CHARLES L. MOHLER

2

Weed life history: identifying vulnerabilities

Weeds from an ecological perspective

Weeds share certain ecological characteristics that distinguish them from other plants. Specifically, *weeds are plants that are especially successful at colonizing disturbed, but potentially productive, sites and at maintaining their abundance under conditions of repeated disturbance.* That is, weeds are the plants that thrive where soil and climate are favorable to plant growth, but disturbance frequently reduces competition among plants to low levels. Unlike previous conceptions of weediness (Baker, 1965; Harlan & de Wet, 1965; Buchholtz *et al.*, 1967), this ecologically based definition lacks reference to humans and human disturbance. The species people refer to as weeds mostly existed prior to human disturbance, and the repertoire of behaviors that makes them invasive and persistent in human-dominated habitats largely evolved independently of human society. Nevertheless, as discussed in Chapter 10, human activities selectively modify weed characteristics such that weeds are becoming better adapted to human disturbance regimes.

The subcategory of weeds dealt with in this book consists of the weeds of agriculture – specifically, the plants that colonize and increase in the disturbances created by farming. These are sometimes termed *agrestal* weeds, as distinguished from the *ruderal* weeds of roadsides, waste piles, and other non-agricultural disturbances (Baker, 1965). Agricultural weeds share certain life-history characteristics that adapt them for life on farms (Table 2.1). The thesis of this chapter is that *understanding life-history characteristics provides insights into how weed management practices work and how they can be improved.* In particular, *differences between weeds and crops in germination characteristics, seed size, growth rate, and susceptibility of different life stages to stress provide weed management options.*

Relative to most ecosystems, agricultural fields are not stressful environ-

Table 2.1. *Ecological characteristics of agricultural weeds and crops*

Character	Weed	Crop
Maximum relative growth rate (g $g^{-1}d^{-1}$)	Very high	High
Early growth rate (g d^{-1})	Low	High
Shade tolerance	Low	Low
Tolerance of nutrient stress	Low	Low
Nutrient uptake rate	Very high	High
Seed size	Mostly small	Mostly large
Size at establishment	Mostly small	Mostly large
Reproductive rate	High	Varies with crop
Seasonal innate seed dormancy	Frequent	Very rare
Germination in response to tillage related cues[a]	Common	Rare
Seed longevity in soil	Often long	Usually short
Dispersal	Mostly by humans	By humans

Notes:

[a] Light, fluctuating temperature, nitrate.

ments for plants: to get high productivity from crops, the grower reduces stress through seedbed preparation, fertilization, irrigation, and artificial drainage. Moreover, in annual cropping systems, resources greatly exceed the needs of both crop and weeds for several weeks after the crop is planted, and during this period competition has a negligible effect on seedling establishment. The species that do well in these conditions, namely agricultural weeds, prosper because they have very high maximum relative growth rates (see section "Vegetative growth and crop–weed competition" below). This allows them to grow large rapidly and occupy space before resources are monopolized by crops and any ruderal species that happen to be present. The very high relative growth rates of agricultural weeds are coincident with inefficient resource use. Weeds are more susceptible to the negative effects of shade than are species commonly found in less disturbed conditions (Fenner, 1978). Weeds typically accumulate higher concentrations of mineral nutrients than crop species when nutrients are plentiful, but often suffer greater relative declines in growth than crops when nutrients are in short supply (Vengris, Colby & Drake, 1955; Alkämper, 1976). Inherent physiological trade-offs appear to prevent plants from fully adapting to both high and low light levels (Givnish, 1988), or to both high and low nutrient availability (Schläpfer & Ryser, 1996). Agricultural weeds are at one extreme of these adaptive continua.

Because agricultural weeds establish primarily in conditions of low competition, only minimal provisioning of offspring by the mother plant is required. Hence, weed seeds usually weigh only a few milligrams or less (Table

2.2, below). Small seed size allows for production of many seeds by mature individuals. This facilitates colonization of new sites. Moreover, a high reproductive rate is necessary to compensate for high mortality caused by (i) repeated disturbance during the growing season, and (ii) the environmental unpredictability created by crop rotation and variation in weather. Weeds avoid some unpredictability via dormancy mechanisms and germination cues that allow synchronization of establishment with favorable conditions. They also spread risks across years with different environmental conditions by means of perennation and seed banks. Although all these characteristics allow agricultural weeds to prosper in farm fields, they also provide opportunities for weed management.

Each of the properties of agricultural weeds mentioned above is discussed further in the following sections, with a focus on how the nature of weeds indicates their vulnerability to control. The following discussion focuses on broad patterns and generalities regarding various sorts of weeds. Naturally, exceptions exist for each of these generalizations. To avoid undue digression, however, these exceptions are usually not discussed explicitly. Hopefully, understanding of the usual properties shared by many weed species will also clarify the functional significance of the exceptional properties of unusual species.

The life history of weeds

Weeds progress through a series of stages in the life cycle: germination, establishment, growth, reproduction, dispersal, and dormancy. Management tactics generally apply to a particular stage. Moreover, differences in the behavior of species in each stage lead to differences in susceptibility to control by a particular approach. Thus, life history is an organizing principle for the integration of weed management tactics.

Although agricultural weeds commonly share many ecological attributes, they are by no means a homogeneous group of species. In particular, four broad categories of life history can be distinguished (Table 2.2). Annual weeds grow from germination to reproduction within a single growing season. With few exceptions, their seeds persist in the soil for at least a few years and in many cases for decades.

Stationary perennials live from two to several growing seasons (biennials are included in this group). Because they generally do not rejuvenate via vegetative reproduction, they eventually die. As with the annuals, their seeds usually persist in the soil for at least a few years, and often much longer. Under favorable conditions some of these species may set seed the year of

Table 2.2. *Four types of weed life-history strategies*

Character	Annuals	Stationary perennials	Wandering perennials	Woody perennials
Vegetative life span	< 1 year	2 to a few years	Long, indefinite	Long
Vegetative propagation	No	Accidental	Yes	Some species
Usual seed persistence	Years to decades	Years to decades	A few years	Months to years
Energy allocated to seed production	High	Medium high	Medium low	Low
Seed size[a]	Mostly small	Mostly small	Mostly small	Mostly large
Usual mode of establishment	Seeds	Seeds	Vegetative propagules	Seeds
Main dispersal modes	With soil, manure	With soil, wind, feces, crop seed	With soil	Birds, wind
Position in succession	Year 1 (2 in gaps)	Year 1 to 5 (10)	After year 1	Middle
Taxonomy	Monocot and dicot	Mostly dicot	Monocot & dicot	Mostly dicot
Crop types	Annual	Forage, annual	All	Orchard, pasture, swidden, no-till
Examples	*Chenopodium album* *Setaria faberi*	*Rumex crispus* *Poa annua*[b]	*Imperata cylindrica* *Convolvulus arvensis*	*Lantana camara* *Toxicodendron radicans*

Notes:

[a] Seed size ranges and medians from an analysis of 39 annual, 18 stationary perennial, and 16 wandering perennial British weed species of arable land and well-drained grassland reported in Salisbury (1961) were 0.02–35 (1.1), 0.2–3 (1.2) and 0.13–14 (0.7) mg, respectively, indicating no difference in seed size between the three categories.

[b] Because *Poa annua* sets seed during its first season of life, it can behave as an annual in annual cropping systems. However, if left undisturbed it usually lives at least two seasons, and often sets more seed the second year (Law, Bradshaw & Putwain, 1977).

establishment, but often they require longer to mature. Most stationary perennials are broadleaf species. Perennial bunchgrasses are intermediate between stationary and wandering perennials in that most can rejuvenate indefinitely, but have limited capacity for spreading vegetatively.

Because wandering perennials reproduce by vegetative spread and fragmentation, the life span of a genetic individual is indefinite and potentially very long. Although most of these species produce seeds, most reproduction is by vegetative propagation. Seeds of many wandering perennials persist for more than one year, but relatively few have great seed longevity; consequently, wandering perennials are rarely well represented in the seed bank.

Woody weeds are perennials that develop persistent shoot structures. Although some species spread clonally, most reproduce primarily by seed. Their seeds are often relatively large, short-lived, and dispersed by wind or birds. As explained later, they are problems in long-lived crops like orchards and permanent pastures, and are increasingly problematic in no-till planted annual crops (J. Cardina, personal communication). Woody weeds with a vining growth habit (lianas) are often the most difficult to control because they can sprawl laterally and can rapidly reach an orchard canopy by using the crop trees for support.

The contrasting life-history characters of the four groups express ecological rather than physiological trade-offs. For example, propagation by rhizomes is probably not physiologically related to lack of persistence in the seed bank. Basically, adaptation to different stages of ecological succession has grouped characteristics into suites, thereby forming four ecologically distinct types of weed species.

Following a severe disturbance like tillage, annuals predominate because they can survive the disturbance event in a physiologically dormant state as seeds. The stationary perennials are similarly tied to establishment shortly after tillage. However, because they persist in a vegetative state for a longer period, their allocation of resources to roots is greater, and consequently, their seedling growth rate tends to be lower. Thus, in the first year after disturbance, annuals often predominate even if stationary perennials are abundant in the seed bank. However, because stationary perennials start growth with greater reserves during the second season of life compared with newly germinated annuals they are better able to compete with established perennial crops after the first year. Consequently, they are particularly common in hay fields.

In pre-agricultural landscapes, wandering perennials were probably found primarily after the first year of regrowth in fertile, disturbed locations like areas where animals congregated or flood deposited soil along streams. Today, wandering perennial agricultural weeds like *Elytrigia repens* and *Cirsium arvense* are commonly found in well-vegetated, abandoned fields, roadsides, and even disturbed forest. To spread under highly competitive conditions in closed vegetation, they were selected to substantially provision vegetative propagules. Seeds probably served primarily for the risky enterprise of long-distance dispersal.

The advent of tillage greatly changed conditions of life for wandering perennials. Tillage separates daughter plants from the parent and spreads them within and between fields. Simultaneously, tillage removes the competing vegetation. This puts spreading perennials in the advantageous position of having well-provisioned propagules establishing with relatively little competitive pressure. Consequently, many of the world's worst weeds are wandering perennials (Holm *et al.*, 1977). Essentially, these species have characteristics that evolved in response to conditions quite different from present-day agriculture, but they were fortuitously pre-adapted to thrive under moderate tillage. However, deep and frequently repeated tillage is often detrimental to these species (Chapter 4).

Woody perennial weeds are primarily problems in orchards and pastures. Although they help restore soil and eliminate pests and disease during the regenerative phase of shifting agricultural systems (swidden), they can also reduce crop productivity during the cropping phase (Staver, 1991). Woody perennials are poorly adapted to cropping systems with annual tillage for two reasons. First, only a few of these species form persistent seed banks, and consequently, synchronizing establishment with an annual crop is rarely possible. Second, wood is an energetically expensive way to hold up a plant relative to fiber and turgor pressure. Consequently, woody plants grow more slowly than herbs when young (Grime & Hunt, 1975), and as young plants they are rarely competitive with herbaceous annual crops. Because tillage prevents woody weeds from surviving more than one year, they are poorly adapted to most annual cropping systems. Nevertheless, their long life span, tall stature, and vigorous resprouting after cutting and browsing make them serious weeds in tree crops and pastures, and a significant nuisance in no-till planted annual crops.

Parasitic weeds constitute an additional life-history category not included in Table 2.2. To the extent that they behave like other vascular plants (e.g., seed production, seed dispersal), the principles discussed in this book apply to them as well as to weeds that affect the crop primarily through competition for resources. To the extent that they behave more like pathogens (e.g., germination in the presence of host roots, source of nutrition), their study is a specialized field beyond the scope of this book. Several recent books treat the

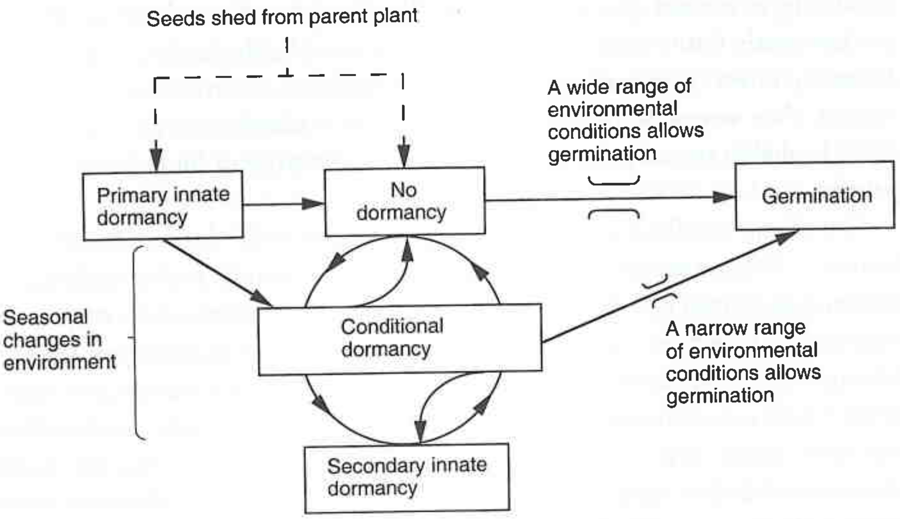


Figure 2.1 Dormancy/germination states of weed seeds. (Redrawn from Egley (1995) based on the concepts of Baskin & Baskin (1985, 1998*a*).)

ecology and management of parasitic weeds (Musselman, 1987; Pieterse, Verkleij & ter Borg, 1994; Hosmani, 1995).

Dormancy and germination

Seasonal and aseasonal germination

Weed seeds often undergo several changes in dormancy state between seed shed and germination (Figure 2.1) (Baskin & Baskin, 1985). These changes represent an adaptive response to the problem of immobility: a seed has little control over where it lands, but through dormancy response to environment, it can choose when to germinate. When first shed from the parent plant, seeds may lack dormancy and be ready to germinate if environmental conditions are favorable. This is commonly the case for those winter annuals like *Galium aparine* that commonly shed seeds in mid to late summer (Håkansson, 1983). Seeds of these species need to be ready for immediate germination since winter annuals usually do best when they establish early in the autumn.

Alternatively, seeds may have innate dormancy when shed (primary innate dormancy). Innate dormancy may be due to impermeable (hard) seed coats, chemical germination inhibitors in the seed coat or embryo, a cold or heat requirement, or other physiological mechanisms (Povilaitis, 1956; Baskin & Baskin, 1985; Taylorson, 1987). Such mechanisms are found in most weedy species of the temperate zone (Baskin & Baskin, 1988) and provide means for matching the period of germination to weather conditions that are suitable for establishment and growth of the plant. With time, seed coats break down, chemical inhibitors are leached away, and cold or heat requirements are satisfied by winter or summer temperatures, depending on the species. The seed then becomes capable of germination.

Nondormant seeds still may not germinate, however, if environmental conditions are unfavorable. Frequently, seeds remain in a quiescent state until appropriate temperatures, water, light, and other germination cues indicate that conditions are favorable for germination and establishment. For some species, seeds that can not germinate because appropriate conditions are lacking may enter a secondary state of innate dormancy (e.g., *Ambrosia artemisiifolia* – Baskin & Baskin, 1980; *Arabidopsis thaliana* – Baskin & Baskin, 1983). In that state, the seed must undergo another period of chilling, heating, leaching, etc., before germination is again possible. The transition into (and out of) innate dormancy is gradual: the seed passes through a series of conditional dormancy states in which the range of environmental conditions that trigger immediate germination becomes increasingly narrow (Baskin & Baskin, 1998*a*, pp. 50–64). Seeds of many species may cycle between innate dormancy and non- or conditional dormancy for several years before the environment happens to favor germination in an appropriate season.

Due to these dormancy processes, most weed species germinate at particular times of year. For example, Chepil (1946) observed the timing of emergence of 59 species in Saskatchewan and grouped the species into five categories. The categories of peak emergence were (i) early spring (e.g., *Bromus tectorum*, *Chenopodium album*, *Plantago major*), (ii) mid spring (e.g., *Setaria viridis*, *Cirsium arvense*), (iii) summer (e.g., *Amaranthus retroflexus*, *Capsella bursa-pastoris*, *Portulaca oleracea*), (iv) autumn (e.g., *Sophia multifida*, *Lepidium perfoliatum*), and (v) no consistent period of peak emergence (e.g., *Taraxacum officinale*, *Sinapis arvensis*, *Medicago lupulina*). Other authors have found similar variation in the emergence times of temperate weeds (Figure 2.2) (Lawson, Waister & Stephens, 1974; Roberts & Neilson, 1980; Roberts & Potter, 1980; Håkansson, 1983; Roberts, 1984), although some have also found species with bimodal germination in spring and fall (e.g., *Veronica hederifolia* in Figure 2.2).

