 1930; previous chapter). To understand how these dormancy mechanisms contribute to late-season emergence, in this experiment I compared embryo and coat-imposed dormancy of seeds collected from agricultural and ruderal habitats.

3.2 Materials and Methods

Plant Material

Giant ragweed dispersal units were collected from eight agricultural populations and six ruderal populations in central Ohio during October of 2004 and 2005 (Table 3.1). The collection process involved clipping plant stems below seed-bearing inflorescences and transporting plant material in paper bags to an unheated greenhouse for drying. Following one week of drying, plant material was mechanically threshed to separate dispersal units from inflorescence structures. Chaff and hollow dispersal units were removed with forced air and dispersal units were stored dry at 0 °C. For each population, seedling emergence and seed dormancy was determined in the year of harvest.
Field emergence

On November 10, 2004 and November 4, 2005, artificial seed banks were established in a common environment at the Ohio State University Waterman Research Farm and Laboratory in Columbus, OH (Columbus, OH 39°59’ N, 83°01’ W). The site was clear of vegetation throughout the experiment. Soil at the site was a Kokomo silty clay loam (fine, mixed, mesic Typic Argiaquolls) and there was no history of giant ragweed in the area. Population seed banks were arranged in a completely randomized design with four replicates. To construct seed banks, sections of polyvinyl chloride pipe (30 cm diameter, 15 cm length) were buried flush with the soil surface. From within each pipe, 12.5 cm of soil was removed and blended with 500 dispersal units (Hartzler et al. 1999). The soil-seed mixture was then poured back into the pipe. Two data loggers (Onset Computer Corporation, Bourne, MA) recorded soil temperature at 5 cm every 15 minutes. Daily average temperature was calculated as one half the sum of minimum plus maximum.

Beginning March 28, 2004 and March 20, 2005, seedlings with fully expanded cotyledons were counted and removed by pulling every three to four days. The removal process caused minimal soil disturbance. Following the conclusion of emergence, observations were summed and expressed as cumulative percent of the total. Replicates were averaged and plotted as a function of time.
Dormancy loss treatments

Dormancy loss treatments consisted of stratification (cold, moist storage) followed by a germination assay and treatments were replicated four times. Dispersal units were stratified at 2 °C for eight intervals. For 2004, stratification intervals were: 0, 14, 28, 42, 63, 77, 91, and 112 days. For 2005, stratification intervals were: 0, 14, 28, 49, 70, 84, 98, and 112 days. Stratification was performed within insulated boxes (60 X 30 X 30 cm) stored inside low-temperature chambers. Stratification medium was one part sand, one part field soil. The stratification system allowed for stable thermal and hydro environments with minimum fungal attack on dispersal unit surfaces.

Following stratification intervals, 40 dispersal units from each treatment group were subject to a germination assay. Twenty of the dispersal units were left intact and 20 were dissected to extract the embryo. For each group (dispersal unit and embryo) dormancy was quantified as the absence of visible radicle elongation in fourteen-day germination assays conducted at 12 °C and 20 °C, continuous light (30 μmol m⁻² s⁻¹). Embryos destined for 12 °C germination assays were obtained from dispersal units dissected in a room at approximately 4 °C. Embryos for 20 °C germination assays were taken from dispersal units at room temperature. At the conclusion of germination assays, embryos and dispersal units that did not exhibit radicle elongation were collected. Dispersal units were sliced along the longitudinal axis to expose the embryo. Viability of remaining dispersal units and embryos was determined by applying pressure to the embryo. Firm, nondamaged embryos indicated dormancy. Dormancy was expressed as a percent of total viable (the number of seedlings + the number of dormant). For 2004, the
dormancy loss treatment at 20 °C was conducted prior to the dormancy loss treatment at 12 °C. For 2005, the dormancy loss temperature treatments were conducted simultaneously.

For each population, embryo and coat-imposed dormancy loss was assessed with two measurements: final dormancy, and stratification time to 50% dormancy loss. Final dormancy was the percentage of dormant embryos or dispersal units for the 112 day stratification interval. Stratification time to 50% dormancy loss was determined with a four parameter sigmoidal model fit (Sigma Plot, version 10.0) to average percent dormancy as a function of stratification time. The four parameter sigmoidal model follows:

\[
\text{Dormancy (\%) } = 100 - \left( y_0 + \frac{A}{1 + \exp\left(-\frac{\text{time} - x_0}{b}\right)} \right) 
\]

where \(y_0\) = the minimum dormancy, \(A\) = the difference between the minimum and maximum dormancy, \(\text{time}\) = stratification time in days, \(x_0\) = stratification time at 50% of the distance between minimum and maximum dormancy (stratification time to 50% dormancy loss), and \(b\) = the stratification time interval between 75% and 25% of the dormancy function.

For analysis, years were combined. Final dormancy and stratification time to 50% dormancy loss were analyzed with generalized linear mixed models with parameters estimated by restricted maximum likelihood in SAS version 9.1 (Littell et al. 2006). Habitat was treated as a fixed effect. For analysis of final percent dormancy, year and population were random effects. For analysis of stratification time to 50% dormancy
loss, year was the random effect. Generalized linear models allow for modeling of non-
normal data by specification of the probability distribution from which the response
function originates. Furthermore, generalized linear models allow for linear modeling of
range-restricted data by use of a link function to transform response means onto a scale in
which covariates are additive (Schabenberger and Pierce 2002). Final percent dormancy
was modeled with a binomial distribution and a logit-link function. Stratification time to
50 % dormancy loss was modeled with a Poisson distribution with a log-link function.
Previous researchers have found these distributions and link functions appropriate for
analysis of similar data (Andersson et al. 2002; Willenborg et al. 2005). Agricultural and
ruderal habitats were declared significantly different according to the F-test calculated
based on Wald statistics ($\alpha = 0.05$). Parameter estimates for final percent dormancy on
the logit scale were back-transformed according to:

$$V_a = 100 \left( \frac{e^x}{1 + e^x} \right) \quad [2]$$

where $x$ is the logit estimate from the model, and $V_a$ is the approximate percent viable
seed after back transformation. Parameter estimates for time to 50 % dormancy loss on
the log scale were back transformed according to:

$$ST_{50a} = e^x \quad [3]$$

where $x$ is the log estimate from the model, and $ST_{50a}$ is the approximate stratification
time to 50 % dormancy loss after back transformation.
3.3 Results and discussion

For populations from ruderal environments, seedling emergence reached greater than 95% before May 1 (Figure 3.1A). For populations from agricultural environments, seedling emergence occurred more gradually from April to July. Similar emergence patterns were observed in 2005 and 2006. As seedling emergence in agricultural populations continued, soil temperatures gradually increased (Figure 3.1B). Therefore, if seed dormancy contributed to late-season emergence, differences between habitats were expected to be greater when dormancy was quantified at colder temperatures.

Variation among populations was greater for the agricultural habitat compared to the ruderal habitat. Increased variation among agricultural populations was probably due to the nature of selection in each habitat. Agricultural weed control selects for late-season emergence. Selection for late-season emergence is limited by the competitive disadvantage seedlings have in crop canopies (Harrison et al. 2001). In ruderal environments, competition from coexisting summer annual and perennial species selects for early-season emergence (Abul-Fatih and Bazzaz 1979b). Selection for early-season emergence is limited by low temperatures characteristic of early spring. I propose that the selection pressures and limits were more uniform across time and location for ruderal environments as compared to agricultural environments.

Dispersal units from ruderal habitats were less dormant than dispersal units from agricultural habitats (Table 3.2). The dormancy difference between habitats was larger when dormancy was quantified at the colder temperature. This confirms that dispersal
unit dormancy and its interaction with soil temperature contributed to late-season emergence in agricultural populations.

Increased dormancy at colder temperatures was because of increased embryo dormancy (Table 3.3). This conclusion is supported by three observations. First, the habitat difference for embryo dormancy (22 % at 12 °C) was nearly the same as the habitat difference for dispersal unit dormancy (26 % at 12 °C). Second, ruderal embryos displayed little difference between dormancy assay temperatures (10 % dormant at 12 °C; 5 % dormant at 20 °C) while in contrast agricultural embryos were inhibited by the reduced temperature (32 % dormant at 12 °C; 12 % dormant at 20 °C). Third, time to 50 % dormancy loss indicated no difference among habitats in all but one comparison, embryo dormancy loss at 12 °C. Overall results indicate increased embryo dormancy contributes to late-season emergence in agricultural populations compared to ruderal populations. In particular, the inability of the embryo to germinate at low temperatures contributes to prolonged patterns of seedling emergence.

Adaptive seedling emergence patterns contribute to the success of several weed species including *Ranunculus repens* (Harris et al. 1998), *Amaranthus tuberculatus* (Leon et al. 2006), and *Xanthium strumarium* (Blais and Lechowicz 1989). Mortimer (1997) attributed altered emergence patterns to selection for increased dormancy and reduced response to cold stratification. Leon et al. (2006) described a heat-shock protein unique to dormant biotypes of *Amaranthus tuberculatus* and concluded differences in seed dormancy regulatory mechanisms. In this experiment, I found that increased embryo dormancy contributes to late-season emergence in agricultural populations compared to
ruderal populations. In particular, the inability of the embryo to germinate at low temperatures contributes to prolonged patterns of seedling emergence.