Several points can be made regarding these studies. First, most "winter annual" agricultural weeds are only facultatively tied to autumn germination. Only a few have secondary dormancy mechanisms that prevent spring germination (e.g., winter annual races of *Arabidopsis thaliana*, Baskin & Baskin, 1983), and so most agricultural weeds that show a winter annual phenology are found in spring-sown crops as well (Hald, 1999). Second, little overlap in

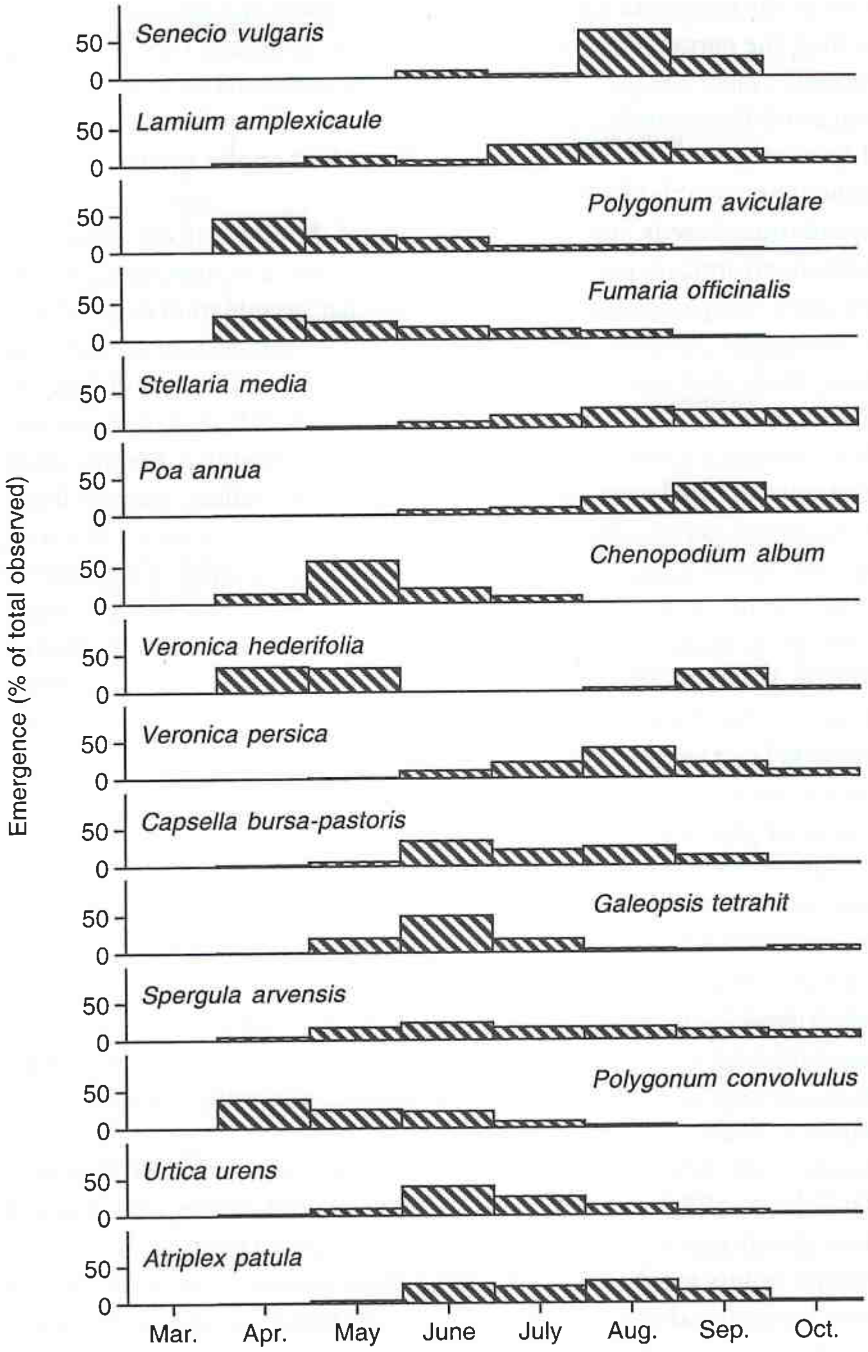


Figure 2.2 Seasonality of emergence in 15 weed species (from Lawson, Waister & Stephens, 1974, experiment I). Data are percent of total counts observed three weeks after soil disturbances performed at monthly intervals in the southern United Kingdom.

the time of germination may occur between species characteristic of early versus late spring (e.g., Figure 2.2). For some species, early and late spring are apparently very different seasons. Third, although most species have times of the year in which germination is most probable, at least some seeds germinate over a wide range of other seasons. This occurs because the dormancy mechanisms are less than perfect in matching germination to one particular season. However, that variability provides adaptation to environmental unpredictability. Finally, the species that have a very broad season of germination tend to be small-statured, rapidly maturing plants, with broad-amplitude temperature tolerance. Such species are well adapted to gardens and mixed high-intensity vegetable farms where the cropping conditions are unpredictable, and therefore, early catastrophic mortality is frequent.

A large comparative study by Forcella *et al.* (1997) illustrates the importance of understanding how dormancy affects the seasonality of seedling emergence. By examining percentage emergence of several weed species in relation to environmental conditions at 22 site and year combinations, they identified soil temperature and moisture thresholds that induced secondary dormancy in *Setaria faberi*, *S. viridis*, *Polygonum convolvulus*, *P. pennsylvanicum*, and *Amaranthus* spp. (mostly *A. retroflexus*). Once the threshold for one of these species has been passed during a growing season, the seeds are induced into secondary dormancy. Few individuals are likely to emerge after that date, and a grower can modify management plans accordingly.

Probably the principal utility of understanding periodicity of weed seed germination is that it allows disruption of weed life cycles. Two approaches are mentioned here and discussed in depth in Chapters 4, 6, and 7. First, if the time of germination is known for the dominant weeds in the seed bank, crop planting dates can be adjusted so that either (i) the crop emerges before the weeds and thereby obtains a competitive advantage, or (ii) weeds are allowed to germinate and are then destroyed during seedbed preparation. Second, by rotating between crops with radically different planting dates, a grower can block the establishment and reproduction of particular groups of weeds in any given year. Thus, for example, in a fall-sown grain crop, spring germinating weeds will either remain dormant or, if they do germinate, suffer heavy competition from the already well-established crop. Those that do not germinate are subjected to another year of mortality risk as seeds, reducing weed pressure on later crops. Alternation of early spring grains or vegetables with late spring- or summer-planted soybean or vegetable crops may be equally effective in disrupting weed life cycles.

Why tillage promotes the germination of weed seeds

Tillage promotes germination of most agricultural weeds, provided the soil disturbance comes at a time of year when the seeds are not innately dormant. Agricultural weeds have adapted to respond to cues associated with soil disturbance because their small seedlings make them poor competitors early in life. Vigorous, well-established plants are unlikely to be present immediately after soil disturbance, and hence weedy species have been selected for germination under conditions that indicate soil disturbance. Relative to undisturbed soil with established vegetation, recently tilled ground tends to be warmer, have higher diurnal temperature fluctuations, higher nitrate concentration, and better aeration (Gebhardt *et al.*, 1985; Cox *et al.*, 1990; Dou, Fox & Toth, 1995). Perhaps most importantly, when tillage or natural processes stir soil, exposure to light prompts seed germination (Sauer & Struik, 1964).

Each of these factors promotes the germination of some common agricultural weeds (Table 2.3). For example, *Rumex crispus*, *Chenopodium album*, and *Panicum dichotomiflorum* have a higher percentage germination when exposed to fluctuating temperatures than when exposed to a constant temperature with the same mean (Henson, 1970; Totterdell & Roberts, 1980) or when separately tested against the two temperature extremes (Fausey & Renner, 1997). *Amaranthus retroflexus* germinates best at 30–40 °C (McWilliams, Landers & Mahlstede, 1968; Weaver & Thomas, 1986), a soil temperature that is unlikely to occur under the shade of established vegetation.

Tillage and other soil disturbances stimulate decomposition of organic matter and nitrification of the ammonium released by decomposition. The presence of nitrate thus indicates not only enhanced availability of mineral nutrients, but also the elimination of competing vegetation. In any case, nitrate indicates favorable growing conditions, and germination of several weed species, including *Chenopodium album* and *Plantago lanceolata*, increases in response to elevated nitrate concentrations (Williams & Harper, 1965; Pons, 1989).

Gas exchange in the soil during tillage probably prompts germination of many weed species. Although oxygen concentration influences germination (Edwards, 1969; Popay & Roberts, 1970; Brennan *et al.*, 1978), oxygen levels near the soil surface are rarely low enough to directly inhibit germination, except when the soil is saturated with water (Egley, 1995). Several studies have

Table 2.3. *Factors associated with tillage that have been shown to promote the germination of weed seeds*

Factor	Species	+Factor (%)[a,b]	−Factor (%)[a,b]	Reference
Light	*Alopecurus myosuroides*	86	0	Froud-Williams (1985)
	Amaranthus retroflexus	98	14	Kigel (1994)
	Brassica arvensis	78	53	Povilaitis (1956)
	Datura ferox	96	1	Scopel, Ballaré & Sánchez (1991)
	Lolium multiflorum	95	82	Schafer & Chilcote (1970)
	Poa annua	89	1	Froud-Williams (1985)
	Portulaca oleracea	28	12	Povilaitis (1956)
Alternating temperature	*Poa annua*	92	47	Froud-Williams (1985)
	Rumex crispus	100	0	Totterdell & Roberts (1980)
	Sonchus arvensis	57	3	Håkansson & Wallgren (1972)
	Sorghum halepense	20	7	Ghersa, Benech Arnold & Martinez-Ghersa (1992)
	Stellaria media	93	47	Roberts & Lockett (1975)
Nitrate	*Chenopodium album*	92	55	Williams & Harper (1965)
	Erysimum cheiranthoides	89	57	Steinbauer & Grigsby (1957*a*)
	Plantago lanceolata	48	25	Pons (1989)
	Plantago major	93	3	Steinbauer & Grigsby (1957*b*)

Notes:

[a] +Factor: seeds germinated in light, in alternating temperature regime, and in nitrate solution. −Factor: seeds germinated in dark, at constant temperature equal to the mean of the alternating regime, and in water.

[b] The numbers given for percentage germination are mostly means taken over several chilling treatments, populations, seed types, etc., but not over treatments that involve variation in other factors listed in the table. In a few cases, the numbers are from selected treatments that demonstrate the effect.

mination (Wesson & Wareing, 1969*b*; Holm, 1972), the effect could not be attributed to improved oxygen availability alone. Holm (1972) further observed that imbibed *Abutilon theophrasti* and *Ipomoea purpurea* produced ethanol, acetone, and acetaldehyde when oxygen concentrations dropped below 6% and demonstrated that these compounds inhibited germination of seeds, even in normal air. He therefore proposed that moderate reduction in oxygen by respiration in the soil results in anaerobic seed metabolism, which produces volatile germination inhibitors. In the absence of air exchange, these enforce seed dormancy. Thus, tillage probably prompts germination of weed seeds both by venting volatile inhibitors from the surface soil and by moving deeply buried seeds to near-surface conditions where air exchange is improved.

Although ethylene and carbon dioxide concentrations are also commonly elevated in undisturbed soil, these compounds appear to play a small role in inhibiting seed germination. Ethylene affects germination of only a small proportion of weed species, and usually promotes, rather than inhibits, germination (Taylorson, 1979). Similarly, concentrations of carbon dioxide up to 5% tend to enhance, rather than inhibit, germination (Baskin & Baskin, 1987; Egley, 1995).

One of the most important cues promoting germination of seeds in the seed bank is light. In a classic study, Wesson and Wareing (1969*a*) collected soil at night, screened it in the dark, and then placed it in trays in a greenhouse in either the light or dark. Averaged over three experiments at different times of year, they found 12 times more dicot seedlings and 26 times more grass seedlings in the light treatment. Many subsequent studies have shown that germination of a great range of weed species is promoted by light (Taylorson, 1972; Stoller & Wax, 1974; Froud-Williams, 1985; Baskin & Baskin, 1986). Some species of weed seeds germinate in response to very small amounts of light. For example, conditional dormancy in *Datura ferox* and *Amaranthus retroflexus* can be broken by the equivalent of a few milliseconds of sunlight (Scopel, Ballaré & Sánchez, 1991; Gallagher & Cardina, 1998). Moreover, many species, like *Spergula arvensis* and *Stellaria media*, that lack light sensitivity when shed from the parent plant quickly develop it after incorporation into the soil (Wesson & Wareing, 1969*b*; Holm, 1972).

Because light-sensitive germination is controlled by the phytochrome system, light depleted in red wavelengths by passage through a plant canopy is inhibitory to germination of light-sensitive species (Górski, 1975). In fact, even some species with moderately high germination in the dark are severely inhibited by light that has passed through plant leaves (King, 1975; Silvertown, 1980). Thus, germination under established vegetation is held in check not only by the amount of light but also by its spectral composition.

Although the several factors discussed above promote germination individually, the effects are most pronounced when several factors combine. Vincent & Roberts (1977), Bostock (1978), Roberts & Benjamin (1979), and Kannangara & Field (1985) demonstrated that two- and three-way interactions among light, nitrate, and fluctuating temperature enhanced germination of 13 out of the 15 weed species they studied. Presumably, the several factors acting in concert provide a more certain signal that competition has been eliminated than any of the factors acting singly.

Germination in response to tillage is both a fact that must be dealt with in the design of agricultural systems and a tool for manipulation of weed populations. For example, shallow cultivation between crop rows is often preferable to deep cultivation. A shallow cultivation tends to eliminate the weeds

all role in
y a small
ibits, ger-
xide up to
xin, 1987;

eds in the
lected soil
nhouse in
ıt times of
rass seed-
ıat germi-
ıon, 1972;
36). Some
s of light.
retroflexus
ıt (Scopel,
ıy species,
hen shed
o the soil

tochrome
nt canopy
5). In fact,
e severely
ıg, 1975;
is held in
sition.
tion indi-
combine.
979), and
y interac-
germina-
he several
tition has

ılt with in
eed popu-
en prefer-
the weeds

---

that were prompted to germinate in response to seedbed preparation without cueing germination of many additional seeds. In contrast, a deep cultivation tends to bring up seeds that are then prompted to germinate by disturbance-related cues. Dynamics of the seed bank in response to tillage is discussed further in Chapter 4.

The germination response of weeds to soil disturbance can also be used to induce inappropriate germination. For example, species with broad seasonality of germination can be stimulated to establish at times that are unsuitable for survival to reproduction, thereby depleting the seed bank. A more common application is to use shallow cultivations with intervening rests before planting to flush out and kill many of the weeds that would otherwise establish with the crop. Use of this "false seedbed" method is analyzed in Chapter 4.

Not all species of weeds are sensitive to germination cues associated with soil disturbance. Most of these are relatively large seeded species (Table 2.4, below) that presumably have sufficient resources in the seedling stage to establish in the face of some competition from established vegetation. Many have hard, impermeable seed coats that prevent water uptake and germination, or other dormancy mechanisms that prevent germination until the seed coat is physically altered (Table 2.4). In the field, temperature extremes or desiccation typically break physical dormancy (Baskin & Baskin, 1998*a*, pp. 114–20). Response to these factors spreads germination over several years and, to some extent, also cues germination to appropriate times of the year. Some large-seeded weeds also have innate physiological dormancy mechanisms (Wareing & Foda, 1957). Thus, large-seeded weeds have mechanisms that match germination to appropriate environmental conditions, but only a few (e.g., *Solanum viarum* – Akanda, Mullahey & Shilling, 1996) sense the removal of competitors through a strong response to light, alternating temperature, or nitrate.