The physiological basis for *A. trifida* embryo dormancy is not known. But embryo dormancy has been studied in other species including *Helianthus annuus* (Asteraceae) (Le Page-Degivry and Garello 1992). In general, the preservation of embryo dormancy is associated with the *de novo* synthesis of the growth inhibitor, abscisic acid (for review see Foley 2001). Furthermore, associated with dormancy alleviation is a decreased capacity for abscisic acid synthesis (Bianco et al. 1997; Foley 2001). Yoshioka et al. (2003) found that abscisic acid is part of the temperature-sensory mechanism in winter annual seeds. For 17 out of 19 winter annual species, germination permissive temperatures widen following application of fluridone, an abscisic acid inhibitor. Therefore, abscisic acid may have a role in *A. trifida* embryo dormancy and its interaction with soil temperature.
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<th>Latitude</th>
<th>Longitude</th>
<th>Description</th>
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<td>39° 53’ N</td>
<td>83° 33’ W</td>
<td>Corn field</td>
</tr>
<tr>
<td>2004</td>
<td>Agricultural</td>
<td>39° 51’ N</td>
<td>83° 40’ W</td>
<td>Corn field</td>
</tr>
<tr>
<td>2004</td>
<td>Agricultural</td>
<td>39° 50’ N</td>
<td>83° 25’ W</td>
<td>Corn field</td>
</tr>
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<td>2004</td>
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<td>39° 49’ N</td>
<td>83° 22’ W</td>
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</tr>
<tr>
<td>2004</td>
<td>Ruderal</td>
<td>39° 59’ N</td>
<td>83° 15’ W</td>
<td>Forest border</td>
</tr>
<tr>
<td>2004</td>
<td>Ruderal</td>
<td>39° 62’ N</td>
<td>83° 17’ W</td>
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</tr>
<tr>
<td>2004</td>
<td>Ruderal</td>
<td>39° 51’ N</td>
<td>83° 40’ W</td>
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<td>Agricultural</td>
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<td>Corn field</td>
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<tr>
<td>2005</td>
<td>Ruderal</td>
<td>39° 53’ N</td>
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<td>2005</td>
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<td>39° 51’ N</td>
<td>83° 11’ W</td>
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<td>2005</td>
<td>Ruderal</td>
<td>39° 51’ N</td>
<td>83° 40’ W</td>
<td>Railroad border</td>
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</tbody>
</table>

Table 3.1  Sites for *Ambrosia trifida* dispersal unit collections in 2004 and 2005.
Figure 3.1. **A** Seedling emergence of ruderal and agricultural populations during 2005 and 2006 in a common garden experiment. Each line represents a population. **B** Average daily soil temperature at 5 cm.
<table>
<thead>
<tr>
<th></th>
<th>Final dormancy (%)</th>
<th>Time to 50% dormancy loss (days)</th>
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</thead>
<tbody>
<tr>
<td></td>
<td>12 °C</td>
<td>20 °C</td>
</tr>
<tr>
<td>Agricultural</td>
<td>0.891 a (71)</td>
<td>0.420 a (60)</td>
</tr>
<tr>
<td>Ruderal</td>
<td>-0.205 b (45)</td>
<td>-0.225 b (44)</td>
</tr>
<tr>
<td>Difference</td>
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<td>(16)</td>
</tr>
</tbody>
</table>

Table 3.2 Generalized linear model analysis for final percent dormancy and stratification time to 50% dormancy loss for agricultural and ruderal dispersal units for 2005 and 2006.

* Parameter estimates for final dormancy are on the logit scale. Estimates within a column followed by the same lower case letter are not significantly different according to F-test calculated on the basis of Wald statistics (α = 0.05). Values in parentheses present approximate mean values on the original scale and were obtained by back transformation with Equation [2].

** Parameter estimates for time to 50% dormancy loss are on the log scale. Estimates within a column followed by the same lower case letter are not significantly different according to F-test calculated on the basis of Wald statistics (α = 0.05). Values in parentheses present approximate mean values on the original scale and were obtained by back transformation with Equation [3].

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### Table 3.3. Generalized linear model analysis for final percent dormancy and stratification time to 50% dormancy loss for agricultural and ruderal embryos for 2005 and 2006.

<table>
<thead>
<tr>
<th></th>
<th>Final dormancy (%)</th>
<th>Time to 50% dormancy loss (days)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>12 °C</td>
<td>20 °C</td>
</tr>
<tr>
<td>Agricultural</td>
<td>-0.739 a (32)</td>
<td>-1.996 a (12)</td>
</tr>
<tr>
<td>Ruderal</td>
<td>-2.201 b (10)</td>
<td>-2.933 b (5)</td>
</tr>
<tr>
<td>Difference</td>
<td>(22)</td>
<td>(7)</td>
</tr>
</tbody>
</table>

* Parameter estimates for final dormancy are on the logit scale. Estimates within a column followed by the same lower case letter are not significantly different according to F-test calculated on the basis of Wald statistics ($\alpha = 0.05$). Values in parentheses present approximate mean values on the original scale and were obtained by back transformation with Equation [2].

** Parameter estimates for time to 50% dormancy loss are on the log scale. Estimates within a column followed by the same lower case letter are not significantly different according to F-test calculated on the basis of Wald statistics ($\alpha = 0.05$). Values in parentheses present approximate mean values on the original scale and were obtained by back transformation with Equation [3].
CHAPTER 4

A HYDROTHERMAL SEEDLING EMERGENCE MODEL FOR AMBROSIA TRIFIDA IN OHIO

4.1 Introduction

Real-time knowledge of weed seedling emergence patterns can facilitate scheduling of weed control practices (Forcella 1998). There are several approaches to modeling weed seedling emergence. The most straightforward is to anticipate emergence based on past observations (Stoller and Wax 1973; Ogg and Dawson 1984; Egley and Williams 1991; Buhler and Owen 1997; Hartzler et al. 1999). While relatively simple to devise, pure empirical emergence models can fail during years when atypical weather occurs during the normal emergence period (Grundy 2003). Another approach to emergence modeling is to quantify the components of seedling emergence (seed dormancy loss, seed germination and seedling growth) over a range of controlled conditions and extrapolate the results to field settings (Benech-Arnold and Sánchez 1995;
Vleeshouwers 1997; Vleeshouwers and Kropff 2000). Such mechanistic models account for the influence of the environment on seedling emergence but require extensive experimentation.

All seedling emergence models are limited by the inherent germination behaviors of the seed populations used for development (Forcella et al. 2000). Emergence patterns are known to vary among weed populations (Harris et al. 1998; Brainard et al. 2006) and can change in response to selection pressures (Clements et al. 2004). To account for diverse and plastic seedling emergence, models need to be developed for specific ecotypes and should be updated regularly. In addition, users need confidence that emergence models are responsive to unusual weather conditions. All of this is difficult to accomplish unless models combine the developmental simplicity of empirical models and the robustness of mechanistic models.

The soil conditions most influential on seedling emergence patterns are temperature and moisture (Grundy and Mead 2000). When the soil is adequately hydrated, the rate of seedling emergence is dependent on soil temperature. When the soil becomes too dry, the progression of seedling emergence is interrupted. A thermal time scale responsive to soil water potential, or hydrothermal time, accounts for the influence of the soil environment on the progression of seedling emergence (Finch-Savage and Phelps 1993; Forcella et al. 2000; Roman et al. 2000; Leguizamón et al. 2005). Thermal unit temperatures and hydric unit water potentials are based on the biological limitations of seedling emergence; therefore, hydrothermal time accumulates only when conditions are conducive to seedling emergence. But, the amount of data required for hydrothermal
calculations limits applicability (Myers et al. 2004). To simplify hydrothermal calculations, direct observations of the soil environment can be replaced with simulations based on readily available information (Forcella 1993; Ekeleme et al. 2005; Masin et al. 2005).

Researchers have formulated a hydrothermal seedling emergence model for giant ragweed using historical observations of seedling emergence (Forcella 1998). The current model does not accurately project giant ragweed seedling emergence in the eastern U.S. Corn Belt. Discrepancies are probably because of inherent emergence pattern variation among giant ragweed populations. In common garden experiments, Sprague et al. (2004) and Schutte et al. (2006) found emergence pattern differences between eastern and western U.S. Corn Belt populations as well as between agricultural and ruderal populations. Giant ragweed from the western Corn Belt and ruderal habitats exhibited synchronous seedling emergence in early spring. In contrast, giant ragweed from eastern Corn Belt agricultural fields displayed a prolonged period of seedling emergence that continued throughout the growing season. The contribution of within population diversity to population emergence patterns is unknown. Giant ragweed populations exhibit high levels of phenotypic diversity for dispersal unit morphology (Sako et al. 2001) and response to herbicide (Patzoldt and Tranel 2002).

The objectives of this research were to 1) develop a hydrothermal seedling emergence model for agricultural giant ragweed populations in Ohio, 2) validate the model, and 3) determine the contribution of individual plants to the population emergence pattern.
4.2 Materials and Methods

Emergence model development

*Field experiment*

I utilized observations of seedling emergence and simulated soil environments based on meteorological records, soil characteristics and geographic location to develop the giant ragweed emergence model. An experiment was conducted during 2001, 2002 and 2003 at the Western Branch Experiment Station of the Ohio Agricultural Research and Development Center near South Charleston, OH (39°52’ N, 83°40’ W; elevation 0.34 km). The study site was a fallow field sectioned into four replicates. The site had a history of corn and soybean production and giant ragweed infestation. The soil was a Crosby silt loam (fine, mixed, active, mesic Aeric Epiqualfs) with 15% sand, 65% silt, 20% clay, and 2.2% organic matter in the Ap horizon.

Quadrats were established at the beginning of each year and were maintained free of vegetation by hand weeding. Beginning March 1, giant ragweed seedlings in two 1-m² quadrats were counted and removed at weekly intervals. Seedling emergence was defined as full expansion of cotyledons, and seedlings were removed with minimal soil disturbance. At the end of each year, weekly seedling emergence observations were converted to cumulative percent emergence and averaged across four replicates.