Survival of weed seeds in the soil

The seeds of most annual and stationary perennial weeds persist in the seed bank for at least a few years, and many remain viable for decades if conditions are favorable. Excavations from dated archaeological strata indicate that some agricultural weed species, including *Chenopodium album*, *Stellaria media*, and *Lamium purpureum*, probably remain viable for several hundred years (Odum, 1965), although movement of younger seeds into the strata by soil animals cannot be excluded with certainty. However, the cool, moist, dark, undisturbed environments of such sites are highly favorable to

Table 2.4. *Characteristics of some species with negligible response to germination cues associated with tillage*

Species	Seed size, mg	Innate dormancy[a]	Wounding/ hard seed[b]	Light[a]	Alternating temperature[a]	NO_3[a]	References
Abutilon theophrasti	4–10	0,(+)	H	0,+,(−)		0	LaCroix & Staniforth (1964), Holm (1972), Fawcett & Silfe (1978), Horowitz & Taylorson (1984, 1985), Warwick & Black (1988)
Avena ludoviciana		0,+	W	−	0	0	Thurston (1960), Froud-Williams (1985)
Bromus sterilis	8	0		0	0	0	Froud-Williams (1985), Thompson, Band & Hodgson (1993)
Convolvulus arvensis	10	0	H	0	(+)		Weaver & Riley (1982)
Xanthium strumarium	50–60	+	W	0	(+)		Wareing & Foda (1957), Kaul (1965), Weaver & Lechowicz (1983)

Notes:

[a] +, −, and 0 indicate that the factor promoted, inhibited or had no effect on germination in the studies cited. Parentheses indicate that the effect was weak. Blanks indicate that information was unavailable.

[b] H, hard seeds; W, wounding increases germination, but seeds are not hard in the usual sense.

Table 2.5. *Half-life and annual loss of seeds from soil for 20 weed species, computed from seed survival over a five-year period*[a]

	Loss per year (%)		Half-life (years)	
	Cultivated	Uncultivated	Cultivated	Uncultivated
Capsella bursa-pastoris	43	24	1.2	2.6
Chenopodium album	31	8	1.9	8.3
Euphorbia helioscopia	54	21	0.9	3.0
Fumaria officinalis	34	16	1.7	4.1
Matricaria matricarioides	33	28	1.8	2.1
Medicago lupulina	30	22	2.0	2.8
Papaver rhoeas	38	30	1.4	2.0
Poa annua	26	22	2.3	2.8
Polygonum aviculare	47	16	1.1	4.0
Polygonum convolvulus	50	25	1.0	2.4
Senecio vulgaris	[b]	45	[b]	1.2
Spergula arvensis	60	30	0.8	2.0
Stellaria media	54	32	0.9	1.8
Thlaspi arvense	50	10	1.0	6.8
Tripleurospermum maritimum ssp. *inodorum*	36	23	1.6	2.6
Urtica urens	37	17	1.5	3.7
Veronica hederifolia	[b]	13	[b]	5.1
Veronica persica	54	22	0.9	2.8
Vicia hirsuta	36	30	1.6	2.0
Viola arvensis	40	15	1.4	4.2

Notes:

[a] Seeds were mixed with the top 15 cm of soil and either left undisturbed or mixed four times per year.

[b] No seeds viable after five years.

Source: From Roberts & Feast (1972).

seed survival (Villiers, 1973), whereas seed longevity is much less in agricultural fields (Table 2.5). Often the logarithm of seed density plotted against time follows a straight line for weed seed banks (Roberts & Dawkins, 1967; Roberts & Feast, 1973), although in some cases the mortality rate is somewhat higher or lower during the first year (Figure 2.3). Thus, seed survival times are often better characterized by the half-life of the population rather than the maximum age achieved by the most persistent individual. Studies on weed seed survival lead to two general conclusions. First, a substantial portion of the seeds of even relatively persistent species disappears from the soil each year, and second, soil disturbance increases the rate of disappearance (Table 2.5) (Roberts & Feast, 1972; Lueschen & Andersen, 1980; Froud-Williams, Chancellor & Drennan, 1984; Warnes & Andersen, 1984; Barralis, Chadoeuf & Lonchamp, 1988).

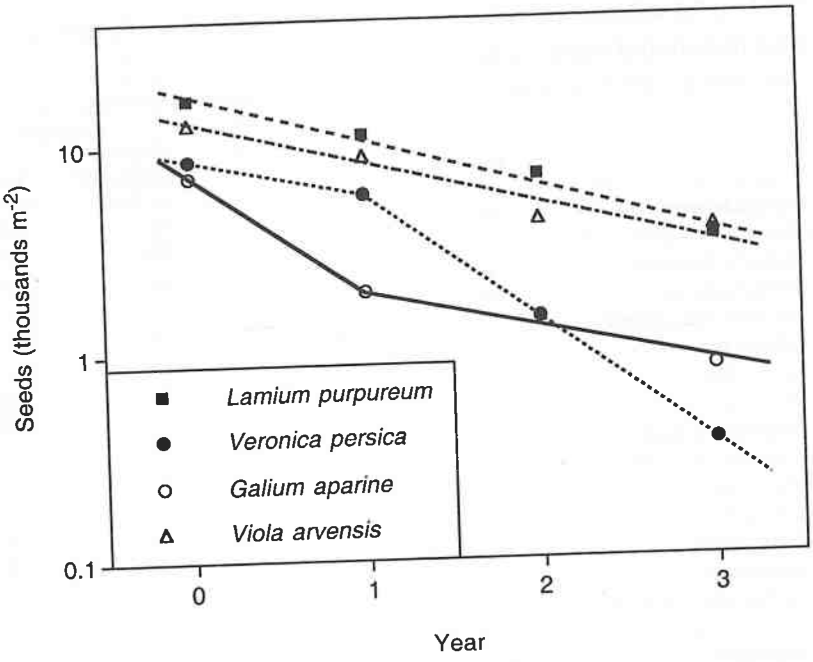


Figure 2.3 Decline in density of viable seeds through time in a field annually tilled and planted with winter wheat or winter oilseed rape. (After Wilson & Lawson, 1992.)

Sources of seed mortality

Factors affecting the rate of seed mortality in the soil include (i) the action of seed predators, including vertebrates, invertebrates, fungi, and bacteria, (ii) physiological aging and exhaustion of reserves through respiration, and (iii) germination at depths in the soil or times of year that are unsuitable for emergence. Strictly speaking, the latter involves the death of seedlings rather than seeds, but it is customarily treated as a source of seed mortality. Several studies have partitioned the sources of weed seed mortality, and of the three factors listed above, inappropriate germination often causes the greatest reduction in seed density (Roberts, 1972). For example, Schafer & Chilcote (1970) found that after burial for 60 days at 10 cm depth, 11% to 13% of *Lolium multiflorum* seeds were nonviable whereas 40% to 64% had died after germination. Zorner, Zimdahl & Schweizer (1984*a*, 1984*b*) and Gleichsner & Appleby (1989) found that *in situ* germination was the largest source of mortality for deeply buried *Avena fatua*, *Kochia scoparia*, and *Bromus rigidus* (*B. diandrus*) seeds, but that loss of viability increased as a cause of mortality with shallower placement. Wilson (1972) noted (i) that *A. fatua* lost dormancy more quickly at the soil surface and (ii) that the seeds on the soil surface rapidly lost weight whereas seeds that had been cultivated into the soil did not. He hypothesized that seeds on the soil surface physiologically initiated germination, but died prior to emergence of the radical. Many *Abutilon theophrasti* seeds on the soil surface imbibe and the seed coat breaks, but germination does not proceed further due to subsequent desiccation (C. L. Mohler, personal observation). In contrast, most *A. theophrasti* seeds buried 1 cm deep emerge successfully. Seed movement by tillage implements and seed survival at different depths in the soil profile are considered further in Chapter 4.

A problem with the above studies and observations is that the species investigated lack strong tillage-cued germination mechanisms and, with the exception of *K. scoparia*, all are relatively large-seeded. Whether the many small-seeded species that rely on environmental cues to inform them of proximity to the soil surface and lack of competition also suffer large mortality due to inappropriate germination remains to be determined. The technical problems of investigating causes of seed loss in small-seeded species with great longevity in the soil are substantial: few seeds are likely to lose viability or germinate inappropriately in any given time interval, and recovering tiny seedlings in the white thread stage is difficult.

Physiological aging of seeds involves loss of membrane integrity, deterioration of organelles, and accumulation of damage to DNA (Abdalla & Roberts, 1968; Villiers, 1973; Roberts, 1988). These aging processes proceed most rapidly when seeds are in warm conditions with seed moisture in the 8% to 15% range (Abdalla & Roberts, 1968; Villiers & Edgcumbe, 1975). In contrast, fully imbibed dormant seeds are metabolically active and apparently capable of repairing structural and genetic damage (Villiers & Edgcumbe, 1975; Elder & Osborne, 1993). These observations probably explain why mortality due to loss of viability increases toward the soil surface: conditions near the surface are warmer than deep in the soil profile and are periodically too dry to maintain seeds in a fully imbibed state. Eventually, even imbibed seeds die, presumably due to accumulation of lethal levels of damage to membranes and DNA (Osborne, 1980; Villiers, 1980). The extent to which depletion of food reserves is involved in the aging process is poorly studied.

Seed predators consume significant numbers of weed seeds in some agroecosytems. Prior to dispersal from the parent, predation is primarily by host-specific natural enemies. Pre-dispersal seed predators may occasionally consume a substantial proportion of the seeds produced (Forsyth & Watson, 1985), but particularly in annual crops, they may have difficulty in locating their host plants, as explained in the section "Survival after emergence" below. After seeds have dispersed from the parent, they are attacked by a range of generalist seed predators including birds, small mammals, earthworms, insects, and fungi (Wilson & Cussans, 1972; Grant, 1983; Brust & House, 1988; Fellows & Roeth, 1992). Seed predation, and the manipulation of agricultural systems to increase predation on weed seeds, are discussed further in Chapters 5 and 8.

What types of species survive better in soil?

Species vary greatly in their ability to survive in the soil seed bank, and certain broad patterns exist that predict which species survive well in the soil. Understanding trends in seed survival across species provides a means for targeting ecological management strategies at particular classes of weeds. It also provides a basis for guessing the likely seed persistence of unstudied species.

A first broad pattern across species is that many broadleaf weeds are able to survive in the seed bank for several decades (Chancellor, 1986), whereas seeds of only a few grass species survive in substantial numbers for more than 5 to 10 years (Dawson & Bruns, 1975; Froud-Williams, 1987, Baskin & Baskin, 1998*b*). Moreover, the seeds of some grass weeds do not persist longer than a single year (e.g., *Bromus diandrus* – Harradine, 1986; Gleichsner & Appleby, 1989; *Bromus sterilis* – Roberts, 1986), whereas few, if any, broadleaf agricultural weeds appear to have seed survival times as short as that. Both of the annual grasses tested by Conn & Deck (1995) (*Avena fatua* and *Hordeum jubatum*) were reduced to < 1% viability by 3.7 years of burial and were completely gone after 9.7 years. In contrast, mean survival of the 13 annual broadleaf species they tested was 32% after 3.7 years, and all but one of the broadleaf species had at least a few surviving seeds after 9.7 years. Burnside *et al.* (1996) counted seedlings emerging from seed samples that had been left in the soil for 1 to 17 years. After 12 years of burial, the 14 annual broadleaf species averaged 10% germination, whereas germination of the 11 annual grasses averaged only 2%. Nevertheless, some economically important weedy annual grasses, notably *Echinochloa crus-galli*, *Bromus secalinus*, and several species of *Setaria*, retained moderate viability into their second decade of burial.

A second broad pattern among species is that annual and stationary perennial weeds tend to form persistent seed banks, whereas wandering perennials and woody weeds usually do not. For example, of the 22 terrestrial grass species tested by Roberts (1986), the weedy, short-lived *Avena fatua*, *A. sterilis* ssp. *ludoviciana*, and *Poa annua* had the greatest emergence 2 years after sowing, whereas many of the rhizomatous species were completely gone by that time. In the study of Burnside *et al.* (1996), seven stationary perennial broadleaf species (including biennials) averaged 37% germination after 8 years of burial and 25 annual broadleaf species averaged 15%, whereas nine wandering broadleaf perennials had an average germination of only 5%. In a study of the flora of northwestern Europe that emphasized arable weeds and grassland species, Thompson *et al.* (1998) showed greater persistence of monocarpic (single fruiting – in this context, annual and biennial) species relative to polycarpic (multiple fruiting) species.

A third pattern across species is that those with weak dormancy mechanisms often have shorter longevity than species with well-developed dormancy mechanisms (Bostock, 1978; Roberts, 1986). The greater persistence of species with dormancy is due to reduction of inappropriate germination rather than to greater retention of viability (Roberts, 1972). Experimental support for the importance of innate dormancy for seed survival comes from studies showing that seed lots of several weed species that were dormant when buried retained viability in the soil better than initially nondormant seed lots (Taylorson, 1970; Naylor, 1983; Zorner, Zimdahl & Schweizer, 1984*b*).

A fourth general pattern is that small, round-seeded species tend to persist in the seed bank longer than species with large or elongate seeds. Thompson, Band & Hodgson (1993) surveyed 97 species and found that few species with seeds larger than 2 mg or with variance in diaspore relative dimension greater than 0.2 persisted longer than 5 years in the soil. In the non-agricultural conditions in which seed persistence evolved, incorporation into the soil was probably more difficult for large or elongate seeds than for small, round ones. The latter can wash into cracks, or be ingested by earthworms more easily than the former. Since seed survival is lower on the soil surface than deep in the profile, species with a low probability of incorporation into the seed bank probably experienced little selection favoring mechanisms that allow long persistence. Large seeds are also more likely to be eaten by small mammals (Hulme, 1994), and possibly selection rarely favors mechanisms that allow long residency in the soil of large-seeded species for this reason. The exceptions to the general pattern occur primarily in the Leguminosae, Convolvulaceae, and Malvaceae, which include many species with large, hard seeds (Taylorson, 1987). Seeds of most of these species have toxins that may help defend them against mammalian seed predators (e.g., *Senna obtusifolia, Ipomoea purpurea*) (Kingsbury, 1964, p. 314; Friedman & Henika, 1991).

Seed persistence and weed management

Persistence of seeds in the soil has consequences for many aspects of weed management. By allowing a given generation of seeds to test the suitability of several growing seasons, a seed bank buffers annual species against a year in which little reproduction is possible (Cohen, 1966). This protects the weed against local extinction, but from the grower's point of view, it makes weeds with seed banks highly resistant to eradication. However, complete eradication is rarely necessary, and knowledge of seed longevity of a species allows some predictability regarding how long perfect control of the weed is required to reduce weed pressure by a given amount (Donald & Zimdahl, 1987). Similarly, rotation into a sod crop allows several years for mortality to reduce the seed bank (Thurston, 1966; Warnes & Andersen, 1984). The effect of rotation on seed banks is discussed further in Chapter 7.

Seed longevity of a species also has a large effect on its response to different tillage regimes, and, as explained in Chapter 4, may be an important factor contributing to the shift from broadleaf species to grasses with reduced tillage. Finally, accumulation of high densities of seeds in the soil allows dispersal in soil clinging to animals, vehicles, and tillage machinery, and this is probably an important route for dispersal of weeds between fields (see section "Dispersal of seeds and ramets" below).

Hazards of establishment

The period of establishment may be defined as the time between germination and the production of the first true leaf. This is the most poorly studied stage in the weed life cycle, except with respect to its sensitivity to herbicides. The few quantitative data available indicate that this phase of the life cycle represents a major bottleneck for some species (Boutin & Harper, 1991). Several mortality factors act on establishing weeds, including exhaustion of seed reserves, drought, seedling predation, disease, physical disturbance, and expression of morphological and genetic defects. Data on the effects of all these phenomena are scarce.

One of the most important factors is exhaustion of seed reserves during emergence. The probability of emergence for a newly germinated seedling is a function of depth of burial, the energy content of the seed, and the resistance of the soil. Although the soil in most tilled seedbeds is probably sufficiently loose to not greatly impede emergence, penetration of the shoot through compact soil requires more energy (Morton & Buchele, 1960), and this probably prevents some weed emergence in no-till systems (Mohler & Galford, 1997).

The seeds of most agricultural weeds weigh less than 2 mg and few exceed 10 mg (Table 2.6) (Stevens, 1932; Thompson, Band & Hodgson, 1993). Consequently, successful emergence requires that weed seeds germinate within a few centimeters of the soil surface (Chancellor, 1964; see also literature review and summary table in Mohler, 1993). In contrast to the many

Table 2.6. *Propagule weight of annual weeds and crops*

Weed species[a]	Propagule weight (mg)	Embryo plus endosperm weight (mg)	Crop species[b]	Propagule weight (mg)
Abutilon theophrasti	9.5	5.1	Maize	250
Ambrosia artemisiifolia	4.4	2.4	Soybean	220
Brassica kaber	2.2	1.8	Wheat	39
Chenopodium album	0.74	0.47	Oat	35
Amaranthus retroflexus	0.44	0.29	Rye	27

Notes:

[a] Weeds are the five most common annual weeds in agronomic crops in New York state (Bridges, 1992).