*Hydrothermal time*

Soil microclimate at the 1 cm depth was simulated by the Soil Moisture and Temperature (SMT²) model, which can be downloaded from the worldwide web at [http://www.ars.usda.gov/mwa/ncsrl](http://www.ars.usda.gov/mwa/ncsrl) (Spokas et al. 2007). The SMT² model establishes a
one-dimensional vertical profile from the soil surface down to 1.8 m, sectioned into
discrete nodes to define microclimates at specific depths. Fluxes in and out of the system
are governed by atmospheric conditions at the soil surface. SMT\(^2\) simulates incident
solar radiation with Solar Calc, a model that estimates hourly solar radiation based on
latitude, longitude, and elevation of the field site, along with daily precipitation, and daily
minimum and maximum air temperatures (Spokas and Forcella 2006). To estimate soil
water potential, SMT\(^2\) requires data on soil texture and soil organic matter. A summary
of the total inputs for SMT\(^2\) include: latitude, longitude, elevation, daily precipitation,
daily minimum and maximum temperature, soil texture, and soil organic matter. For this
experiment, meteorological data for SMT\(^2\) were collected from a weather station located
approximately 0.5 km from the study site. On January 1 of each year, soil environment
simulations began with soil saturated conditions.

Simulated soil temperatures and water potentials were used to calculate
hydrothermal days:

\[
\text{Hydrothermal day} = \theta_H \times \theta_T
\]  

[1]

where \(\theta_H = 1\) when \(\psi > \psi_b\) otherwise \(\theta_H = 0\); and \(\theta_T = T - T_b\) when \(T > T_b\) otherwise \(\theta_T = 0\).

Daily average soil water potential is represented by \(\psi\), \(\psi_b\) is base water potential of
seedling emergence, \(T\) is daily average soil temperature and \(T_b\) is base temperature of
seedling emergence (Roman et al. 2000). Giant ragweed base temperature of emergence
\((T_b)\) was extrapolated from the literature as 2°C (Abul-Fatih and Bazzaz 1979b). To
determine the base water potential of emergence \((\psi_b)\) from the findings of Abul-Fatih and
Bazzaz (1979), I utilized their experiment in which giant ragweed seed germination was
measured along a gradient of soil water content. Soil water content was converted to soil water potential from curves characteristic for soil textures (Campbell 1977). Abul-Fatih and Bazzaz (1979) provided the soil type used in their experiments and texture was estimated from the soil textural triangle. It is important to note that the base water potential for seedling emergence was not the base water potential for seed germination.

Hydrothermal days were accumulated from March 1 to provide hydrothermal time ($\theta_{HT}$):

$$\theta_{HT} = \sum_{March \ i}^{i} \text{Hydrothermal day}$$  \[2\]

March 1 is currently considered the earliest time with potential for emergence. Typically emergence initiates during mid-to-late March.

*Modeling seedling emergence*

Cumulative percent emergence for each year was plotted as a function of calendar day using the following four parameter Weibull model:

$$Y = M \left[1 - \exp\left(-k \left(\theta_{HT} - z\right)^c\right)\right]$$  \[3\]

where $Y$ is the cumulative percent emergence, $M$ is the asymptote, $k$ is the rate of increase, $\theta_{HT}$ is hydrothermal time, $z$ is the lag phase and $c$ is a curve shape parameter (Brown and Mayer 1988). The Weibull model was fit to observed emergence values through an iterative process in which one or more of the following parameters was adjusted: asymptote ($M$), rate ($k$) lag phase ($z$) and curve shape ($c$), as well as the base water potential for seedling emergence ($\psi_b$). Model parameters and base water potentials were adjusted until projected seedling emergence resembled actual seedling emergence. Model fit was assessed by the coefficient of determination. The end-result was a single model that described seedling emergence for 2001, 2002 and 2003.
Emergence model validation

The seedling emergence model was validated at South Charleston, OH in 2005 and at Columbus, OH in 2006. The South Charleston site included tilled and no-tillage fields. The tilled field was chisel-plowed in the fall prior to planting and received two passes with a disk-cultivator-harrow during the spring. The Columbus site was a no-tillage field at the Ohio State University Waterman Agricultural and Natural Resources Laboratory (39°59’ N, 83°01’ W; elevation 0.24 km). Soil at the Columbus, OH site was a Kokomo silty clay loam (fine, mixed, mesic Typic Argiaquolls) with 18% sand, 41% silt, 41% clay, and 2.8% organic matter in the Ap horizon. At each site, precipitation as well as minimum and maximum temperature were recorded daily at an onsite weather station. Validation environments were divided into four blocks and within each block, giant ragweed seedlings were counted and removed from two permanent 1-m² quadrats at weekly intervals. Seedling emergence observations were converted to cumulative percent of total emergence, averaged across replicates, and plotted as a function of calendar day.

Hydrothermal time was calculated with soil environments estimated by the SMT² model as previously described and used to project seedling emergence with the Weibull model ([3]). Projected emergence was superimposed on plots of actual seedling
emergence versus calendar day. The difference between predicted and actual seedling emergence values was assessed by the root mean square error (RMSE) calculated as follows:

\[
RMSE = \sqrt{\frac{\sum_{i=1}^{n} (x_i - y_i)^2}{n}}
\]

where \(x_i\) represents actual cumulative percent seedling emergence, \(y_i\) is predicted cumulative percent seedling emergence, and \(n\) is the number of observations (Mayer and Butler 1993). RMSE provides an indication of the typical difference between predicted and actual values in units of percent seedling emergence.

Seedling emergence of progeny from individual plants

To determine the contribution of individual plants to population emergence patterns, an experiment was conducted to identify the seedling emergence periods of progeny collected from individuals, hereafter referred to as half-sib families. In 2003, a giant ragweed population was established in a cornfield at the Columbus site. The field had a history of giant ragweed and was an old-field successional area for 19 years prior to 2003. On October 20, 2003, 25 half-sib families were collected. Individual plants used as seed sources were chosen by selecting giant ragweed individuals every 1.2 m along a 30-m transect through the center of the field. Half-sib families were stored in brown paper bags and kept in the laboratory at ambient conditions. From each half-sib family, 40 of the heaviest seeds without visible damage were divided into four samples of 10 seeds each and used in a field experiment was conducted at the Columbus site to determine emergence patterns among half-sib families. Treatments (half-sib families)
were arranged in a randomized complete block with four replicates. Half-sib family seed samples were planted within open-topped baskets (22 cm by 38 cm, 6 cm depth) constructed from fiberglass mesh (0.8 mm²). Twenty-five baskets aligned in a row formed a block. The experiment was installed on November 21, 2003.

The following spring, seedlings were counted and removed every three to five days. The area was maintained free of vegetation by hand weeding. The half-sib family seedling emergence period was characterized as the interval between median time of first emergence and median time of final emergence. The median was used rather than the average because the median best reflected the central tendency (Zar 1999). Time was quantified on a hydrothermal scale based on onsite meteorological observations entered into the SMT² model as described previously. The total number of seedlings was expressed as a percent of the number of seeds buried (10) and averaged across four replicates. Average percent emergence and emergence intervals were subjected to correlation analysis to determine the extent to which seedling number and emergence interval was related. Nonsignificant correlation coefficients (α = 0.05) indicated variable emergence intervals resulted from inherently different timing mechanisms and not differences from in the number of seedlings that emerged.
4.3 Results and Discussion

Seedling emergence model development

Giant ragweed seedling emergence patterns were similar in 2001, 2002 and 2003 (Figure 4.1). In each year, cumulative percent emergence increased rapidly during April, leveled off in May and increased again in June. This pattern of emergence is consistent with grower’s observations in Ohio of two giant ragweed seedling flushes during a season. According to the current understanding of seedling emergence, interruptions in the progress of cumulative percent emergence are because of suboptimal soil temperature and moisture conditions (Benech-Arnold et al. 2000). However, meteorological records indicate the period in which the rate of seedling emergence declined (May) was not subject to cold temperatures or reduced precipitation (Figure 4.2). Accordingly, hydrothermal time continued to accumulate during May while emergence showed a temporary lag before resuming at a slower rate (Figure 4.3).

A single four parameter Weibull model did not describe the biphasic pattern of emergence (data not shown); therefore, I divided the emergence season and modeled cumulative percent emergence with two successive Weibull functions (Table 4.1). The first described emergence from 0 to 600 HTT; the second described emergence from 600 HTT to conclusion. The soil environment was simulated at the 1-cm depth but giant ragweed seedlings can emerge from depths as deep as 16 cm (Abul-Fatih and Bazzaz 1979b). Therefore, the simulated soil environment did not capture the microenvironment of each seed. Nonetheless, these results indicate that giant ragweed seedling emergence is
relatively insensitive to dry conditions in the top 1 cm of soil. In other words, giant ragweed emergence, especially late-season emergence, continues during periods of little rainfall because it can emerge from depths where moisture remains adequate.

The applicability of seedling emergence models for weed control can be limited by the diversity of seedling emergence patterns (Grundy 2003). The potential for emergence variation was illustrated by Brainard et al. (2006) who found that emergence patterns of Powell amaranth (Amaranthus powellii) varied among farms in central New York State. To expand the utility of hydrothermal seedling emergence models, projections need to be customized for specific emergence environments (Page et al. 2006). The more complicated the modeling procedure, the less likely it will be used on a widespread basis. In this chapter, I present an approach to hydrothermal seedling emergence modeling that did not require extensive instrumentation or data collection.

Seedling emergence model validation

Two successive Weibull models projected seedling emergence well (Figure 4.4). The RMSE values of this experiment (8.21, 8.04, 9.87) compared favorably to other seedling emergence models. Ekeleme et al. 2005 proposed a hydrothermal seedling emergence model for tropic ageratum (Ageratum conyzoides) with RMSE values ranging from 5.8 to 10.1, and Roman et al. 2000 proposed hydrothermal seedling emergence models for common lambsquarters (Chenopodium album) with RMSE values that ranged from 6.5 to 37.1.
The shape of the cumulative emergence curve reflects variation in hydrothermal requirements among seeds within the population. Typically, seed-to-seed variation in hydrothermal time requirements is continuous (Bradford 1996), and as a result, cumulative seedling emergence in response to hydrothermal time is described by a single sigmoidal curve (Shrestha et al. 1999). I modeled giant ragweed seedling emergence with a double sigmoidal curve which indicates two subpopulations within the general population (Kao 1959). The origins of giant ragweed seedling emergence subpopulations are unknown. Giant ragweed seed dormancy loss is influenced by burial depth (Harrison et al. 2007), but the biphasic emergence pattern was apparent in two tillage environments and at two locations. These results suggest biphasic giant ragweed emergence is independent of soil environment and is common in Ohio agricultural fields.

Seedling emergence periods of progeny from individual plants (half-sib families)

Because seed germination behavior is known to differ among half-sib families (Andersson and Milberg 1998; Norman et al. 2002; Lacerda et al. 2004), I analyzed an agricultural giant ragweed population to determine if half-sib families exhibited different emergence periods corresponding to the first and second seedling flush. Consistent with the above results, seedling emergence exhibited a rapid, early season flush, followed by a more gradual flush (Figure 4.5A). The percent emergence for the second flush was not as large as the previous populations studied. Giant ragweed seedling emergence encounters heavy selection pressure and late-season emergence is not advantageous in successional environments (Abul-Fatih and Bazzaz 1979b) because of to competition from established
biennials and perennials. Therefore, the diminished second flush of the population investigated in this study may have been a consequence of selection pressures associated with the 19-year period prior to 2003 in which the study site was undergoing old-field succession.

Examination of half-sib family emergence periods indicated that the early and late seedling flushes observed for the population did not result from “early” and “late” emergence periods within each family (Figure 4.5B). Rather, the second seedling flush observed for the population was the consequence only of those half-sib families with prolonged emergence periods. However, the factors that would result in biphasic emergence among progeny of single maternal phenotype require further study. Evolutionary ecology theory predicts individuals in unpredictable establishment environments “bet-hedge” or diversify offspring germination so that at least some encounter optimum conditions for seedling establishment (Cohen 1966). While empirical evidence supports the bet-hedging hypothesis (Biere 1991; Philippi 1993), the general mechanisms of offspring diversification are poorly understood. With regards to giant ragweed, knowledge of the factors that diversify offspring emergence and identification of individuals prone to bet-hedging will increase our understanding of giant ragweed success in agricultural environments and can improve integrated weed management strategies.
Figure 4.1. Giant ragweed cumulative percent emergence as a function of calendar day during 2001, 2002, and 2003. Presented are averages with standard errors.
Figure 4.2. Weather conditions at South Charleston, OH. Gray bars represent weekly total precipitation. Solid line presents daily average temperature.
Figure 4.3. Cumulative percent emergence as a function of hydrothermal time. Data was combined from 2001, 2002 and 2003. Hydrothermal time ([2]) was calculated with base temperature of emergence ($T_{\text{base}}$) at 2°C and base water potential of emergence ($\psi_{\text{base}}$) at -10 MPa.
Table 4.1. Emergence model parameters determined from four parameter Weibull model ([3]) fit to cumulative percent emergence plotted as a function of hydrothermal time. Model parameters include: $M =$ upper asymptote, $k =$ rate parameter, $z =$ lag phase, and $c =$ curve shape parameter.

<table>
<thead>
<tr>
<th>Model</th>
<th>$M$</th>
<th>$z$</th>
<th>$c$</th>
<th>$k$</th>
<th>$T_b$ ($^\circ$C)</th>
<th>$\Psi_b$ (MPa)</th>
<th>$R^2$</th>
</tr>
</thead>
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<td>0 to 600 HTT</td>
<td>60</td>
<td>60</td>
<td>1.60</td>
<td>0.00027</td>
<td>2.0</td>
<td>-10</td>
<td>0.88</td>
</tr>
<tr>
<td>600 HTT to conclusion</td>
<td>40</td>
<td>600</td>
<td>1.23</td>
<td>0.00060</td>
<td>2.0</td>
<td>-30</td>
<td>0.84</td>
</tr>
</tbody>
</table>
Figure 4.4. Emergence model validation at South Charleston, OH in till and no-till conditions during 2005 and validation at Columbus, OH in no-till conditions during 2006. Solid line presents projected emergence and data points are average actual emergence with standard errors.
Figure 4.5. **A** Population emergence pattern. Data points are averages of twenty-five half-sib families with standard errors. **B** Emergence periods for half-sib families of the population presented in top figure. Each half-sib family is represented by a bar. The left edge of the bar represents the median day of first emergence; the right edge of bar represents the median day of final emergence. Emergence interval was the difference between the first and final day of emergence. Emergence intervals were not correlated with average percent emergence ($r = 0.12$, $P = 0.58$).
5.1 Introduction

As indicated by seedling emergence spread in time, weed species produce seeds with varying durations in the seed bank. Diversity in seedling emergence time is advantageous in establishment environments that are characterized by temporal heterogeneity (Cohen 1966). Understanding the production of seeds with different capacities for seed bank persistence will increase our knowledge of plant adaptations to disturbed environments.

Seed bank longevity is one of several adaptations to heterogeneous establishment environments. Others include seed dispersal and seed size, that represent adaptations to spatial heterogeneity (Willson and Traveset 2000; Leishman et al. 2000; Moles and Westoby 2004). Venable and Brown (1988) proposed that since seed size, seed dispersal and seed bank longevity represent adaptations to establishment environment heterogeneity, they form a coevolutionary syndrome where strong selection for one
coincides with weaker selection for the others. Evidence in support of Venable and Brown’s coevolutionary syndrome comes from interspecific variation in seed size and seed bank longevity within some floras. For example, among the herbaceous plants in grasslands of north-western Europe (Thompson et al. 1993) and central Argentina (Funes et al. 1999), species that produce small, compact seeds tend to persist in the seed bank more than species that produce large seeds.

The applicability of Venable and Brown’s coevolutionary syndrome within a species is not well understood. Many have reported individuals within a population that produce uniquely sized seeds (Byers et al. 1997; Telenius and Torstensson 1999; Simons and Johnston 2000; Susko and Lovett-Doust 2000; Halpern 2005), and many others have reported individuals produce unique seed germination behaviors (Andersson and Milberg 1998; Meyer and Allen 1999b; Herrera 2000; Norman et al. 2002; Cruz et al. 2003; Schütz and Rave 2003; Lacerda et al. 2004). Within-species variation in seed size and seed germination was reported by Simons and Johnston (2000) who found that Lobelia inflata seed size was influenced by maternal identity and that rate of germination under controlled conditions was inversely proportional to seed size. Furthermore, previous research with Avena fatua suggested a genetic relationship between seed size and seed bank persistence (Adkins et al. 1986). Avena fatua lines that were bred for decreased seed dormancy produced seeds that were larger than A. fatua lines bred for increased seed dormancy. Interindividual variation of seed size has not been explicitly related to seed bank persistence.
In addition to maternal identity, seed germination behavior is frequently influenced by the time of seed maturation (Lacey and Pace 1983; Roach 1986; Baskin and Baskin 1995; Cardina and Sparrow 1997; El-Keblawy and Al-Rawai 2006). Differences among maturation times occur as a result of changes in the environment during the maturation period (Roach and Wulff 1987). Many influential environmental factors have been identified and the most important include: temperature, day length, and soil moisture (Baskin and Baskin 1998; Gutterman 2000).

The degree that seed germination behavior is influenced by the maternal plant environment varies among genotypes (Alexander and Wulff 1985; Schmitt et al. 1992). Working with genetically pure lines of *A. fatua* and *Bromus tectorum*, previous researchers found that the seed germination of dormant genotypes was more influenced by the maturation environment than nondormant genotypes (Sawhney and Naylor 1979; Meyer and Allen 1999a).

The overall objective of this experiment was to identify seeds within a population that were more likely to persist in the seed bank by considering individual differences in seed size and maturation environment responses. Specifically, I hypothesized that maternal family seed size was inversely related to seed bank longevity. Furthermore, I expected seed bank longevity to be influenced by seed maturation time and that smaller-seeded maternal plants (more dormant genotypes) were influenced by the maturation environment more than larger-seeded maternal plants (less dormant genotypes). As a result, the most persistent fraction of the seed population was anticipated to originate from small-seeded individuals at a particular time during the seed maturation period.
To test these hypotheses, I utilized *Ambrosia trifida*, a problematic weed of corn and soybean production in the eastern U.S. corn-belt (Loux and Berry 1991; Gibson et al. 2005). The reproductive dispersal unit of *A. trifida* is a hardened involucre that encases a single achene (Barkley et al. 1986). *Ambrosia trifida* dispersal units have several characteristics that are optimumal for this experiment. First, the general shape and size of *A. trifida* dispersal units are consistent within an individual so that each individual produces a distinct morph (Sako et al. 2001). Second, *A. trifida* dispersal units are relatively large (up to 14mm length, 10mm width (Sako et al. 2001)) which eases recovery from soil seed banks. Finally, within *A. trifida* populations, dispersal units reach maturity asynchronously over a period of 42 days during the autumn (Harrison et al. 2001).