[b] Crops are the five annual agronomic crops with the greatest hectarage in New York state (New York Agricultural Statistics Service, 1994).

Source: Adapted from Mohler (1996).

small-seeded weeds that emerge best from a depth of 0.5 to 1.0 cm, most agronomic crops and many vegetable crops have much larger seeds (Table 2.6). Consequently, they are usually planted at 3 to 5 cm. As discussed in Chapter 4, this difference in emergence depth allows pre- and post-emergence cultivation in the crop row. In some systems, it also allows directed feeding of water and nutrients to the crop (Chapter 5). In addition, the difference in seed size between crops and weeds makes possible the use of crop residue and dust mulches (Chapter 5) and greatly facilitates the use of crop competition for weed management (Chapter 6). Conversely, the relatively small difference between the seed size of crop species and large-seeded weeds like *Xanthium strumarium*, *Avena fatua*, and *Ipomoea hederaceae* helps explain why these species are so difficult to control.

Herbivores and damping off fungi have their greatest impact on weed density during the establishment phase because very small plants have few resources for defense and recovery. Cover by residue and the crop canopy is a major factor regulating the effectiveness of naturally occurring generalist seedling predators (see Chapter 5). Frequently, the inundative release of biological weed control agents is most effective when the weeds are small (e.g., Pitelli, Charudattan & Devalerio, 1998).

The susceptibility of a weed to physical disturbance decreases as it grows. First, as the plant grows, stems and roots thicken and toughen with fiber. Consequently, impact with a hoe or cultivator tine is less likely to cause fatal breakage to a large old plant than to a small young one. Second, plants grow by repeated addition of metamers, units consisting of a leaf, the subtended bud(s), and an internode (White, 1979). Potentially, a weed can lose most of its shoot and still regrow into a full-sized plant, provided a single bud is left. Modular growth below ground similarly allows recovery from drastic damage to the root system. However, for most herbaceous dicot species, a seedling that is broken between the root and base of the cotyledons will not survive. At this stage the weed has only one shoot meristem, and its loss is fatal. Establishing monocot seedlings are somewhat less susceptible to damage than dicots because they lack the long hypocotyl between the root and shoot meristems, but they too may fail to recover following loss of a substantial portion of the cotyledon or primary root. Thus, very small weeds in the white thread and cotyledon stages are more easily controlled by mechanical means than are weeds that are more developed. Cultivation techniques specifically aimed at establishing weed seedlings are discussed in Chapter 4.

Surprisingly, the biology of mechanical weed management has been little studied. For example, conventional wisdom among farmers holds that rotary hoeing is most effective if the soil is not immediately wetted afterward by rain or irrigation, and some experimental evidence confirms this view (Lovely, Weber & Staniforth, 1958). However, the phenomenon has only been studied at the level of the field, and not at the level of the individual weed. To what extent is the elimination of weeds by a pre-emergence operation with a rotary hoe or tine weeder due to (i) direct damage, (ii) desiccation from loss of intimate contact with soil, or (iii) reburial of white thread seedlings that have already expended their seed reserves?

Vegetative growth and crop–weed competition

Once a cohort of weeds has established in a field, its success depends primarily on its survival, discussed in the following section, and its growth, discussed here. Two types of growth rate are relevant to understanding the growth potential of weeds. Absolute growth rate is the addition of biomass per unit time (g week^{-1}), whereas relative growth rate (RGR) is the biomass added per unit biomass per unit of time (g g^{-1} week^{-1}). In most species, RGR declines as the plant grows (Grime & Hunt, 1975; Spitters & Kramer, 1985; Ascencio & Lazo, 1997). This occurs because (i) a greater proportion of tissue is nonphotosynthetic in larger plants, (ii) maintenance respiration increases disproportionately with plant size, (iii) self-shading increases as plants grow, and (iv) larger leaves have less favorable source/sink relationships for photosynthesis (Chapin, Groves & Evans, 1989). Since RGR varies with plant size and with environmental conditions, the maximum RGR achieved by young plants in an optimal environment forms a useful basis for comparing species.

Agricultural weeds have the highest maximum RGR of any large category

a single bud is left.
from drastic damage
pecies, a seedling that
vill not survive. At this
ss is fatal. Establishing
o damage than dicots
ot and shoot meristems.
ubstantial portion of the
the white thread and cot-
ical means than are weeds
pecifically aimed at estab-

management has been little
ng farmers holds that rotary
ately wetted afterward by rain
e confirms this view (Lovely,
omenon has only been studied
f the individual weed. To what
nergence operation with a rotary
(ii) desiccation from loss of inti-
white thread seedlings that have

weed competition

lished in a field, its success depends
ne following section, and its growth
ate are relevant to understanding the
rowth rate is the addition of biomass
ative growth rate (RGR) is the biomass
me (g g^{-1} week^{-1}). In most species, RG
& Hunt, 1975; Spitters & Kramer, 198
because (i) a greater proportion of tissue
(ii) maintenance respiration increases d
) self-shading increases as plants grow, a
le source/sink relationships for photos
989). Since RGR varies with plant size
he maximum RGR achieved by young pl
s a useful basis for comparing species.
highest maximum RGR of any large cate

---

of plants. For example, in Grime & Hunt's (1975) analysis of growth rate of 132 British species, annuals had the highest maximum RGR of the several groups analyzed, and the agricultural annuals were mostly in the higher end of this class. Perennial agricultural weeds also have high RGR. For example, *Poa annua* and *Convolvulus arvensis* had the highest and third highest RGR measured. Grime & Hunt (1975) also compared occurrence of species in four RGR categories in 29 British habitats. Plants of manure piles had the greatest proportion of high RGR species, followed by those of enclosed pastures, arable land, and meadows. In short, productive agricultural habitats tend to favor plants with high RGR.

From a management perspective, the most important plants to compare with weeds are crops. Seibert & Pearce (1993) compared growth parameters of four weed and two crop species (Table 2.7). They found that RGR declined as seed size increased, such that *Xanthium strumarium*, an exceptionally large-seeded weed, behaved more like the crops. High RGR for the small-seeded weed species was primarily due to higher leaf area ratio (LAR, leaf area/plant weight) rather than higher net assimilation rate (NAR, change in plant weight/leaf area). That is, differences in growth rate due to seed size were attributable to morphology rather than physiology. The smaller-seeded species (weeds) put a greater proportion of plant mass into leaves (high LWR, leaf weight ratio) and had thinner leaves (high SLA, specific leaf area) than the large-seeded weed (*X. strumarium*) and the crops. The proportion of biomass invested in roots was lower in the weeds, but their root diameter was less so that total length of roots increased more quickly than in the crops. To some extent the particular patterns found by Seibert & Pearce (1993) probably depended on the choice of species. Chapin, Groves & Evans (1989) decreased this problem by comparing weed, domestic, and progenitor taxa in a single genus, *Hordeum*. They too found that seed size explained most of the variation in RGR, and again, the weeds had smaller seeds and higher RGR than the crops. The reason was that large seeds make large seedlings, and larger plants tend to have lower RGR regardless of whether the comparison is within a species or between species.

Because small-seeded weeds have a higher RGR than the larger-seeded crops, they tend to catch up in size eventually. As an extreme example, the initial 500-fold difference in the seed size of maize and redroot pigweed (Table 2.6) may be reduced to a two-fold difference in the size of the mature plants if each species is allowed to grow without competition (Mohler, 1996). Although the large initial size of most crop species gives them a lower RGR than many weeds, the larger size is still competitively advantageous. At emergence, the crop has a greater leaf area and a larger root system than the weed.

Table 2.7. *Seed size and growth parameters for some weeds and crops*

Species	Seed weight (mg)	RGR ($g\ g^{-1}\ d^{-1}$)[a]	NAR ($g\ dm^{-2}\ d^{-1}$)[b]	LAR ($cm^2\ g^{-1}$)[c]	SLA ($cm^2\ g^{-1}$)[d]	LWR ($g\ g^{-1}$)[e]	RWR ($g\ g^{-1}$)[f]	Root diameter (mm)[g]	RLI ($cm\ cm^{-1}\ d^{-1}$)[h]
Amaranthus reroflexus	0.41	0.349	0.298	198	326	0.597	0.189	0.22	0.343
Chenopodium album	0.44	0.335	0.254	224	329	0.674	0.153	0.20	0.285
Abutilon theophrasti	7.8	0.244	0.145	190	326	0.583	0.214	0.46	0.274
Xanthium strumarium	38	0.187	0.224	136	237	0.560	0.217	0.35	0.227
Sunflower (domestic)	61	0.197	0.241	140	276	0.495	0.272	0.42	0.227
Soybean	158	0.155	0.176	132	242	0.539	0.241	0.64	0.201
Correlation with ln (seed weight)		−0.99**	−0.59	−0.94**	−0.86*	−0.84*	0.86*	0.86*	−0.93**

Notes:

[a] RGR: relative growth rate = g increase in plant weight g^{-1} plant weight d^{-1}.

[b] NAR: net assimilation rate = g increase in plant weight dm^{-2} leaf area d^{-1}.

[c] LAR: leaf area ratio = cm^2 leaf area g^{-1} plant weight.

[d] SLA: specific leaf area = cm^2 leaf area g^{-1} leaf weight.

[e] LWR: leaf weight ratio = g leaf weight g^{-1} plant weight.

[f] RWR: root weight ratio = g root weight g^{-1} plant weight.

[g] Average of root diameters at 0, 7, 14, 21, and 28 days after emergence.

[h] RLI: relative rate of root length increase from 0 to 28 days after emergence.

* Significant at $p < 0.05$ level.

** Significant at $p < 0.01$ level.

Source: From Seibert & Pearce (1993)

Therefore, the crop's absolute growth rate is initially greater, and usually remains greater for at least several weeks (Dunan & Zimdahl, 1991; Tanji, Zimdahl & Westra, 1997).

Use of the initial advantage conferred to the crop by relatively large size and high absolute growth rate is a key concept in ecological weed management (Mohler, 1996). A major strategy in most annual crops is to design the cropping system so that the initial size advantage still holds at the time the crop and weeds grow into physical contact. With few exceptions, both crops and weeds are adapted to open habitats, and both are intolerant of shade (Blackman & Black, 1959; Knake, 1972; Loomis & Connor, 1992, pp. 274–5; McLachlan *et al.*, 1993; Bello, Owen & Hatterman-Valenti, 1995). Consequently, if the crop is in the superior position, it will suppress the growth of the weeds, whereas if the weeds grow above the crop canopy, then yield reduction is likely to be severe. Which outcome occurs depends on (i) the relative timing of emergence, (ii) the time course of height growth for the two species, and (iii) how rapidly the crop canopy closes. Factors that can be manipulated to affect the relative timing of emergence include planting date (Chapters 4 and 6), cultivation (Chapter 4), and mulch (Chapter 5). Factors that can be manipulated to affect the growth of crops relative to weeds include the planting date (Chapter 6), the use of allelopathic materials (Chapter 5), and the timing, type, and spatial distribution of fertilizer and irrigation water applied to the crop–weed community (Chapter 5). Finally, the speed with which the crop canopy closes can be increased through narrow row spacing, dense planting, intercropping, use of fast-growing cultivars, and choice of planting dates that optimize crop growth rate (Chapters 6 and 7).

The effectiveness of these tactics depends on the morphology of the weed species present in the field. For example, a tall, erect weed species is unlikely to be suppressed by a low-growing crop unless the emergence of the weed is substantially delayed relative to the crop. To some extent, weeds change shape in response to shade. For many broadleaf species, including *Polygonum arenastrum* (*P. aviculare*), *Cassia (Senna) obtusifolia*, *Abutilon theophrasti*, and *Xanthium strumarium*, branch length is reduced when the plant is shaded or crowded by competitors (Geber, 1989; Regnier & Stoller, 1989; Regnier & Harrison, 1993; Smith & Jordan, 1993). Shade or crowding also inhibits release of lateral buds in some species, particularly on the lower parts of the main shoot (*Abutilon theophrasti*, *Datura stramonium* but not *Xanthium strumarium* – Regnier & Stoller, 1989; *Amaranthus retroflexus* – McLachlan *et al.*, 1993). These changes presumably channel resources into height growth rather than lateral spread and thereby improve competition for light. Several studies on *Amaranthus retroflexus* have shown that the vertical distribution of biomass and leaf area shifts upward as competition increases (Légère & Schreiber, 1989; McLachlan *et al.*, 1993; Knezevic & Horak, 1998). Differences in branching of *C. obtusifolia* emerging on different dates and located at various distances from the soybean row allowed that species to maintain a nearly constant proportion of leaves above the crop, regardless of the timing of competition (Smith & Jordan, 1993). Since morphological flexibility allows some weed species to overtop even competitive crops like soybean, either the tactics discussed above need to create a substantial size differential between the crop and weed or else tall weeds will need to be dealt with by other means.

Plants compete for nutrients and water as well as for light. This is apparent from the many studies in which perennial cover crops growing beneath a main crop reduced yield less in a wet year or when irrigated, even though the cover crop was kept short (Chapter 7) (Mohler, 1995; Teasdale, 1998). Similarly, a short weed like *Taraxacum officinale* can reduce yield of a tall crop like sweet corn in a dry year (Mohler, 1991), even though shading by the crop reduces transpiration by the weed.

In annual cropping systems, the soil is unoccupied by roots at the beginning of the season, and usually nutrients and water are relatively abundant. Under such conditions, the outcome of below-ground competition between the crop and weed depends primarily on the rate at which the two species occupy the soil with roots, and their relative rates of uptake. Andrews & Newman (1970) showed that root density is critical in competition for nutrients. Because small-seeded species tend to have a higher rate of root elongation (Table 2.7) (Seibert & Pearce, 1993), weeds tend to rapidly occupy the soil volume to the detriment of the crop. Probably because weeds are adapted to exploit the brief pulse of nutrient availability that follows disturbance, they also usually have substantially higher macronutrient concentrations in the shoot than do the crops with which they compete (Vengris *et al.*, 1953; Alkämper, 1976; Qasem, 1992). They thus sequester nutrients that would otherwise be available to the crop. Given that weeds have this double competitive advantage, fertilization often favors weeds more than crops (Chapter 5) (Vengris, Colby & Drake, 1955; Alkämper, 1976; Lawson & Wiseman, 1979; Dyck & Liebman, 1994). Consequently, directing water and nutrients toward the crop rather than the weeds is a critical component of weed management. This can be achieved by fertilizing and irrigating directly in the crop rooting zone, timing the application of fertilizer or manure to correspond to the needs of the crop, and using organic materials that inhibit root growth of weeds (Chapter 5).

Below-ground competition works differently in perennial systems where the soil is permanently occupied with roots (Grubb, 1994). In perennial communities, the competitive dominant is usually the species that can deplete the limiting resource to the lowest level (Tilman, 1982). Thus, in unfertilized grasslands, the superior competitor is usually the species that reduces the nutrient element in shortest supply (often nitrogen) to the lowest concentration when the several species are grown in monoculture (Tilman & Wedin, 1991*a*, 1991*b*). However, the ability to compete on low-nutrient soils is usually associated with a low ability to adjust growth rate in response to resource availability (Lambers & Poorter, 1992). Consequently, when grassland is fertilized, large, fast-growing species tend to overtop and shade out species adapted to low-nutrient conditions (Smith, Elston & Bunting, 1971). Since fast-growing species grown under favorable conditions tend to have higher concentrations of nitrogen (protein), minerals, and water, and lower concentrations of secondary compounds than slow-growing species (Lambers & Poorter, 1992), their palatability is high. That is, the potentially fast-growing species tend to be desirable forage species (i.e., the "crop"). Thus, fertilizing a weedy grassland tends to have the opposite effect on the competitive balance between crops and weeds of fertilizing a weedy annual crop. However, legumes complicate this picture somewhat. In low-nitrogen soils, nitrogen-fixing legumes tend to have an advantage relative to other species (Donald, 1961), despite relatively slow growth (Grime & Hunt, 1975). Where legumes have been abundant for a while, however, nitrogen accumulates, and taller-growing grasses tend to displace them (Turkington & Harper, 1979). Dung deposition also favors tall-growing grasses that displace legumes and contributes to a shifting mosaic of species in pasture communities (Lieth, 1960). Weed management in pastures is discussed further in Chapter 9.