5.2 Materials and Methods

*Seed collection*

*A. trifida* dispersal units were collected from a natural stand at The Ohio State University Waterman Agricultural and Natural Resources Laboratory at Columbus, OH during 2004 and 2005. Soybeans were planted at the Columbus site on May 15, 2004 and May 9, 2005. *A. trifida* populations developed after planting and soybean plants were removed during the final week of June and a giant ragweed monoculture was maintained in a 30 m x 23 m area.
On September 16, 2004 and September 21, 2005, giant ragweed individuals were selected haphazardly with the criteria that individuals have at least 60 mature dispersal units and sufficient immature dispersal units to supply an additional collection. All mature dispersal units were removed from each individual, and individual collections were stored separately in paper bags. Seed maturity was assessed by the absence of green color and free separation from the inflorescence with a slight touch to the conical beak. In 2004 the selected plants were revisited on September 23 and October 1 and the seed collection process repeated. In 2005 the selected plants were revisited on October 1 and October 11. As a result, seeds were collected from each individual at three maturation times: early, middle and late.

Day length, temperatures and precipitation varied during the maturation period and patterns were somewhat consistent between years. Day length decreased from 13 hrs 3 min on September 1, to 10 hrs 30 min on October 15. Daily average air temperature and daily total precipitation were recorded by an onsite weather station. In general, temperatures decreased as seed maturation progressed. The dispersal unit maturation periods of both years were characterized by a large rain event (6 cm in 2004, 10 cm in 2005) between the early and middle maturation times.

Seed collections were stored dry at room temperature. Each dispersal unit was individually inspected and weighed. Dispersal units with predispersal damage (Harrison et al. 2001) and dispersal units that weighed less than the collection mean minus the standard error were discarded. Sixty dispersal units were required from early, middle and late collections for a total of one hundred eighty dispersal units per plant. *A. trifida*
dispersal unit production varies according to local conditions. Bassett and Crompton
(1982) reported typical *A. trifida* individuals produce 275 dispersal units and Harrison et
al. (2001) found up to fifty percent of seed rain can be hollow or damaged. The
experiment included 20 individuals in 2004, and 27 individuals in 2005. Dispersal unit
harvesting included more individuals but because of the abundance of hollow seeds and
predispersal damage, many individuals were removed from the experiment. Hereafter,
the progeny from an individual plant is referred to as a “maternal family” and maternal
families are identified by the year of seedling emergence.

*Field experiment*

In general, seed banks are divided into two types: active and persistent. The
‘active’ seed bank is the collection of seeds capable of germination during a particular
year (Zhang et al. 1998). The ‘persistent’ seed bank describes seeds that remain viable in
the soil for more than one emergence season (Walck et al. 1993). For this experiment,
longevity in the active seed bank was measured by monitoring seedling emergence over
time and the persistent seed bank was measured by seed recovery.

The field experiment was conducted at The Ohio State University Waterman
Agricultural and Natural Resources Laboratory on a Crosby silt loam soil (fine, mixed,
active, mesic Aeric Epiaqualfs) with no history of giant ragweed. The experiment was
designed in a split-plot with four complete blocks. Maternal family was the main-plot
factor and maturation time was the sub-plot factor. For each sub-plot, 12 seeds were
placed in open-top baskets constructed from fiberglass mesh (0.8 mm$^2$) (Figure 5.1).
Baskets were incorporated into the soil so that the top was even with the soil surface and
depth to basket bottom was 4 cm. This depth was chosen because it allows for seedling emergence (Abul-Fatih and Bazzaz 1979b) and prevents dispersal unit escape from baskets. Preliminary research indicated dispersal units settle to basket bottoms. Basket burial depth was verified during the emergence season (2005 emergence season mean depth = 5.8 ± 0.3 cm; 2006 emergence season mean depth = 4.2 ± 0.5 cm). The study was installed on December 2, 2004 and November 20, 2005.

Following one winter, seedlings were counted and removed every three to five days. Seedling emergence was defined as complete cotyledon expansion and seedlings were removed with minimum soil disturbance. Occasionally seedling cotyledons were encased by involucre hulls. These hulls were collected for later analysis. Throughout the study, the site was kept free of vegetation by hand-weeding and glyphosate applications at 0.94 kg ai/ha. The seedling emergence season was declared complete when no seedlings were observed for 28 consecutive days (August 8, 2005 and August 14, 2006). At that time, mesh baskets were unearthed and brought to the laboratory.

Dispersal units were recovered by passing soil through slotted sieves (2 mm X 13 mm). Intact dispersal units were cross-sectioned along the longitudinal axis to reveal the embryo. Embryo integrity was determined by applying pressure with a scalpel. Dispersal units with firm, undamaged embryos were considered viable.

From seedling emergence counts and observations of dispersal units, additional dispersal unit fates were deduced. Additional fates included: fatal germination (34% in 2005; 9% in 2006), nonviable embryos (8% in 2005; 3% in 2006), parthenocarpic dispersal units (5% in 2005; 1% in 2006) and damage from Diptera larvae (19% in 2005,
13% in 2006). Recovery success was determined from the sum of dispersal units recovered plus involucre hulls collected from emerged seedlings. This system accounted for 96% of the dispersal units initially buried and the number of missing dispersal units was independent of year, individual and maturation time (α = 0.05).

Dispersal unit size

Previous researchers distinguished maternal families from two-dimensional dispersal unit profiles (Sako et al. 2001). For each maternal family, 10 dispersal units per collection time were scanned (200 dpi) with a flatbed scanner. Dispersal unit images were converted to black and white in order to enhance the contrast between dispersal unit and background. The dispersal unit perimeter was the border between the dispersal unit and background. The area within the perimeter was calculated with an image analysis software package (Rasband 2007). Areas were pooled across years and subjected to analysis of variance. Maternal family dispersal unit area was the mean across maturation times.

Data analysis

The active and persistent seed banks of *Ambrosia trifida* were described by dichotomous variables. *Ambrosia trifida* seedling emergence during a particular year occurs in two successive flushes; one prior to May 1 and one after May 1 (previous chapter). Longevity in the active seed bank was described by the percent of emergence after May 1 (binary response, 0 = before May 1, 1 = after May 1). The persistent seed bank was described by the percent of buried dispersal units that were viable at the conclusion of the emergence season (binary response, 0 = germinated, 1 = persistent).
Maternal family dispersal unit area effects on the active and persistent seed banks were determined with generalized linear mixed models fit by restricted maximum quasi-likelihood in SAS version 9.1 (Littell et al. 2006). Generalized linear models allow the probability distribution of the response function to be specified, and provide a link function for mean transformation of a range-restricted response onto a scale in which covariates are additive (Schabenberger and Pierce 2002). The active and persistent seed banks were modeled with binomial distributions and a logit-link function. The fixed effect was family area which was entered as a continuous variable. Year was treated as a random effect. The significance of parameter estimates were measured with t-tests based on the estimate divided by its standard error. When significant ($\alpha = 0.05$), the influence of family area was further assessed with odds ratios. The odds ratio describes the change in the probability of an event when the independent variable increases by one unit. Values above one indicate that the frequency of the event increases, and values between zero and one indicate that it decreases (Hosmer and Lemeshow 2000).

Dispersal unit maturation time effects on the active and persistent seed banks were determined separately for each year. A generalized linear mixed model modeled the active and persistent seed bank with binomial distributions and the logit-link function. Dispersal unit maturation time was entered as a fixed effect, block was entered as a
random effect. Maturation times were compared with pairwise t-test (\(\alpha = 0.05\)). To present maturation time means, parameter estimates were back transformed with the following equation:

\[
V_a = 100 \left( \frac{e^x}{1 + e^x} \right)
\]  

[1]

where \(x\) is the logit estimate from the model, and \(V_a\) is the approximate percent viable after back transformation.

The influence of maturation time was defined by the pair of times that exhibited the greatest difference. The magnitude of the maturation time effect was determined for maternal families and the association between family maturation time effect and dispersal unit area was assessed with Pearson correlation coefficients.

Seed bank responses to maternal family dispersal unit area were integrated with responses to maturation time. First, maternal plants were ranked by cohort dispersal unit size and then pooled into thirds: small, medium, and large. Then for each size class, mean persistent seed bank was determined for early, middle and late maturation times.

5.3 Results

Individual plants produced morphologically distinctive dispersal units (Figure 5.2). Maternal family dispersal unit area was negatively associated with the probability of seedling emergence after May 1st (Table 5.1) and the probability of viability at the conclusion of the emergence season (Table 5.2). On average, a 1 mm\(^2\) increase of
dispersal unit area increased the odds of emergence after May 1 0.934 times.
Furthermore, a 1 mm$^2$ increase in dispersal unit area increased the odds of viability after
the first emergence season 0.932 times.

Dispersal unit maturation time did not influence the probability of emergence
after May 1 in 2005 ($F_{2, 6} = 1.38, P = 0.254$) but did affect the probability of emergence
after May 1 in 2006 ($F_{2, 6} = 44.35, P < 0.01$) (Figure 5.3). Dispersal unit maturation time
influenced the probability of viability after the one emergence season in both 2005 ($F_{2, 6}
= 59.92, P < 0.01$) and 2006 ($F_{2, 6} = 20.38, P < 0.01$). Maturation time effects on
viability after one emergence season were not consistent between years (Figure 5.4).

For the probability of emergence after May 1 in 2006, the magnitude of the
maturation effect was not related to maternal family dispersal unit area ($r = -0.01, P =
0.97$). For the probability of viability after one emergence season, the magnitude of the
maturation effect was negatively associated with family dispersal unit area in 2005 ($r = -
0.45, P = 0.05$) and not associated with family dispersal unit size in 2006 ($r = -0.14, P =
0.48$). Integration of dispersal unit viability results for 2005 indicated that the most
persistent fraction of the seed population was produced late in the maturation season by
individuals characterized by small dispersal units (Figure 5.5).

5.4 Discussion

Consistent with the results of Sako et al. (2001), there was considerable dispersal
unit polymorphism among individuals (Figure 5.2). This experiment further
demonstrated the genetic control of dispersal unit morphology by measuring dispersal
unit size throughout the maturation period. With such a high degree of genetic control on dispersal unit size, the coevolutionary syndrome between seed size and seed bank persistence proposed by Venable and Brown (1988) can be tested.

Results of this experiment suggested the presence of a coevolutionary syndrome within *A. trifida* populations. Maternal family dispersal unit size was inversely related to seedling emergence after May 1 (longevity in the active seed bank) and viability following one emergence season (persistent seed bank formation). This indicates smaller dispersal units would be advantageous in temporally heterogeneous environments. But for the coevolutionary syndrome to be complete, there must be an environment where smaller dispersal units are disadvantaged and larger dispersal units are advantaged.

Working with dispersal units pooled from several *A. trifida* individuals, Harrison et al. (2007) found that larger dispersal units exhibited greater emergence from deeper depths as compared to smaller dispersal units. Furthermore, smaller dispersal units exhibited longer seed bank durations than larger dispersal units. Although the experiment used dispersal units pooled from several individuals, the strong genetic effect on dispersal unit size reported here suggests that small and large seed collections consisted of different genotypes. The results of Harrison et al. (2007) are in agreement with the results of this experiment, and therefore, the coevolutionary syndrome between seed size and seed bank persistence is applicable within *A. trifida* populations.

The implication of this finding is that *A. trifida* populations with variable dispersal unit sizes are collections of genotypes with different seedling emergence strategies. Increased longevity in both the active and persistent seed bank is a
consequence of genotypes with an adaptation for seed bank persistence, not genotypes with a multitude of emergence strategies. Such information influences the scope of weed management (Clements et al. 2004). The adaptability of *A. trifida* to environments with different establishment conditions (Hartnett et al. 1987) is based on the preservation of genetic diversity.

In addition to maternal family dispersal unit size, time of maturation time influenced soil longevity. The maturation time effect was inconsistent across years which meant that changes in daily average air temperature, daily precipitation, and day length during the seed maturation periods were not the primary causes for the observed variation in soil longevity. Other influential maturation environment conditions vary on a finer scale (Baskin and Baskin 1998; Gutterman 2000). Without knowledge of the environmental factor that caused the maturation time effect, maturation time variation among individuals cannot be ascribed to different sensitivities to the maturation environment. Nonetheless, by considering maternal genotype and asynchronous maturation, I was able to identify the most persistent fraction of a seed population in one year. Combined, the results of this experiment indicate that, in addition to the seed bank environment, the genetics and environment of the maternal plant influence a seed’s duration in the seed bank.
Figure 5.1. Field experiment design. Subplots (individual maturation time) consisted of open-top, mesh basket (10 cm x 7 cm; 4 cm deep). Main plots (individual) were three successive baskets.
Figure 5.2. Columns represent two maternal families collected over time. Relative differences between and within families are representative of the material used in this investigation. Analysis of variance indicated that 68% of the variation in dispersal unit area was attributable to the maternal family.
<table>
<thead>
<tr>
<th>Parameter</th>
<th>Estimate</th>
<th>SE</th>
<th>DF</th>
<th>t-value</th>
<th>P</th>
<th>Odds ratio</th>
</tr>
</thead>
<tbody>
<tr>
<td>Intercept</td>
<td>1.376</td>
<td>0.98</td>
<td>44</td>
<td>1.40</td>
<td>0.16</td>
<td></td>
</tr>
<tr>
<td>Dispersal unit area</td>
<td>-0.067</td>
<td>0.03</td>
<td>44</td>
<td>-2.01</td>
<td>0.05</td>
<td>0.934</td>
</tr>
</tbody>
</table>

Table 5.1. Generalized linear model with a binomial distribution and logit-link function for the effects of maternal family dispersal unit area on the probability of emergence after May 1 (active seed bank).
<table>
<thead>
<tr>
<th>Parameter</th>
<th>Estimate</th>
<th>SE</th>
<th>DF</th>
<th>t-value</th>
<th>P</th>
<th>Odds ratio</th>
</tr>
</thead>
<tbody>
<tr>
<td>Intercept</td>
<td>0.477</td>
<td>0.80</td>
<td>44</td>
<td>0.59</td>
<td>0.55</td>
<td></td>
</tr>
<tr>
<td>Dispersal unit area</td>
<td>-0.071</td>
<td>0.03</td>
<td>44</td>
<td>-2.48</td>
<td>0.02</td>
<td>0.932</td>
</tr>
</tbody>
</table>

Table 5.2. Generalized linear model with a binomial distribution and logit-link function for the effects of maternal family dispersal unit area on the probability of viability after one emergence season (persistent seed bank).
Figure 5.3. Parameter estimates for the effects of maturation time on the probability of seedling emergence after May 1st determined from a generalized linear model with a binomial distribution and a logit-link function. Values above bars are means on the logit scale. Bars represent the approximate means on the original scale and were obtained by back transformation with Equation 1. Maturation times of a year with the same lower case letter are not significantly different according to pairwise t-tests ($\alpha = 0.05$).
Figure 5.4. Parameter estimates for the effects of maturation time on the probability of seed bank persistence after one emergence season determined from a generalized linear model with a binomial distribution and a logit-link function. Values above bars are means on the logit scale. Bars represent the approximate means on the original scale and were obtained by back transformation with Equation 1. Maturation times of a year with the same lower case letter are not significantly different according to pairwise t-test ($\alpha = 0.05$).
Figure 5.5. Integration of seed size and maturation time results for the persistent seed bank in 2005. Symbols represent the mean for one-third of the maternal families grouped according to maternal family dispersal unit size.
A.1 Introduction

The impact of a glyphosate application on crop yield is largely dependent upon application timing. While glyphosate is better than most herbicides at controlling larger weeds, it is most effective on weeds less than a height specific for a species (Hoss et al. 2003). After weeds have grown taller than the specific height, glyphosate applications have reduced benefits on crop yield due to inconsistent weed control. Furthermore, crops with a head start on weeds acquire a greater proportion of limited resources and suppress weed growth (Zimdahl 1980). Once a crop has developed a sufficient competitive advantage, glyphosate applications have little benefit towards crop yield. Accordingly, there is a period during the early stages of crop development when glyphosate should be applied according to weed height. This period is hereafter referred to as the “glyphosate management interval”.

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Previous researchers have defined the glyphosate management interval in a variety of units including: weed height exclusively (Krausz et al. 1996; Gower et al. 2003; Dalley et al. 2004), weed growth stage (Sikkema et al. 2005), crop growth stage (Vangessel et al. 2000; Myers et al. 2005), and combinations of crop growth stage and calendar days (Choudhary and Bordovsky 2006). Knezevic et al. (2002) proposed standardizing weed control scheduling after crop emergence on a scale of growing degree days (GDD) accumulated from crop emergence or planting. The authors stated that accumulated growing degree days provides a continuous and precise scale that is biologically meaningful and allows for comparison among crops (Knezevic et al. 2002).

Previous researchers have used GDD to describe the weed control concept similar to the glyphosate management interval, the critical weed-free period (Knezevic et al. 2002; López-Ovejero et al. 2005; Williams 2006). Both the critical weed-free period and glyphosate management interval describe the length of time required to provide a crop the competitive advantage over later-emerging weeds.

Giant ragweed is among the most competitive weeds of row-crop agriculture. Season-long interference of one giant ragweed plant m$^{-2}$ has been found to reduce soybean yield by over 75% (Webster et al. 1994), and 1.7 giant ragweed plants per 10 m$^2$ reduced corn yield by 18% (Harrison et al. 2001). Furthermore, growers in the eastern U.S. Corn Belt regard giant ragweed as one of the most problematic in corn and soybean production (Loux and Berry 1991; Gibson et al. 2005). Giant ragweed control is difficult because of its seedling emergence phenology. In agricultural fields, emergence typically initiates in late-March and continues to July (Sprague et al. 2004; Schutte et al. 2007).
Seedlings are capable of rapid growth (Abul-Fatih and Bazzaz 1979a) and can be competitive within the crop canopy (Harrison et al. 2001). As a result, giant ragweed control requires an extended glyphosate management interval (Jeschke and Stoltenberg 2004). For giant ragweed control in the eastern U.S. Corn Belt, current glyphosate application guidelines are applications when giant ragweed plants are no more than 6 inches tall followed by a second application three weeks later (Johnson et al. 2007). Glyphosate management intervals based on GDD have not been reported for corn and soybean fields with heavy giant ragweed infestations. The objective of this experiment was to determine the glyphosate management interval in growing degree days for corn (Zea mays) and soybean (Glycine max) fields heavily infested with giant ragweed (Ambrosia trifida L.).

A.2 Materials and Methods

Study site

Field experiments were conducted at the Western Branch Experiment Station of the Ohio Agricultural Research and Development Center in Clark County, OH (39°52’ N, 83°40’ W). The area had a history of tilled row-crop production and giant ragweed infestation. The soil type was Crosby silt loam (fine, mixed, active, mesic Aeric Epiaqualfs) with an organic content of 2.2% in the Ap horizon. The experiment was established in 2000 and maintained until 2006. Data for 2004 was not included because of unusually late planting due to bad weather.
Field experiment

The experimental design was a three-factor factorial arranged in a split-split-plot design with four complete blocks. The main plot factor was tillage (no-till and till), subplot factor was crop (corn and soybean), and sub-subplot factors were weed control (weedy control, glyphosate management interval, and weed-free control). No-till corn data was excluded because of heavy and inconsistent pathogen pressure. Main plots were 11.4 m by 55 m, subplots were 18.3 m by 11.4 m, and sub-subplots were 3.8 m by 18.3 m. Tillage treatments were conducted continuously on the same plots throughout the experiment but crop treatment locations varied by year. From 2000 to 2004, corn and soybean treatments were continuous, but in 2005 and 2006, corn and soybean plots were rotated. Glyphosate application treatments were applied continuously to the same plots throughout the experiment.