Survival after emergence

Rates of natural mortality due to disease, herbivory, and drought are usually low for established weeds in annual crops. In the absence of post-emergence weed control, survival rates for annual weeds from the cotyledon stage to maturity usually lie between 25% and 75% (Table 2.8) (Chancellor & Peters, 1972; Naylor, 1972; Sagar & Mortimer, 1976; Weiss, 1981; Mack & Pyke, 1983; Lapointe *et al.*, 1984; Mohler & Callaway, 1992). Sometimes, however, rates of survival to maturity exceed 90% (Young, 1986) or approach 0% (Lindquist *et al.*, 1995) (Table 2.8). Given the high reproductive rates of annual weeds (see the following section), their reported survival rates seem surprisingly high, and probably indicate that most weed mortality occurs prior to emergence or is due to post-emergence control measures. Mortality rate usually decreases with increasing plant size or age (Weiss, 1981; Mohler & Callaway, 1992; Buhler & Owen, 1997).

Table 2.8. *Survival of seedlings emerging in maize in July from establishment to maturity (or for some* A. theophrasti, *death by hard frost)*

Species	Year	Till	No-till	Rye + Till	Rye + No-till
Amaranthus retroflexus	1986	0.27	0.44	0.25	0.46
	1987	0.33	0.55	0.20	0.55
	1991	0.78	0.82		
	1992	0.58	0.49		
Chenopodium album	1986	0	0	0.15	0
	1987	0.61	0.41	0.43	0.33
Portulaca oleracea	1986	0	0.04	0	0
	1987	–	0.31	–	–
Digitaria sanguinalis	1986	–	0.81	–	0.58
	1987	–	0.84	–	0.79
	1991	0.78	0.70		
	1992	0.60	0.16		
Abutilon theophrasti	1991	0.94	0.96		
	1992	0.63	0.48		

Notes:
No comparisons were significant except for till vs. no-till for *A. retroflexus* in 1986 and 1987, *C. album* in 1987, and *D. sanguinalis* in 1992.
Source: Data for 1986 and 1987 from Mohler & Callaway (1992); data for 1991 and 1992 from C. L. Mohler (unpublished).

Drought occasionally causes substantial mortality during the growth phase in some weed populations (Blackman & Templeman, 1938), but based on the several studies cited above, it does not appear to be a major limiting factor for most annual weeds. Usually drought will have greatest effect on population size during establishment rather than during growth and maturation. Once the weed has a well-established root system, a drought that kills many weeds is likely to severely damage the crop as well.

For introduced weed species, the low mortality rates may be partially due to escape from host-specific natural enemies. However, even in their native range most annual agricultural weeds probably escape serious attack because they represent unpredictable and ephemeral resources (Feeny, 1976). Crop rotation and year-to-year variation in the success of weed control practices create large fluctuations in the density of particular weed species. Moreover, weed populations tend to be patchy (e.g., Wilson & Brain, 1991; Cardina, Sparrow & McCoy, 1996), and because they are usually mixed in with a larger population of a more dominant plant species, namely the crop, they are probably hard for host-specific herbivores to locate (Root, 1973). In an exceptional case, monarch butterfly larvae defoliated 31% to 78% of young *Asclepias syriaca* in soybean in Minnesota (Yenish *et al.*, 1997). However, defoliation by monarch larvae was generally much less in maize due to lower weed seedling density, and in wheat because of a denser canopy during egg-laying by the adults. Thus, temporal variability, patchiness, and interference by the crop with search behavior of host-specific herbivores mitigate against effective control of weeds by these agents in annual crops. These obstacles could be overcome by mass application of host-specific herbivores. Mass application of herbivores for weed control has not been tried on a field scale, though Kremer & Spencer (1989*a*, 1989*b*) studied a seed-feeding scentless plant bug on *Abutilon theophrasti* for that purpose.

Many annual weed species, including *Amaranthus retroflexus* and *Chenopodium album*, are highly palatable to humans, indicating that they have poor physical and chemical defenses against generalist herbivores and pathogens (Feeny, 1977). However, management practices, especially tillage, tend to reduce populations of generalist enemies like mollusks (Hunter, 1967). Moreover, the growth rate of annual weeds is so high that once they are beyond the seedling stage they often increase in biomass faster than the herbivores can feed. Thus, once they have established, annual weeds usually escape control by generalist natural enemies as well as host-specific ones.

The generally small response of survival of annual weeds to variation in tillage and mulch (Table 2.8) indicates that manipulation of naturally occurring populations of herbivores and pathogens probably has limited potential for post-emergence weed management in annual cropping systems. This contrasts with the substantial management potential inherent in naturally occurring seed predators (see Chapter 8). Nevertheless, naturally occurring herbivores and pathogens may provide significant weed control in some systems, and these cases need to be identified, and programs developed that exploit this potential. For most annual weeds, the most effective approach to use of natural enemies for post-emergence control will usually be inundative release of pathogens (Chapter 8).

Survival rates of perennial weeds during the period from seedling to first reproduction are typically much lower than for annuals. For example, Mortimer (1976) established four perennials in small plots in grassland (type unspecified) that was (i) turned with a spade, (ii) killed with herbicides and the dead surface vegetation removed, or (iii) clipped to 7.5 cm and then left undisturbed. Proportion of plants surviving over an eight-month period ranged from 0.01 to 0.18 (Figure 2.4). *Poa annua* and *Plantago lanceolata* survival was several-fold lower in the undisturbed grassland than in the plots with inverted soil. In nearly every case, exclusion of invertebrates with insecticides and molluskicides increased survival, although many of the differences were too small to be significant individually (Figure 2.4). Other studies have found

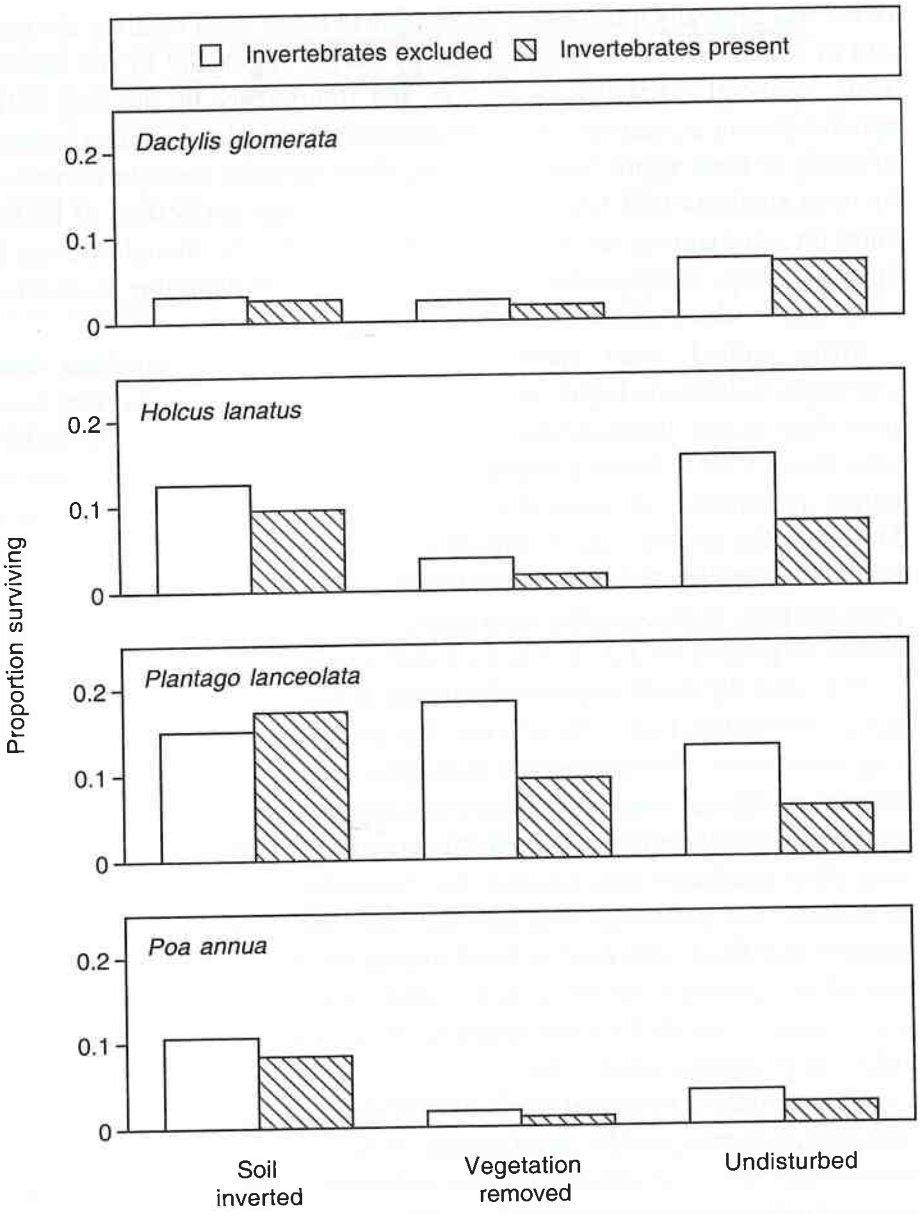


Figure 2.4 Survival of four perennial species from seedling to adult during an eight-month period (September to May) in three grassland disturbance conditions in northern Wales, UK. (After Mortimer, 1976.)

similarly low or even lower survival rates for perennial weeds in perennial vegetation (Forcella & Wood, 1986; McEvoy *et al.*, 1993; Qi, Upadhyaya & Turkington, 1996). In contrast with annual weeds, perennial weeds in perennial vegetation like pastures and hay meadows remain in the same location for an extended period. This makes them easier for herbivores to find and allows the build-up of enemies to effective levels. Even more importantly, the dense, diverse crop provides shelter for the herbivores that attack young weeds, and the shady, moist conditions within the sward facilitate attack by pathogens. In addition, the weed suffers competitive pressure from the crop, and in pastures suffers from grazing and trampling by livestock. These factors can be manipulated to decrease weed survival in perennial systems (Chapters 8 and 9).

Life span and seed production

The potential postgermination life span of weeds in agricultural systems varies from a few months to decades. In most arable cropping systems, actual life span is rarely more than a few years due to periodic tillage. Some annuals are truly monocarpic: resources in vegetative tissues are remobilized to fill seeds and the plant senesces after seed set (e.g., *Chenopodium album*, *Setaria faberi*). However, many annuals shed seeds continuously through much of the growing season and for a substantial proportion of the weed's life span (e.g., *Galinsoga ciliata*, *Digitaria sanguinalis*).

Continuously fruiting annuals tend to dominate the weed flora of fall-sown cereals (Figure 2.5), perhaps because most sprawling species are continuously fruiting and a sprawling habit is well adapted for surviving winter conditions. The early seed production of continuously fruiting annuals like *Portulaca oleracea* and *Stellaria media* adapts them well to cropping systems in which disturbance occurs throughout the growing season; consequently, they are common weeds in gardens and vegetable farms. In contrast, the true monocarpic annuals are more sensitive to frequent weeding or cultivation, but because they do not expend resources on reproduction early in life, they are better able to grow tall and compete with large-statured crops. Consequently, monocarpic annuals tend to dominate the weed flora of tall crops such as maize, and crops such as oat that are rarely cultivated (Figure 2.5).

The seed production capacity of weeds varies greatly both within and between species. In most populations, a few individuals produce many seeds, whereas most individuals produce far fewer (Figure 2.6) (Salisbury, 1942; Mack & Pyke, 1983). This variation in seed production is largely the result of

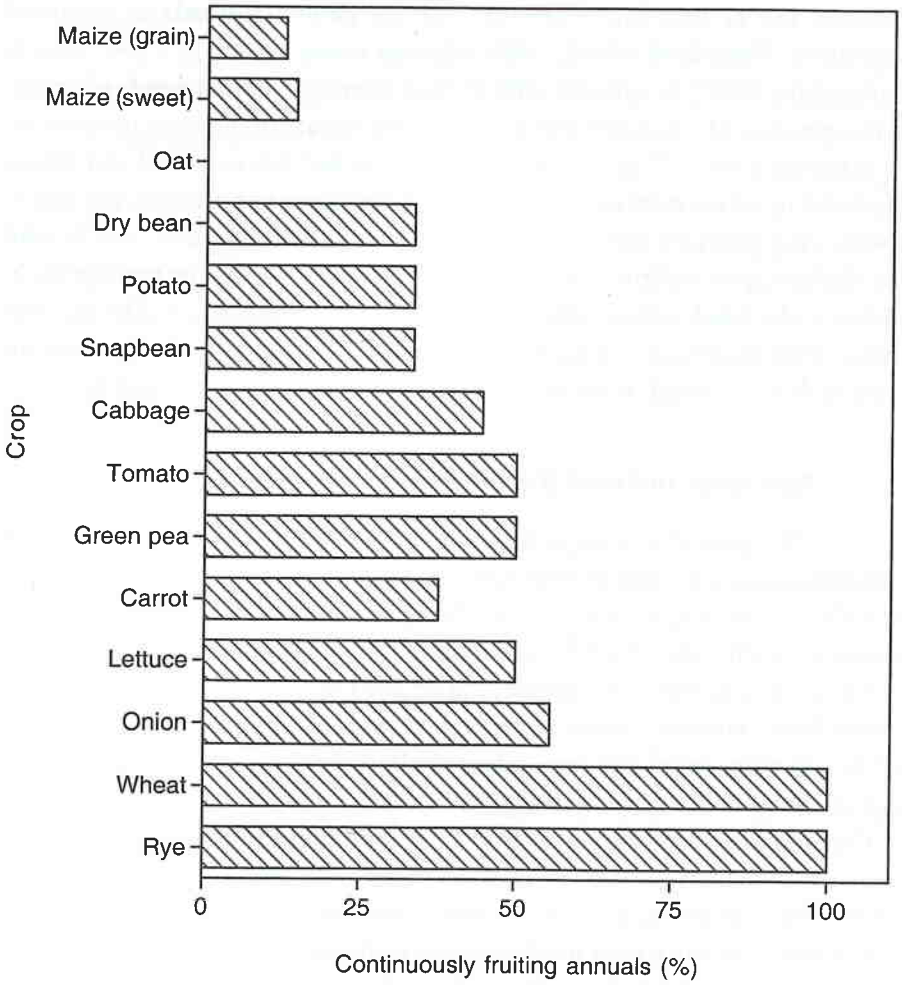


Figure 2.5 Continuous fruiting annuals as a percentage of the common annual weeds in 14 crops in New York state (data from Bridges, 1992). From top to bottom: spring grain crops (sweet corn grouped with maize grain), spring vegetable crops (roughly in decreasing order of competitive ability), winter grain crops.

exponential growth magnifying small differences in seed size, access to nutrients, proximity to crop plants, etc. The extreme skewness in the distribution of seed production over individuals in most weed populations indicates that hand, chemical, or mechanical killing of the largest weeds can reduce weed densities in subsequent crops even if all individuals are not destroyed. Mechanical methods for attacking the large weeds that emerge through crop canopies are discussed in Chapter 4.