Tillage treatments consisted of chisel-plow the fall prior to planting and two passes with a disk-cultivator-harrow during spring. Corn was planted in rows spaced 76 cm apart and soybean was planted in rows spaced 38 cm apart. Within one week of planting, corn plots were fertilized with ammonium nitrate 34-0-0 at 225 kg N ha\(^{-1}\) applied with a manual drop spreader. We used full-season, glyphosate-resistant varieties. Additional planting details are presented in Table 1.

At planting, the entire study was sprayed with a tank mixture of glyphosate at 1.1 kg ai ha\(^{-1}\), s-metachlor at 1.19 kg ai ha\(^{-1}\), 1% (v/v) ammonium sulfate delivered at 140 L ha\(^{-1}\) to control emerged vegetation and provide residual control of monocot weeds. Weedy controls received no further weed control. Glyphosate management intervals
were characterized by both calendar days and GDD from planting (Table 2). In 2005, two glyphosate management intervals were accommodated by dividing sub-subplots to 3.8 m by 9.15 m. GDD was calculated as:

$$\text{GDD} = \left[ \frac{(T_{\text{max}} + T_{\text{min}})}{2} \right] - 10^\circ\text{C}$$

where $T_{\text{max}}$ is the daily maximum air temperature, $T_{\text{min}}$ is the daily minimum air temperature. Daily minimum and maximum air temperatures were obtained from an onsite weather station.

During the glyphosate management interval, plots were sprayed with glyphosate at 1.1 kg ai ha$^{-1}$, and 1% (v/v) ammonium sulfate with a carrier volume of 140 L ha$^{-1}$ whenever giant ragweed populations attained a height of 10 cm. Depending upon the year, glyphosate management interval treatments received one or two herbicide applications. Weed-free treatments were maintained with glyphosate applied in a manner identical to glyphosate management intervals or hand-weeding.

Temperatures during the first sixty days following crop planting were compared to long-term averages during the same time period. Daily average air temperatures were calculated as one half the sum of minimum and maximum air temperatures reported by the US National Oceanic and Atmospheric Administration National Climatic Data Center ([NOAA NCDC] 2007). Long-term average temperatures were daily temperatures from 1961 to 1990.

Yields were determined from two corn rows and five soybean rows in the center of each plot. During 2000 to 2003 and 2006 harvest row length was 15.2 m, and in 2005 harvest row length was 7.6 m. A plot combine was used for harvesting. Grain yields
were adjusted to 13% moisture prior to analysis. A grain sample was obtained from each plot and the proportional weight of grain to giant ragweed seed provided a correction factor for giant ragweed contamination. Giant ragweed densities at harvest were determined in three 0.25 m$^2$ quadrats positioned front, center and rear of treatment plots. In two of the three quadrats, above-ground giant ragweed biomass was harvested and dried at 55 °C for 7 days. Giant ragweed biomass was expressed on a per plant basis and averaged across crop and tillage treatments. The relationship between giant ragweed biomass and glyphosate management interval was assessed by combining data from 2000 to 2005.

**Data analysis**

Glyphosate management interval treatment yields were expressed as a percent of weed-free yields and are hereafter referred to as relative yield. For each of the following subplots (till corn, till soybean and no-till soybean), one data set was formed by combining all years and plotting relative yields as a function of glyphosate management interval. The relationship between relative yield and glyphosate management interval was summarized by the three parameter Gompertz function:

$$RY = a \exp (- b \exp (- k*time))$$  \[2\]

where $RY$ is relative yield, $a$ is the yield upper asymptote (set to one hundred percent), $b$ and $k$ are constants, and $time$ is calendar day or growing degree day (GDD) from planting to final glyphosate application. The three parameter Gompertz model has been used previously to describe the interval from planting in which a crop needs to be kept weed-free in order to obtain a desired yield (Knezevic et al. 2002). Gompertz model
parameters were determined iteratively by the modified Gauss-Newton method in a
nonlinear regression procedure (PROC NLIN) of SAS version 9.1. The coefficients of
determination between predicted and actual relative yields provided indications of model
performance (Schabenberger and Pierce 2002).

Nonlinear regressions were compared in a manner similar to Harrison et al.
(2001). First, redundancy among nonlinear regressions was tested with the following $F$-
test (Zar 1999):

\[ F = \frac{SS_t - SS_p}{(m + 1)(k - 1)} \frac{SS_p}{DF_p} \]

where $SS_t$ is the total residual sum of squares from regression of the combined data set;
$SS_p$ is the pooled residual sum of squares, equal to the sum of the residual SS from the
individual regressions; $m$ is the number of independent variables and $DF_p$ is the pooled
residual degrees of freedom from individual regressions. When the above $F$-test found
that individual regressions were estimates of the same population, variance homogeneity
was then evaluated with an $F$-test of the variance ratio (Clewer and Scarisbrick 2001).
Subplots were combined when the variance ratio $F$-test indicated variances were equal.

A.3 Results and discussion

Giant ragweed was the dominant weed in this experiment and giant ragweed
densities in weedy control plots averaged $55 \pm 11$ plants m$^{-2}$ in no-till soybeans, $84 \pm 15$
plants m$^{-2}$ in till soybeans, and $53 \pm 11$ plants m$^{-2}$ in till corn. Descriptions of natural of
giant ragweed populations are scant but Abul-Fatih and Bazzaz (1979a) reported a natural population with a density of 33 plants m$^{-2}$. With relatively high giant ragweed densities, the study site of this experiment is representative of crop fields with heavy giant ragweed infestations.

The first sixty days after planting was characterized by higher than normal temperatures during 2000, 2002, 2005 and 2006 (Figure 1). In 2001, the temperatures during the first sixty days after crop planting resembled normal. In 2003, the crop establishment period was characterized by below normal temperatures. Noteworthy in 2003 was twenty-one consecutive days during which daily average temperatures never matched or exceeded normal temperatures. No other growing season contained such a prolonged period of abnormal temperatures.

As expected, crop yield was greatly reduced when weeds were not controlled after planting. For both crops, yields for weedy controls were at least ninety percent lower than weed-free controls. Relative yields plotted as a function of the glyphosate management interval in calendar days did not exhibit a recognizable pattern because the 2003 glyphosate management interval produced a lower than expected relative yield (Figure 2). The low yield in 2003 may have been due to below average temperatures. Similarly, Halford et al. (2001) found the number of calendar days in which weeds had to be controlled increased during a year that was cooler. Thus calendar day-based recommendations can underestimate the glyphosate management interval during years characterized by below normal temperatures.
In contrast to calendar days, relative yield plotted as a function of glyphosate management interval in GDD exhibited a sigmoidal pattern (Figure 3). Therefore, the effects of glyphosate application timing are more predictable as a function of GDD than calendar days and GDD-based recommendations account for abnormally cool years. The relationships between relative yield and glyphosate management interval in GDD were described with Gompertz functions. The $F$ test for comparing nonlinear models indicated that till and no-till soybean regressions represented the same population, therefore, the data were combined.

For both corn and soybeans, the Gompertz functions increased rapidly from approximately 350 GDD to 500 GDD. During early-summer, a typical calendar day accumulated 18 to 22 growing degrees. Therefore, during the period between 350 GDD to 500 GDD, a few days difference in glyphosate application timing had tremendous impact on crop yield. The Gompertz functions projected that yields of glyphosate management interval treatments were equivalent to yields of weed-free controls following 450 GDD from planting in corn and 600 GDD from planting in soybean. Perhaps due to taller plants and increased light capture earlier in the season (Mohler 2001a), corn developed a competitive advantage over giant ragweed earlier in the growing season than soybean. Glyphosate applications after 450 GDD in corn and 600 GDD in soybean are not warranted since at this time the crop is able to resist interference from newly emerged giant ragweed. Glyphosate applications scheduled exclusively by weed height may not identify the point of diminished returns since the competitive ability of crops is not accounted for.
In this experiment, the ability of corn and soybean to suppress ragweed was further indicated by reductions in giant ragweed biomass (Figure 4). Smaller giant ragweed plants produce fewer seeds (Abul-Fatih and Bazzaz 1979c). Accordingly, Harrison et al. (2001) found that giant ragweed fecundity decreased when emergence occurred four weeks after crop emergence compared to giant ragweed emergence synchronous with crop emergence. Therefore, properly timed glyphosate applications not only protect yield but also are important components of long-term giant ragweed management.