Most annual weeds produce a few thousand seeds per individual when

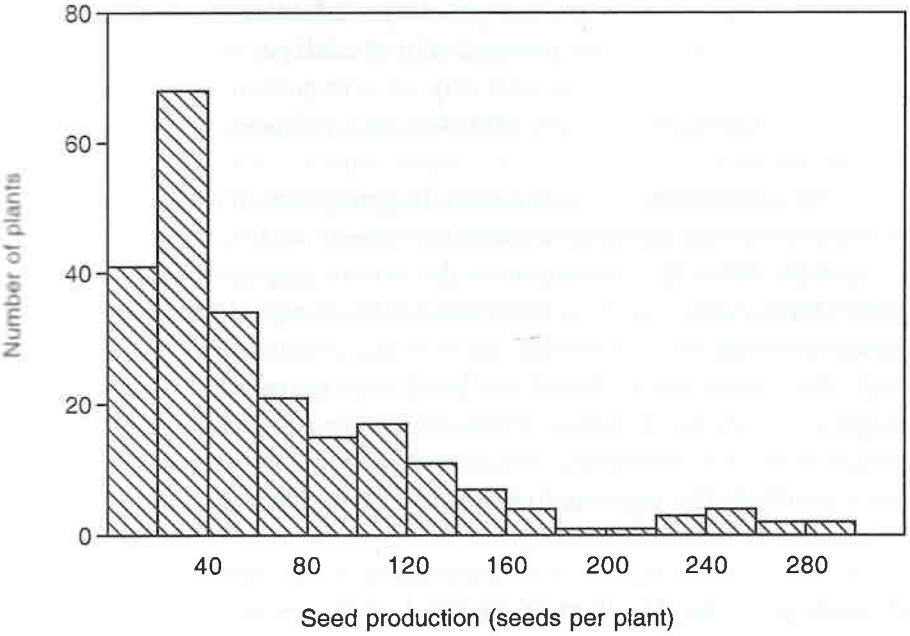


Figure 2.6 Distribution of estimated seed production by 231 individuals of *Amaranthus retroflexus* in no-till sweet corn plots. (C. L. Mohler & M. B. Callaway, unpublished data; see Mohler & Callaway, 1995.)

growing with minimal competition, though some produce 10 000 to 25 000 seeds per plant (Stevens, 1932; Salisbury, 1942), and a few like *Salsola iberica* and *Echinocloa crus-galli* may produce over 100 000 seeds per plant (Young, 1986; Norris, 1992). A few annuals (e.g., *Veronica hederifolia*) produce fewer than 100 seeds per individual (Salisbury, 1942; Boutin & Harper, 1991). Stationary perennial weeds show a similar range in seed production to annuals (Stevens, 1932; Salisbury, 1942), except that monocarpic perennials (biennials) tend to produce more seeds (Stevens, 1932), probably because the observed reproductive output is based on resources captured over more than one season of growth. Comparable data for wandering perennials are lacking, but given that they allot resources to vegetative spread, their seed production probably tends to be less on a per ramet basis. Some wandering perennials (e.g., biotypes of *Cynodon dactylon*) produce no viable seeds at all (Horowitz, 1972; Kigel & Koller, 1985).

Although most weed species potentially produce very many seeds per plant, the actual productivity in a crop is usually much less. C. L. Mohler & M. B. Callaway (unpublished data) found that *Amaranthus retroflexus* produced up to 253 000 seeds per plant, but that individuals emerging in unplanted plots in July as effects of an atrazine application dissipated averaged only 770 seeds per plant, probably due to a short growth period. Moreover, when growing with sweet corn, *A. retroflexus* averaged only 28 seeds per plant. Thus, cultural practices and competition from the crop act as important regulators of weed seed production (Zanin & Sattin, 1988; Mohler & Callaway, 1995; Blackshaw & Harker, 1997).

Several models have shown that including the effects of seed production on future crops lowers economic weed density thresholds by a factor of 3 to 8 relative to the effect of competition on the current crop alone (Cousens *et al.*, 1986; Doyle, Cousens & Moss, 1986; Bauer & Mortensen, 1992). Some authors have argued that the damage inflicted on future crops by seed production is so great that certain weeds should not be allowed to reproduce at all (*Abutilon theophrasti* – Zanin & Sattin, 1988; *Echinochloa crus-galli* – Norris, 1992). Although extreme efforts to prevent spread of new, localized populations are often justified, the economic utility of a zero tolerance policy for long-established populations remains to be demonstrated.

In any case, measures should be taken to reduce seed production. Depending on the phenology of the weed relative to the crop, a substantial proportion of potential seed production can sometimes be prevented by prompt post-harvest weed control measures (Young, 1986; Kegode, Forcella & Durgan, 1999). This is particularly true for cereals and early season vegetables where harvest of the crop releases the weeds from competition at a time in the season when temperature and day length allow rapid growth and maturation of previously suppressed weeds. For example, Webster, Cardina & Loux (1998) found that killing weeds in July or August following wheat harvest controlled 70% to 95% of various weed species in maize the following spring relative to control plots in which weeds were allowed to mature.

In some grain crops, a large portion of the weed seed produced passes through the combine. For example, Ballaré *et al.* (1987*a*) found that <2% of *Datura ferox* in soybean were shed prior to harvest, and that all three of the combines tested took up nearly all capsules. In such cases, if equipment were added to the combine to capture or destroy weed seeds rather than dispersing them with the chaff, substantial reductions in the annual addition of viable seeds to the seed bank could be achieved. Slagell Gossen *et al.* (1998) proposed attaching hammer mills or roller mills to grain combines to destroy weed seeds before they were returned to the field. They found that both types of mill killed a high percentage of *Bromus secalinus* seeds. In many crop–weed systems, however, the benefit of capturing or killing weed seeds in the combine would be small because most of the seeds disperse prior to harvest (Moss, 1983). Although seed collection and post-harvest weed control usually will not provide effective control by themselves, they can contribute substantially to integrated management of weed populations, especially if crop rotation provides some years in which the crop is removed early in the maturation period of the weed.

The capacity of wandering perennial species to produce vegetative propagules is also large. For example, single tubers of *Cyperus esculentus* planted in California and Zimbabwe grew into clones that in one year produced 6900 and 17700 tubers, respectively (Tumbleson & Kommedahl, 1961; Lapham, 1985). Unlike seed production, which is necessarily preceded by a period of vegetative growth, vegetative reproduction in wandering perennials often begins early in life. Production of new tubers in *Cyperus esculentus* may begin as early as 3 weeks after tubers sprout (Bell *et al.*, 1962). Adventitious buds form on the roots of *Euphorbia esula* and *Cirsium arvense* within 1–2 and 6–8 weeks of seedling emergence, respectively (Selleck, 1958; Bakker, 1960). Consequently, the number of potential individuals produced is roughly proportional to the size of the plant, and tends to increase exponentially when interference is absent (Lapham, 1985). As a result, vigorous competition from a crop is important for reducing vegetative reproduction of wandering perennials (Håkansson, 1968; Håkansson & Wallgren, 1972). Strategies for mechanical control of wandering perennials are discussed extensively in Chapter 4.

Dispersal of seeds and ramets

The spatial scale of dispersal events

Various seed dispersal mechanisms work on greatly differing spatial scales (Figure 2.7). Dispersal of seeds by rain splash or explosive dehiscence of the fruit is generally not effective for more than a few meters, unless assisted by wind. At the other extreme, contaminated crop seed and other agricultural commodities have regularly transported weeds many hundreds of kilometers and have been major sources of intercontinental weed introductions.

Three categories of scale can be usefully distinguished for purposes of managing the spread of weeds: dispersal within fields, between fields, and between regions. Some natural dispersal processes operate primarily at the within-field scale (Figure 2.7). For a weed to spread long distances, other agencies must come into play. Wind, birds, mammals, and water may transport seeds between fields. Natural processes, however, rarely transport species between regions or continents, which is a large part of why regional floras were highly distinct prior to human commerce.

If a newly arrived weed persists within a field, its spread is likely because both natural processes and machinery will tend to disperse the species out

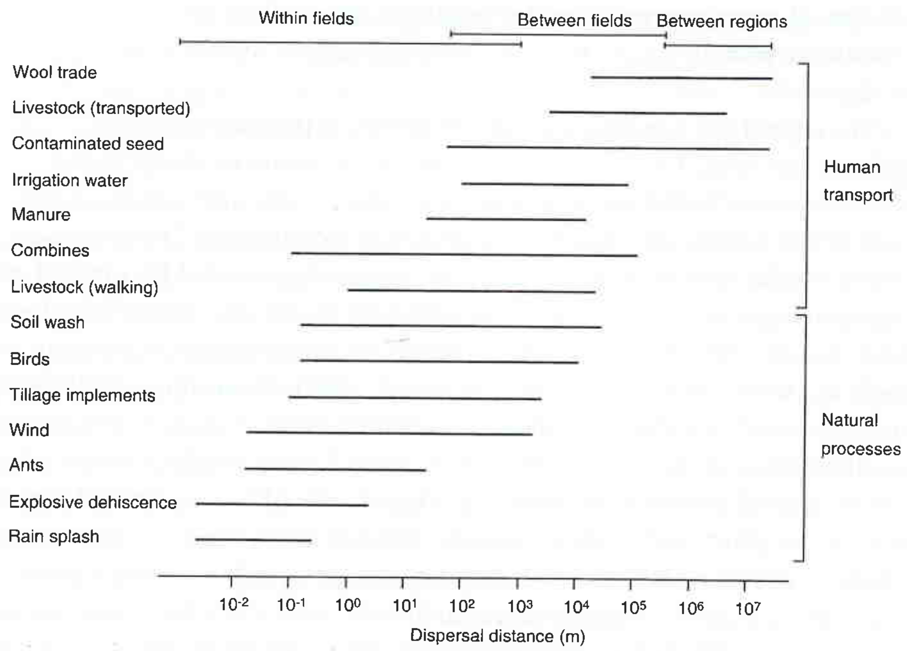


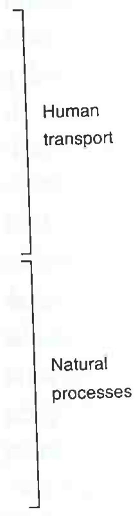
Figure 2.7 Estimated approximate range of dispersal distances for 14 processes that disperse weed seeds.

from its original location. Thus, vigilance and prompt eradication while the population is small are the best defenses against spread within a field. During eradication, care should be taken to avoid spreading the new weed around the field with tillage and cultivation implements.

Although wind, birds, and mammals occasionally move weeds between fields, most spread of weeds between fields is probably the result of human activity. Most of the discussion that follows focuses on dispersal of weeds between fields and regions, areas in which substantial management options exist.

Adaptations for seed dispersal

Weed species have a variety of adaptations for dispersal. Many members of the Compositae and other groups (e.g., *Asclepias* and *Epilobium* spp.) have hairs attached to the seeds that provide buoyancy to aid dispersal by wind. In other species, the plant breaks off at ground level (e.g., *Amaranthus albus*, *Sisymbrium altissimum*), or the inflorescence detaches as a unit (e.g., *Panicum capillare*) and rolls with the wind over the ground surface. Seeds of some species have hairs, spines, or hooks that adapt them to disperse in the fur of animals, and these are often equally effective at attaching to clothing (e.g.,



4 processes

on while the
field. During
d around the

eeds between
ult of human
rsal of weeds
ment options

spersal. Many
and *Epilobium*
id dispersal by
g., *Amaranthus*
s a unit (e.g.,
rface. Seeds of
perse in the fur
clothing (e.g.,

Cenchrus incertus, Arctium lappa). A few agricultural weeds, many of them woody, have fleshy fruits that entice birds to swallow the seeds (e.g., *Solanum* spp., *Toxicodendron radicans*). Since fruit-feeding birds usually lack the sort of alimentary tract required to digest seeds, these are mostly regurgitated or passed out with the feces, often at a considerable distance from the parent plant. Another small group of weed species have explosive dehiscence mechanisms that catapult seeds as much as a few meters from the parent (e.g., *Oxalis stricta* – Lovett Doust, MacKinnon & Lovett Doust, 1985). A very few weeds have oily bodies attached to the seeds (eliasomes) that entice ants to carry the seeds to their nests (e.g., *Fumaria officinalis, Euphorbia esula* – Pemberton & Irving, 1990). After the ants have bitten off the eliasome, the seeds are then discarded and may subsequently germinate. Seed-feeding ants also regularly disperse seeds accidentally during foraging. The effectiveness of these dispersal mechanisms are evaluated with further examples in Salisbury (1961, pp. 97–143) and Cousens & Mortimer (1995, pp. 55–85).

Although some agricultural weed species show obvious adaptations for dispersal, most do not. Of the 50 weeds of arable land discussed by Salisbury (1961), 76% lack any apparent adaptation for dispersal. Consequently, most weed seeds fall close to the parent plant. For example, Howard *et al.* (1991) found that *Bromus sterilis* and *B. interruptus* seeds shed in a winter wheat field fell in a normally distributed pattern about the parent plant with standard deviations of 31 cm and 19 cm, respectively.

Prior to dispersal by humans (see next section), species without obvious dispersal adaptations probably dispersed in soil washed along streams, in mud clinging to large animals, and in the guts of birds and mammals. The seeds of many weed species pass through the digestive tracts of grazing animals without damage (Kirk & Courtney, 1972; Takabayashi, Kubota & Abe, 1979; Blackshaw & Rode, 1991), and may be retained in the gut for several days (Burton, 1948; Özer, 1979), thereby allowing deposition at sites distant from their point of origin. Although most of the seeds ingested by seed-eating birds are probably destroyed, a few apparently pass through the digestive tract unharmed (Proctor, 1968; Aison, Johnson & Harger, 1984).

The frequency distribution of distance traveled by wind-dispersed seeds is typically very skewed (Smith & Kok, 1984; Feldman & Lewis, 1990). Consequently, most wind-dispersed seeds land within a few meters of the parent plant (Plummer & Keever, 1963; Michaux, 1989), but a few seeds may be caught in updrafts and occasionally travel far enough to reach nearby fields. Whereas only 10% of the arable weeds discussed by Salisbury (1961) are wind-dispersed, 28% of the species he lists as common in British upland grasslands have appendages that facilitate wind dispersal. Many of these wind-dispersed grassland weeds thrive on road margins, ditch banks, fence lines, and hedgerows where they are relatively free from trampling and grazing by animals and cutting by mowing machines. From there, they disperse into fields, especially during the establishment year of leys and during periods when pastures are rested from grazing. Consequently, preventing fruiting of these weeds in ruderal habitats adjacent to farm fields is an important part of their management.

Human dispersal of weeds: risks and potential reductions

Dispersal in contaminated seed

Weed contamination of crop seed has been a major source of introductions at all scales from continents to individual fields. Weed seeds are still regularly transported between countries in seed shipments (Tasrif *et al.*, 1991; Huelma, Moody & Mew, 1996). Probably the only effective method for preventing this is inspection of large samples from every international shipment (Tasrif *et al.*, 1991). This could be facilitated by computer visualization procedures that identify contaminated samples.

Improved seed-cleaning techniques and seed certification programs have greatly reduced the spread of weeds between farms in some regions, and have led to the near elimination of some weed species (Salisbury, 1961). However, even in developed countries, some growers still plant contaminated seed (Tonkin, 1982; Dewey, Thill & Foote, 1985; Dewey & Whitesides, 1990), and this is the norm in most developing countries. For example, Rao & Moody (1990) found an average of 3800 weed seeds per kg (17 species) after rice was processed by farmers in the Philippines, and 660 seeds per kg (15 species) after local commercial cleaning. Use of contaminated seed guarantees that the worst weeds will become ubiquitous throughout all the fields of a farm, and leads to spread between farms when seed is traded. In addition to mechanical cleaning, the propagation of weeds with crop seed can be greatly reduced by reserving one field or part of a field for production of next year's seed, and weeding this area intensively. This reflects the approach used to produce certified seed (Wellington, 1960), but may be more cost-effective than purchasing certified seed for many growers in both developed and developing countries.

Dispersal with manure, feed, and transported animals

Weed seeds may be moved to previously uninfested fields by application of manure. Mt. Pleasant & Schlather (1994) found a total of 13 grass and 35 broadleaf species in manure samples taken from 26 New York dairy farms. On most farms, the density of weed seeds in the manure was too low to significantly change seed density in the soil, but they concluded that manure did have a potential for spreading weeds. In particular, *Abutilon theophrasti* was probably introduced onto many New York farms during the last 30 years in contaminated feed, and then spread from field to field in manure once it had established. Weed density in manure may be greater in less-developed countries where animals are regularly grazed on weedy stubble after crop harvest. Dastgheib (1989) estimated that farmers in Iran were sowing nearly 10 million weed seeds per hectare per year with the sheep manure used to fertilize a wheat/paddy rice double-cropping system.

Mack (1981) documented the spread of *Bromus tectorum* in western North America. From a few initial introductions, probably in contaminated wheat seed, the weed first spread along rail lines and cattle trails, and then outward from these corridors to become a dominant species on much of the rangeland between the Cascade–Sierra Nevada and Rocky Mountains. Apparently, disposal of manure and bedding from cattle cars was particularly effective in creating secondary points of introduction. Since cattle are today often raised in one location, finished in another, and slaughtered at a third, the potential for spread of weeds during cattle transport remains large.

Several strategies can be used to reduce the risk of spreading weeds with manure. One is use of clean concentrates and fodder. Seeds cannot occur in the manure unless they are first present in the feed. Intensive pasture management can prevent weeds from going to seed (Chapter 9) (Sharrow & Mosher, 1982; Popay & Field, 1996). Mowing is also effective in this regard. At the very least, mill screenings should not be fed to animals unless they are first heat-treated to kill weed seeds. Ensiling is highly effective at killing seeds of most weed species (Zahnley & Fitch, 1941; Takabayashi, Kubota & Abe, 1979; Blackshaw & Rode, 1991). Consequently, ensiling forage that is contaminated with a problem weed may be preferable to direct feeding. However, a substantial percentage of *Abutilon theophrasti*, *Convolvulus arvensis*, and *Polygonum convolvulus* seeds can survive ensiling (Zahnley & Fitch, 1941; Blackshaw & Rode, 1991). High-temperature composting, anaerobic fermentation, or oven drying can greatly reduce the number of viable weed seeds in manure (Kirk & Courtney, 1972; Takabayashi, Kubota & Abe, 1979; Bloemhard *et al.*, 1992; Šarapatka, Holub & Lhotská, 1993; Tompkins, Chaw & Abiola, 1998). However, the outside of a compost pile will not heat sufficiently to kill seeds, so simply piling the manure for a few weeks without turning may leave high densities of viable seeds (Cudney *et al.*, 1992). Finally, manure from off the farm should be evaluated for weed seeds before transport.

Dispersal in raw wool and other bulk commodities

Weed species adapted to cling to animal fur may be transported thousands of kilometers in raw wool, and then dispersed with textile wastes. Several hundred species have apparently been introduced into Britain by this route (Dony, 1953; Salisbury, 1961), although many never became naturalized. Weeds probably also move in raw cotton. However, this remains to be documented, and the problem is likely smaller than with wool since cotton fields often have fewer weed species than sheep pastures.

The recent rapid shift of the textile industry from developed to developing countries is probably providing new opportunities for weed introductions in raw fiber. In addition to inspection and quarantine measures, introductions of weeds with textile raw materials can be curtailed by heat treatment or high-temperature composting of wastes prior to application to land.

Dispersal by machinery

Tillage machinery moves few seeds further than three meters within a field and moves most seeds only a meter or less (Howard *et al.*, 1991; Rew, Froud-Williams & Boatman, 1996; Rew & Cussans, 1997; Mayer, Albrecht & Pfadenhauer, 1998). However, the few seeds that are carried long distances can form foci from which the weed can spread in future years. Roots, rhizomes, and tubers of wandering perennials can catch on the shanks of tine implements, particularly once the soil is loosened by primary tillage. Although most fragments do not move far, the few that do can spread an infestation over large areas in a single tillage operation (Schippers *et al.*, 1993).

Few studies have quantitatively examined potential between-field movement of seeds in soil on tires and machinery. Schmidt (1989) observed over 3900 seedlings of 124 species emerging in the soil scraped from an automobile that had been used for field research in Germany. Mayer, Albrecht & Pfadenhauer (1998) found that seeds were moved between fields on tractor tires and a rotary tiller, but not by a plow, rotary harrow, or heavy cultivator. In their experiment, the equipment passed through 25 m of clean soil after encounter with the seeds.

Some idea of the potential for between-field dispersal in soil clinging to tillage machinery can be gathered from the density of seeds in soil. Many species commonly achieve densities of a few thousand seeds per m^2 (Jensen, 1969; Ball & Miller, 1989). Assuming a plowing depth of 20 cm, 1000 seeds per m^2 is about 1 seed per 200 g of soil. This represents a fairly small risk, except that (i) conservation tillage keeps seeds close to the surface where they are more likely to be picked up, (ii) field edges and headlands are typically plowed and cultivated last, and they are usually weedier than the rest of the field

(Marshall, 1989; Wilson & Aebischer, 1995), and (iii) tractor tires can pick up surface-lying seeds from along the field border as they leave. Consequently, seed movement in soil is probably the source of many new weed infestations, particularly of nearby fields. Nevertheless, the risk will usually be small until the weed becomes dense in the potential source field. Movement of vegetative propagules with soil on farm machinery is probably the major method of spread for some species that do not produce viable seeds (e.g., *Panicum repens* – Wilcut *et al.*, 1988).

Several studies on movement of weed seeds by combine harvesters indicate that most seeds are deposited within 10 m of the source but that some are dispersed as far as 50 m or more in the direction of travel (Ballaré *et al.*, 1987*a*; McCanny & Cavers, 1988; Howard *et al.*, 1991; Ghersa *et al.*, 1993; Rew, Froud-Williams & Boatman, 1996). Thus, combines can rapidly spread weeds throughout a field (Ballaré *et al.*, 1987*b*), with significant potential effects on crop yield (Maxwell & Ghersa, 1992).

The spread of weeds between fields by combines is probably also frequent, and prudence indicates that a combine should be cleaned before it is moved into a new field. McCanny & Cavers (1988) found that more seeds lodged in the central divider assembly of the maize header than elsewhere on the combine, and that this could be effectively cleaned by vacuuming. Data on the spread of weeds between fields by combines are badly needed. An interesting study could be made by cleaning trapped seeds out of combines each night as a custom combining operation works its way north through the midwestern USA during grain harvest. Comparison of the weed species removed from the combine after harvesting a field with the flora of the next field on the schedule would indicate the likelihood of long-distance spread of species by this route.

Dispersal in irrigation water

Seeds of most weed species can survive several months of immersion in fresh water (Comes, Bruns & Kelley, 1978), and most will float, particularly if chaff is retained on the seed, or if pieces of inflorescence fall onto the water. Consequently, many species of weed seeds disperse in irrigation water. Wilson (1980) found 77 species of weed seeds in samples of irrigation water in Nebraska, and Kelley & Bruns (1975) observed 77, 84, and 137 species in samples taken in eastern Washington in three years. In both studies, the density of seeds deposited was not sufficiently high to warrant concern, but the potential for introduction of new weed species to fields by irrigation water was substantial. Consequently, Kelley & Bruns (1975) recommended that irrigation water be screened to remove seeds. Both studies found that seed density in water increased as water traveled down canals with weedy banks. In contrast, Kelley & Bruns (1975) found no increase in seeds for water flowing in a canal whose banks were kept free of weeds by grazing, tillage, and burning. Thus, weed control on canal banks can reduce the dispersal of weeds into fields.

Weed dispersal as a management issue

The many studies cited in the preceding sections largely agree that the density of weed propagules dispersing into an area is usually insufficient to create substantial competitive pressure against crops. Instead, weed populations appear to reach competitively effective densities primarily through local population growth. The central problem that human-facilitated weed dispersal poses for management is therefore the prevention of new infestations, including both the arrival of new species onto farms and the multiplication of foci for local population growth within fields. Consequently, from the farmer's perspective, movement of weeds that are already widespread on the farm can largely be ignored, and efforts instead concentrated on preventing the spread of particular weeds that are both competitive and currently absent from all or much of the farm. From the weed scientist's perspective, the key issue with weed dispersal is prevention of the spread of economically damaging species through the landscape. Surprisingly little research directly addresses this problem. Effectively preventing the spread of weeds probably requires region-wide co-ordination of education and containment efforts analogous to infectious disease control activities of public health agencies. This is discussed further in Chapter 10.

Dispersal and spatial pattern

Weed populations usually have noticeably clumped spatial patterns. The most common pattern is for the frequency of occurrence of individuals to follow a negative binomial distribution (Zanin, Berti & Zuin, 1989; Wiles *et al.*, 1992; Mortensen, Johnson & Young, 1993; Mulugeta & Stoltenberg, 1997). For wandering perennial species, much of the clumped pattern is the result of vegetative growth. Variation in soil fertility, tilth, drainage, and the density and vigor of the crop causes variation in plant size of both perennial and annual weeds. In addition, variation in the size, burial depth, and genetic constitution among seeds, and in the time of emergence of seedlings, leads to great variation in the size of annual plants. The resulting clumped distribution of weed biomass in any given year leads to a clumped distribution of density the following year, since reproductive output is correlated with plant size (e.g., Mohler & Callaway, 1995), and most weed seeds only disperse a short distance. Even if a weed is initially distributed uniformly across a field, as

r flowing in
nd burning.
weeds into

y agree that
insufficient
weed popu-
ily through
itated weed
new infesta-
multiplica-
tly, from the
read on the
preventing
ently absent
tive, the key
ally damag-
rch directly
ds probably
nent efforts
th agencies.

ial patterns.
dividuals to
989; Wiles *et*
berg, 1997).
the result of
l the density
erennial and
genetic con-
ngs, leads to
ped distribu-
stribution of
d with plant
perse a short
ss a field, as

---

might happen, for example, if it were introduced in contaminated seed, the high variance in reproductive output among individual plants (Figure 2.6) guarantees that the species will quickly become clumped. However, the initial distribution of a species within the field is usually far from uniform. Often the weed expands from an initial point of establishment, either as an expanding front, or with new inoculation points appearing elsewhere in the field by intermediate-distance dispersal from the original site (Cousens & Mortimer, 1995, pp. 217–42). Some weed populations may be entirely maintained by dispersal from an adjacent habitat that is more suitable for the plant's reproduction. In such cases, the species is likely to be more common along the edge of the field (Marshall, 1989; Wilson & Aebischer, 1995). However, even weeds that are well adapted to farm fields are often more abundant along field edges due to soil compaction, lower crop competition, and inefficient application of herbicides and cultivation (Wilson & Aebischer, 1995).

The persistent storage organs of perennial weeds and the persistent seed bank of many annual weeds insures that weed patches tend to remain in the same locations in successive seasons (Dieleman & Mortensen, 1999). Moreover, all the factors that disperse seeds within a field leave most seeds within a few meters (or less) of the parent plant. Consequently, once a clumped distribution of weeds is formed, it tends to persist. For example, Wilson & Brain (1991) found that *Alopecurus myosuroides* tended to occur in the same locations within a farm year after year. Patches tended to persist even through several years of sod. This is reasonable for a species with a persistent seed bank since dispersal forces are particularly weak after the seeds are in the soil, especially if the ground is not tilled. Thus, although variation in the soil conditions within a field doubtless contributes to the maintenance of some weed patches, the dynamics of reproduction seem sufficient to explain many of the clumped patterns observed.

Dispersal also creates patchiness at larger scales. For example, McCanny, Baugh & Cavers (1988) repeatedly surveyed wild *Panicum miliaceum* populations in two Ontario townships, and found it present in 10% to 20% of the tilled fields. They found that the number of infested fields did not change much, but that the species had a probability of local extinction of 17% to 48% depending on the year. As some populations went extinct, new ones formed by colonization of previously uninfested fields. Perennial weeds and species with persistent seed banks probably behave similarly, but on longer time scales.

Conclusions

The discussion in the preceding sections indicates that agricultural weeds generally share certain properties, including small seed size, high relative growth rate, low early absolute growth rate, intolerance to stress, and high reproductive capacity. They differ from crops in most of these respects, and these differences form the basis for a variety of weed management tactics.

Despite similarities among weeds, weed species differ with respect to longevity, ability to spread vegetatively, temporal pattern of seed production, relative seed size, ability of seeds to persist in the soil, and season of germination. Divergent life history characteristics allow different weed species to prosper in differing sorts of crop production systems and may require divergent management strategies for successful control.

The several life cycle stages of a weed provide separate opportunities for control. Constraining a weed population at several points in the life cycle by using multiple partial controls is the essence of integrated weed management and is the basic approach for meeting the objectives of weed management proposed in Chapter 1. Chapters 4 through 9 discuss methods for attacking weeds at various stages in their life cycle. Often, reduction in the number of individuals passing through a stage improves management options in succeeding stages. In some cases, a particular tactic may be quite impractical unless the population is constrained in other ways as well. Consequently, the potential effectiveness of a particular tactic may be much greater than is indicated by studies that treat the factor in isolation.

REFERENCES

Abdalla, F. H., & Roberts, E. H. (1968). Effects of temperature, moisture, and oxygen on the induction of chromosome damage in seeds of barley, broad beans, and peas during storage. *Annals of Botany*, New Series, **32**, 119–36.

Aison, S., Johnson, M. K., & Harger, T. R. (1984). Role of birds in dispersal of itchgrass (*Rottboellia exaltata* (L.) L.f.) seeds in the southeastern USA. *Protection Ecology*, **6**, 307–13.

Akanda, R. U., Mullahey, J. J., & Shilling, D. G. (1996). Environmental factors affecting germination of tropical soda apple (*Solanum viarum*). *Weed Science*, **44**, 570–4.

Alkämper, J. (1976). Influence of weed infestation on effect of fertilizer dressings. *Pflanzenshutz-Nachrichten Bayer*, **29**, 191–235.

Andrews, R. E., & Newman, E. I. (1970). Root density and competition for nutrients. *Oecologia Plantarum*, **5**, 319–34.

Ascencio, J., & Lazo, J. V. (1997). Growth evaluation during the vegetative phase of dicotyledonous weeds and under phosphorus deficiency. *Journal of Plant Nutrition*, **20**, 27–45.

Baker, H. G. (1965). Characteristics and modes of origin of weeds. In *The Genetics of*

Colonizing Species, ed. H. G. Baker, & G. L. Stebbins, pp. 147–68. New York: Academic Press.

Bakker, D. (1960). A comparative life-history study of *Cirsium arvense* (L.) Scop. and *Tussilago farfara* L., the most troublesome weeds in the newly reclaimed polders of the former Zuiderzee. In *The Biology of Weeds*, ed. J. L. Harper, pp. 205–22. Oxford, UK: Blackwell.

Ball, D. A., & Miller, S. D. (1989). A comparison of techniques for estimation of arable soil seedbanks and their relationship to weed flora. *Weed Research*, **29**, 365–73.

Ballaré, C. L., Scopel, A. L., Ghersa, C. M., & Sánchez, R. A. (1987*a*). The demography of *Datura ferox* (L.) in soybean crops. *Weed Research*, **27**, 91–102.

Ballaré, C. L., Scopel, A. L., Ghersa, C. M., & Sánchez, R. A. (1987*b*). The population ecology of *Datura ferox* in soybean crops: a simulation approach incorporating seed dispersal. *Agriculture, Ecosystems and Environment*, **19**, 177–88.

Barralis, G., Chadoeuf, R., & Lonchamp, J. P. (1988). Longévité des semences de mauvaises herbes annuelles dans un sol cultivé. *Weed Research*, **28**, 407–18.

Baskin, C. C., & Baskin, J. M. (1988). Germination ecophysiology of herbaceous plant species in a temperate region. *American Journal of Botany*, **75**, 286–305.

Baskin, C. C., & Baskin, J. M. (1998*a*). *Seeds: Ecology, Biogeography, and Evolution of Dormancy and Germination*. San Diego, CA: Academic Press.

Baskin, C. C., & Baskin, J. M. (1998*b*). Ecology of seed dormancy and germination in grasses. In *Population Biology of Grasses*, ed. G. P. Cheplich, pp. 30–83. Cambridge, UK: Cambridge University Press.

Baskin, J. M., & Baskin, C. C. (1980). Ecophysiology of secondary dormancy in seeds of *Ambrosia artemisiifolia*. *Ecology*, **61**, 475–80.

Baskin, J. M., & Baskin, C. C. (1983). Seasonal changes in the germination responses of buried seeds of *Arabidopsis thaliana* and ecological interpretation. *Botanical Gazette*, **144**, 540–3.

Baskin, J. M., & Baskin, C. C. (1985). The annual dormancy cycle in buried weed seeds: a continuum. *BioScience*, **35**, 492–8.

Baskin, J. M., & Baskin, C. C. (1986). Seasonal changes in the germination responses of buried witchgrass (*Panicum capillare*) seeds. *Weed Science*, **34**, 22–4.

Baskin, J. M., & Baskin, C. C. (1987). Environmentally induced changes in the dormancy states of buried weed seeds. In *1987 British Crop Protection Conference – Weeds*, pp. 695–706. Croydon, UK: British Crop Protection Council.

Bauer, T. A., & Mortensen, D. A. (1992). A comparison of economic and economic optimum thresholds for two annual weeds in soybeans. *Weed Technology*, **6**, 228–35.

Bell, R. S., Lachman, W. H., Rahn, E. M., & Sweet, R. D. (1962). *Life History Studies as related to Weed Control in the Northeast*. 1. Nutgrass, University of Rhode Island Agricultural Experiment Station Bulletin no. 364. Kingston, RI: University of Rhode Island Agricultural Experiment Station.

Bello, I. A., Owen, M. D. K., & Hatterman-Valenti, H. M. (1995). Effect of shade on velvetleaf (*Abutilon theophrasti*) growth, seed production, and dormancy. *Weed Technology*, **9**, 452–5.

Benvenuti, S., & Macchia, M. (1995). Effect of hypoxia on buried weed seed germination. *Weed Research*, **35**, 343–51.

Blackman, G. E., & Black, J. N. (1959). Physiological and ecological studies in the analysis of plant environment. XI. A further assessment of the influence of shading on the growth of different species in the vegetative phase. *Annals of Botany*, New Series, **23**, 51–63.