In this experiment, I found that giant ragweed height and growing degree days from planting can be integrated to produce robust glyphosate management intervals. Higher glyphosate application rates can be used to control larger weeds (Krausz et al. 1996), providing flexibility within the glyphosate management interval. Although this experiment demonstrated giant ragweed control with multiple glyphosate applications, recent detection of glyphosate-resistant ragweed (Heap 2007) forbids implementation of this approach. Growers in the eastern U.S. Corn Belt are now advised to include two or more herbicide modes of actions for giant ragweed control (Johnson et al. 2007). In particular, researchers advise the use of preemergence herbicides in combination with glyphosate. The growing degree day intervals identified in this study are applicable to pre-emergence plus glyphosate herbicide programs since they indicate the minimum amount of time from planting a herbicide program needs to be effective against giant ragweed. In addition, GDD-based weed control recommendations is that management intervals can be integrated with other management decision tools, such as thermal and
hydrothermal seedling weed emergence models. Thermal and hydrothermal seedling emergence models exist for many species (Forcella 1998; Roman et al. 2000; Myers et al. 2004; Hacault and Van Acker 2006), including giant ragweed (Chapter 4). Seedling emergence projections integrated with herbicide application intervals could provide a more complete management decision tool than either one alone.
<table>
<thead>
<tr>
<th>Year</th>
<th>Planting date</th>
<th>Corn Variety</th>
<th>Till population $10^4$ plants ha$^{-1}$</th>
<th>Soybean Variety</th>
<th>No-till population $10^5$ plants ha$^{-1}$</th>
<th>Till population $10^5$ plants ha$^{-1}$</th>
</tr>
</thead>
<tbody>
<tr>
<td>2000</td>
<td>5/1</td>
<td>Clever 466RR</td>
<td>5.4</td>
<td>AGI 7372RR</td>
<td>1.8</td>
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<td>2001</td>
<td>4/26</td>
<td>Seed Consultants 11R19</td>
<td>7.5</td>
<td>AGI 7372RR</td>
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Table A.1. Varieties, planting dates and population densities for corn and soybean plots. Population densities were determined at harvest.
<table>
<thead>
<tr>
<th>Year</th>
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<th>GDD*</th>
</tr>
</thead>
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</tr>
<tr>
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<td>23</td>
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<tr>
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<td>43</td>
<td>782</td>
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<td>34</td>
<td>588</td>
</tr>
<tr>
<td>2006</td>
<td>29</td>
<td>536</td>
</tr>
</tbody>
</table>

Table A.2. Glyphosate management intervals for 2000 to 2006. In 2005, two management intervals were accommodated by splitting plots (see materials and methods). Time accumulated from the day of planting.

* GDD were calculated with Formula [1] with a base temperature of 10 °C.
Figure A.1. Frequency of days with average temperatures below and above normal during the first sixty days after planting. Normal temperatures were defined as the daily average temperature from 1961 to 1990 during the same time period.
Figure A.2. Relative yield (percent of weed-free control) as a function of glyphosate management interval in calendar days after planting for A) till corn, and B) till and no-till soybean.
Figure A.3. Relative yield (percent of weed-free control) as a function of glyphosate management interval in GDD after planting for A) till corn, and B) till and no-till soybean. Lines represent Gompertz functions (Formula \[2\]) fitted to data.
Figure A.4. Biomass of giant ragweed at harvest as a function of glyphosate management interval in GDD.
Previous researchers identified *Ambrosia trifida*’s prolonged period of seedling emergence as an adaptation to agricultural fields (Hartnett et al. 1987) and a causal factor for *A. trifida*’s success in agricultural fields in the eastern U.S. Corn Belt (Hartzler et al. 1999; Sprague et al. 2004). This dissertation examined the biological and ecological factors that contribute to prolonged seedling emergence. Results can provide direction for management founded on ecological principles.

Late-season emergence is associated with increased embryo dormancy and seedling emergence timing is a consequence of the interaction between embryo dormancy and increasing soil temperature. Analysis of soil temperatures for central Ohio from the past twenty-four years indicated that soil temperature plateaus in late-July to early-August (Figure B.1). Therefore, the latest potential time for *A. trifida* seedling emergence in central Ohio is early-August.
Seedlings that emerge later in the season represent a phenotype that produces offspring characterized by diverse emergence times, a “bet-hedging” phenotype (Cohen 1966). The uncertainty of *A. trifida* seedling emergence timing contributes to the management difficulties (Loux 2006, personal communication). Growers attempt to increase control efficiency by delaying applications until more seedlings have emerged. During this time, plants can become too large for control to be effective. As long as the bet-hedging genotype is present in the giant ragweed population, the optimum time to implement control will be ambiguous. Control schedules can be assisted by seedling emergence projections, but all emergence projections are inaccurate to a degree. Provided the potential yield loss associated with low *A. trifida* population densities (Webster et al. 1994; Harrison et al. 2001), growers cannot afford *A. trifida* control errors. Therefore, it is in the long-term interest of growers to eliminate the bet-hedging phenotype from their fields.

Elimination of the bet-hedging phenotype may not be accomplished with current control recommendations for conventional agriculture. Growers are advised to extend herbicide applications up to six to seven weeks (400 to 500 GDD) after planting, or into early June (Johnson et al. 2007). Previous experience has demonstrated the adaptability of *A. trifida* seedling emergence patterns to agricultural practices. For example, *A. trifida* seedling emergence discontinues when fields are planted (early May) and continues when planting is typically completed. This is advantageous since seedlings avoid destruction caused by planting operations. Furthermore, *A. trifida* populations exhibit phenotypic diversity of seedling emergence phonologies, a requisite for evolution by natural
selection. Therefore, *A. trifida* seedling emergence timing is expected to adapt to current control recommendations, resulting in a greater proportion of *A. trifida* seedlings emerging later in the season. In terms of yield loss, late emerging seedlings may have little immediate influence (Harrison et al. 2001). However, *A. trifida* plants that emerge late are capable of producing seeds (Abul-Fatih and Bazzaz 1979c). Therefore, current herbicide applications will perpetuate the bet-hedging phenotype.

The potential for *A. trifida* seedling emergence in August and the evolutionary significance of late-emerging seedlings suggest a need for full-season control. However, such long-term control potentially increases the economic and environmental cost of crop production. The sustainability of weed control increases by further manipulation of weed biology (Bhowmik 1997) and results of this dissertation can be used to improve biologically-based control of *A. trifida*.

Tactics targeted at dispersal units are promising control tools since *A. trifida* fecundity is low without intentional dispersal unit destruction (Abul-Fatih and Bazzaz 1979b; Harrison et al. 2001). Dispersal units are an important food source for rodents and invertebrates and post-dispersal predation has been proposed as a method to reduce *A. trifida* populations (Harrison et al. 2003). Granivore activity is influenced by environmental conditions (Menalled et al. 2006) and granivores often prefer dispersal units of a particular size (Harrison et al. 2003). *A. trifida* dispersal units mature asynchronously for approximately one month and dispersal units produced early in the maturation period are just as likely to produce late-season seedlings as dispersal units produced early in the maturation period. To promote consumption of dispersal units that
produce problematic seedlings, environmental conditions need to be conducive to granivore activity throughout the entire maturation period. In addition, within the seed rain, the late-emerging genotype is more likely to be represented by smaller dispersal units. Therefore, post-dispersal predation strategies need to ensure small dispersal units are consumed.

The high incidence of *A. trifida* seed death in high temperature soil conditions indicates that dispersal units which do not germinate in the spring are susceptible to death and decay in the summer. In general, spring germination can be avoided by secondary seed dormancy which is the imposition of dormancy after seed dispersal because of the absence of dormancy terminating factors (Benech-Arnold et al. 2000). Davis (1930) reported the incidence of secondary dormancy in *A. trifida*. By moderation of the soil microclimate of the seed germination zone (Van Wijk et al. 1959), winter annual cover crops potentially induce secondary seed dormancy and have been reported to reduce spring emergence of weed seedling emergence (Moore et al. 1994). Therefore, winter annual cover crops can be used to reduce *A. trifida* populations by inhibiting spring germination and subjecting dispersal units to summer soil conditions. Promotion of dispersal unit predation and decay are proposed not to replace but to supplement herbicide control. Multiple control tactics will limit selection for resilience to any one tactic and reduce reliance on herbicide control.

In addition to implications on control of *A. trifida* in agricultural fields, results of this dissertation can direct management decisions to prevent development and spread of weedy populations. In the western U.S. Corn Belt and parts of Europe, *A. trifida*
populations are found in field margins and there is concern for these populations invading agricultural fields. *A. trifida* weediness evolves from selection for increased embryo dormancy. Therefore, to prevent ruderal populations from becoming weedy, transmission of genes involved with embryo dormancy needs to be limited. Furthermore, dispersal unit morphology heterogeneity is an indication of emergence timing variation, and therefore, provides an indication of the potential for agricultural land invasion.

While much of this dissertation did not explicitly examine *A. trifida* management, a better understanding of a trait that renders *A. trifida* difficult to control enabled conclusions that can lead to improved control. Due to concerns for the sustainability of weed control based on a single external input, many have called for a multitactic approach founded on ecological phenomena (Forcella et al. 1993; Swanton and Murphy 1996; Liebman and Gallandt 1997; Cardina et al. 1999; Buhler et al. 2000; Liebman and Davis 2000; Mortensen et al. 2000; Liebman 2001). The effectiveness of these tactics depends on the understanding of weed biology. Therefore, the approach of this dissertation, the study of weed biology with consideration of management implications, can be used to solve weed control problems in the future.
Figure B.1. Soil temperatures at 5 cm from 1982 to 2006 at the Western Branch Experiment Station of the Ohio Agricultural Research and Development Center in Clark County, OH (39°52’ N, 83°40’W). Top line represents maximum daily average soil temperature recorded, bottom line represents minimum daily average soil temperature recorded, and bold line within range presents the average soil temperature.
APPENDIX C

FUTURE RESEARCH NEEDS FOR THE STUDY OF AMBROSIA TRIFIDA
SEEDLING EMERGENCE BIOLOGY AND ECOLOGY

• Determine physiological mechanisms of embryo and coat-imposed dormancy.
• Determine heritability of embryo dormancy.
• Determine spread of genes involved with embryo dormancy.
• Determined the covering-structure responsible for coat-imposed dormancy.
• Identify causes of seed demise in the soil.
• Improve precision of seedling emergence model.
• Validate Soil Moisture and Temperature model predictions in Ohio.
• Develop mechanistic seedling emergence model for A. trifida.
• Determine the effects of the maturation environment on seedling emergence.

• Determine if rates of seed decay justify development of new management strategies to inhibit spring seedling emergence.

• Determine if the environment during dispersal can be manipulated to promote seed predation.
LIST OF REFERENCES


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