Blackman, G. E., & Templeman, W. G. (1938). The nature of the competition between cereal crops and annual weeds. *Journal of Agricultural Science*, **28**, 247–71.

Blackshaw, R. E., & Harker, K. N. (1997). Scentless chamomile (*Matricaria perforata*) growth, development, and seed production. *Weed Science*, **45**, 701–5.

Blackshaw, R. E., & Rode, L. M. (1991). Effect of ensiling and rumen digestion by cattle on weed seed viability. *Weed Science*, **39**, 104–8.

Bloemhard, C. M. J., Arts, M. W. M. F., Scheepens, P. C., & Elema, A. G. (1992). Thermal inactivation of weed seeds and tubers during drying of pig manure. *Netherlands Journal of Agricultural Science*, **40**, 11–19.

Bostock, S. J. (1978). Seed germination strategies of five perennial weeds. *Oecologia (Berlin)*, **36**, 113–26.

Boutin, C., & Harper, J. L. (1991). A comparative study of the population dynamics of five species of *Veronica* in natural habitats. *Journal of Ecology*, **79**, 199–221.

Brennan, T., Willemsen, R., Rudd, T., & Frenkel, C. (1978). Interaction of oxygen and ethylene in the release of ragweed seeds from dormancy. *Botanical Gazette*, **139**, 46–9.

Bridges, D. C. (ed.) (1992). *Crop Losses Due to Weeds in the United States – 1992*. Champaign, IL: Weed Science Society of America.

Brust, G. E., & House, G. J. (1988). Weed seed destruction by arthropods and rodents in low-input soybean agroecosystems. *American Journal of Alternative Agriculture*, **3**, 19–25.

Buchholtz, K. P., Grantz, R. L., Sweet, R. D., Timmons, F. L., & Vostral, H. J. (1967). Subcommittee on Standardization of Abbreviations, Terms and Definitions. *Weeds*, **15**, 388–9.

Buhler, D. D., & Owen, M. D. K. (1997). Emergence and survival of horseweed (*Conyza canadensis*). *Weed Science*, **45**, 98–101.

Burnside, O. C., Wilson, R. G., Weisberg, S., & Hubbard, K. G. (1996). Seed longevity of 41 weed species buried 17 years in eastern and western Nebraska. *Weed Science*, **44**, 74–86.

Burton, G. W. (1948). Recovery and viability of seeds of certain southern grasses and lespedeza passed through the bovine digestive tract. *Journal of Agricultural Research*, **76**, 95–103.

Cardina, J., Sparrow, D. H., & McCoy, E. L. (1996). Spatial relationships between seedbank and seedling populations of common lambsquarters (*Chenopodium album*) and annual grasses. *Weed Science*, **44**, 298–308.

Chancellor, R. J. (1964). The depth of weed seed germination in the field. In *Proceedings of the 7th British Weed Control Conference*, pp. 599–606. London: British Crop Protection Council.

Chancellor, R. J. (1986). Decline of arable weed seeds during 20 years in soil under grass and the periodicity of seedling emergence after cultivation. *Journal of Applied Ecology*, **23**, 631–7.

Chancellor, R. J., & Peters, N. C. B. (1972). Germination periodicity, plant survival and seed production in populations of *Avena fatua* L. growing in spring barley. In *Proceedings of the 11th British Weed Control Conference*, pp. 218–25. London: British Crop Protection Council.

Chapin, F. S. III, Groves, R. H., & Evans, L. T. (1989). Physiological determinants of growth rate in response to phosphorus supply in wild and cultivated *Hordeum* species. *Oecologia*, **79**, 96–105.

Chepil, W. S. (1946). Germination of weed seeds. I. Longevity, periodicity of germination, and vitality of seeds in cultivated soil. *Scientific Agriculture*, **26**, 307–46.

Cohen, D. (1966). Optimizing reproduction in a randomly varying environment. *Journal of Theoretical Biology*, **12**, 119–29.

Comes, R. D., Bruns, V. F., & Kelley, A. D. (1978). Longevity of certain weed and crop seeds in fresh water. *Weed Science*, **26**, 336–44.

Conn, J. S., & Deck, R. E. (1995). Seed viability and dormancy of 17 weed species after 9.7 years of burial in Alaska. *Weed Science*, **43**, 583–5.

Cousens, R., & Mortimer, M. (1995). *Dynamics of Weed Populations*. Cambridge, UK: Cambridge University Press.

Cousens, R., Doyle, C. J., Wilson, B. J., & Cussans, G. W. (1986). Modelling the economics of controlling *Avena fatua* in winter wheat. *Pesticide Science*, **17**, 1–12.

Cox, W. J., Zobel, R. W., van Es, H. M., & Otis, D. J. (1990). Tillage effects on some soil physical and corn physiological characteristics. *Agronomy Journal*, **82**, 806–12.

Cudney, D. W., Wright, S. D., Shultz, T. A., & Reints, J. S. (1992). Weed seed in dairy manure depends on collection site. *California Agriculture*, **46**(3), 31–2.

Dastgheib, F. (1989). Relative importance of crop seed, manure and irrigation water as sources of weed infestation. *Weed Research*, **29**, 113–16.

Dawson, J. H., & Bruns, V. F. (1975). Longevity of barnyardgrass, green foxtail and yellow foxtail seeds in soil. *Weed Science*, **23**, 437–40.

Dewey, S. A., & Whitesides, R. E. (1990). Weed seed analyses from four decades of Utah small grain drillbox surveys. *Proceedings of the Western Society of Weed Science*, **43**, 69–70.

Dewey, S. A., Thill, D. C., & Foote, P. W. (1985). *Weed Seed Contamination of Cereal Grain Seedlots: A Drillbox Survey*, Current Information Series no. 767. Moscow, ID: Cooperative Extension Service, Agricultural Experiment Station, University of Idaho.

Dieleman, J. A., & Mortensen, D. A. (1999). Characterizing the spatial pattern of *Abutilon theophrasti* seedling patches. *Weed Research*, **39**, 455–67.

Donald, C. M. (1961). Competition for light in crops and pastures. In *Mechanisms in Biological Competition, Symposium of the Society for Experimental Biology*, 15, pp. 283–313. New York: Academic Press.

Donald, W. W., & Zimdahl, R. L. (1987). Persistence, germinability, and distribution of jointed goatgrass (*Aegilops cylindrica*) seed in soil. *Weed Science*, **35**, 149–54.

Dony, J. G. (1953). Wool aliens in Bedfordshire. In *The Changing Flora of the British Isles*, ed. J. E. Lousley, pp. 160–3. Oxford, UK: Botanical Society of the British Isles.

Dou, Z., Fox, R. H., & Toth, J. D. (1995). Seasonal soil nitrate dynamics in corn as affected by tillage and nitrogen source. *Soil Science Society of America Journal*, **59**, 858–64.

Doyle, C. J., Cousens, R., & Moss, S. R. (1986). A model of the economics of controlling *Alopecurus myosuroides* Huds. in winter wheat. *Crop Protection*, **5**, 143–50.

Dunan, C. M., & Zimdahl, R. L. (1991). Competitive ability of wild oats (*Avena fatua*) and barley (*Hordeum vulgare*). *Weed Science*, **39**, 558–63.

Dyck, E., & Liebman, M. (1994). Soil fertility management as a factor in weed control: the effect of crimson clover residue, synthetic nitrogen fertilizer, and their interaction on emergence and early growth of lambsquarters and sweet corn. *Plant and Soil*, **167**, 227–37.

Edwards, M. M. (1969). Dormancy in seeds of charlock. IV. Interrelationships of growth, oxygen supply and concentration of inhibitor. *Journal of Experimental Botany*, **20**, 876–94.

Egley, G. H. (1995). Seed germination in soil: dormancy cycles. In *Seed Development and Germination*, ed. J. Kigel, & G. Galili, pp. 529–43. New York: Marcel Dekker.

Elder, R. H., & Osborne, D. J. (1993). Function of DNA synthesis and DNA repair in the survival of embryos during early germination and in dormancy. *Seed Science Research*, **3**, 43–53.

Fausey, J. C., & Renner, K. A. (1997). Germination, emergence, and growth of giant foxtail (*Setaria faberi*) and fall panicum (*Panicum dichotomiflorum*). *Weed Science*, **45**, 423–5.

Fawcett, R. S., & Silfe, F. W. (1978). Effects of field applications of nitrate on weed seed germination and dormancy. *Weed Science*, **26**, 594–6.

Feeny, P. (1976). Plant apparency and chemical defense. In *Recent Advances in Phytochemistry*, vol. 10, *Biochemical Interaction between Plants and Insects*, ed. J. W. Wallace, & R. L. Mansell, pp. 1–40. New York: Plenum Press.

Feeny, P. (1977). Defensive ecology of the Cruciferae. *Annals of the Missouri Botanical Garden*, **64**, 221–34.

Feldman, S. R., & Lewis, J. P. (1990). Output and dispersal of propagules of *Carduus acanthoides* L. *Weed Research*, **30**, 161–9.

Fellows, G. M., & Roeth, F. W. (1992). Factors influencing shattercane (*Sorghum bicolor*) seed survival. *Weed Science*, **40**, 434–40.

Fenner, M. (1978). Susceptibility to shade in seedlings of colonizing and closed turf species. *New Phytologist*, **81**, 739–44.

Forcella, F., & Wood, H. (1986). Demography and control of *Cirsium vulgare* (Savi) Ten. in relation to grazing. *Weed Research*, **26**, 199–206.

Forcella, F., Wilson, R. G., Dekker, J., Kremer, R. J., Cardina, J., Anderson, R. L., Alm, D., Renner, K. A., Harvey, R. G., Clay, S., & Buhler, D. D. (1997). Weed seed bank emergence across the corn belt. *Weed Science*, **45**, 67–76.

Forsyth, S. F., & Watson, A. K. (1985). Predispersal seed predation of Canada thistle. *Canadian Entomologist*, **117**, 1075–81.

Friedman, M., & Henika, P. R. (1991). Mutagenicity of toxic weed seeds in the Ames Test: jimson weed (*Datura stramonium*), velvetleaf (*Abutilon theophrasti*), morning glory (*Ipomoea* spp.), and sicklepod (*Cassia obtusifolia*). *Journal of Agricultural and Food Chemistry*, **39**, 494–501.

Froud-Williams, R. J. (1985). Dormancy and germination of arable grass-weeds. *Aspects of Applied Biology*, **9**, 9–18.

Froud-Williams, R. J. (1987). Survival and fate of weed seed populations: interaction with cultural practice. In *1987 British Crop Protection Conference – Weeds*, vol. 2, pp. 707–18. Croydon, UK: British Crop Protection Council.

Froud-Williams, R. J., Chancellor, R. J., & Drennan, D. S. H. (1984). The effects of seed burial and soil disturbance on emergence and survival of arable weeds in relation to minimal cultivation. *Journal of Applied Ecology*, **21**, 629–41.

Gallagher, R. S., & Cardina, J. (1998). Ecophysiological aspects of phytochrome-mediated germination in soil seed banks. *Aspects of Applied Biology*, **51**, 1–8.

Geber, M. A. (1989). Interplay of morphology and development on size inequality: a *Polygonum* greenhouse study. *Ecological Monographs*, **59**, 267–88.

Gebhardt, M. R., Daniel, T. C., Schweizer, E. E., & Allmaras, R. R. (1985). Conservation tillage. *Science*, **230**, 625–30.

Ghersa, C. M., Benech Arnold, R. L., & Martinez-Ghersa, M. A. (1992). The role of fluctuating temperatures in germination and establishment of *Sorghum halepense*. Regulation of germination at increasing depths. *Functional Ecology*, **6**, 460–8.

Ghersa, C. M., Martinez-Ghersa, M. A., Satorre, E. H., Van Esso, M. L., & Chichotky, G. (1993). Seed dispersal, distribution and recruitment of seedlings of *Sorghum halepense* (L.) Pers. *Weed Research*, **33**, 79–88.

Givnish, T. J. (1988). Adaptation to sun and shade: a whole-plant perspective. In *Ecology of Photosynthesis in Sun and Shade*, ed. J. R. Evans, S. von Caemmerer, & W. W. Adams III, pp. 63–92. East Melbourne, Australia: Commonwealth Scientific and Industrial Research Organization.

Gleichsner, J. A., & Appleby, A. P. (1989). Effect of depth and duration of seed burial on ripgut brome (*Bromus rigidus*). *Weed Science*, **37**, 68–72.

Górski, T. (1975). Germination of seeds in the shadow of plants. *Physiologia Plantarum*, **34**, 342–6.

Grant, J. D. (1983). The activities of earthworms and the fates of seeds. In *Earthworm Ecology*, ed. J. E. Satchell, pp. 107–22. London: Chapman & Hall.

Grime, J. P., & Hunt, R. (1975). Relative growth-rate: its range and adaptive significance in a local flora. *Journal of Ecology*, **63**, 393–422.

Grubb, P. J. (1994). Root competition in soils of different fertility: a paradox resolved? *Phytocoenologia*, **24**, 495–505.

Håkansson, S. (1968). Experiments with *Agropyron repens* (L.) Beauv. II. Production from rhizome pieces of different sizes and from seeds: various environmental conditions compared. *Lantbrukshögskolans Annaler*, **34**, 3–29.

Håkansson, S. (1983). Seasonal variation in the emergence of annual weeds: an introductory investigation in Sweden. *Weed Research*, **23**, 313–24.

Håkansson, S., & Wallgren, B. (1972). Experiments with *Sonchus arvensis* L. III. The development from reproductive roots cut into different lengths and planted at different depths, with and without competition from barley. *Swedish Journal of Agricultural Research*, **2**, 15–26.

Hald, A. B. (1999). The impact of changing the season in which cereals are sown on the diversity of the weed flora in rotational fields in Denmark. *Journal of Applied Ecology*, **36**, 24–32.

Harlan, J. R., & de Wet, J. M. J. (1965). Some thoughts about weeds. *Economic Botany*, **19**, 16–24.

Harradine, A. R. (1986). Seed longevity and seedling establishment of *Bromus diandrus* Roth. *Weed Research*, **26**, 173–80.

Henson, I. E. (1970). The effects of light, potassium nitrate and temperature on the germination of *Chenopodium album* L. *Weed Research*, **10**, 27–39.

Holm, R. E. (1972). Volatile metabolites controlling germination in buried weed seeds. *Plant Physiology*, **50**, 293–7.

Holm, L. G., Plucknett, D. L., Pancho, J. V., & Herberger, J. P. (1977). *The World's Worst Weeds*. Honolulu, HI: University Press of Hawaii.

Horowitz, M. (1972). Development of *Cynodon dactylon* (L.) Pers. *Weed Research*, **12**, 207–20.

Horowitz, M., & Taylorson, R. B. (1984). Hardseededness and germinability of velvetleaf (*Abutilon theophrasti*) as affected by temperature and moisture. *Weed Science*, **32**, 111–15.

Horowitz, M., & Taylorson, R. B. (1985). Behavior of hard and permeable seeds of *Abutilon theophrasti* Medic. (velvetleaf). *Weed Research*, **25**, 363–72.

Hosmani, M. M. (1995). Striga *(a Noxious Root Parasitic Weed)*, 2nd edn. Dharwad, India: S. M. Hosmani.

Howard, C. L., Mortimer, A. M., Gould, P., Putwain, P. D., Cousens, R., & Cussans, G. W. (1991). The dispersal of weeds: seed movement in arable agriculture. In *Brighton Crop Protection Conference – Weeds*, pp. 821–8. Farnham, UK: British Crop Protection Council.

Huelma, C. C., Moody, K., & Mew, T. W. (1996). Weed seeds in rice seed shipments: a case study. *International Journal of Pest Management*, **42**, 147–50.

Hulme, P. E. (1994). Post-dispersal seed predation in grassland: its magnitude and sources of variation. *Journal of Ecology*, **82**, 645–52.

Hunter, P. J. (1967). The effect of cultivations on slugs of arable land. *Plant Pathology*, **16**, 153–6.

Jensen, H. A. (1969). Content of buried seeds in arable soil in Denmark and its relation to the weed population. *Dansk Botanisk Arkiv*, **27**(2), 7–56.

Kannangara, H. W., & Field, R. J. (1985). Environmental and physiological factors affecting the fate of seeds of yarrow (*Achillea millefolium* L.) in arable land in New Zealand. *Weed Research*, **25**, 87–92.

Kaul, V. (1965). Physiological ecology of *Xanthium strumarium* Linn. II. Physiology of seeds in relation to its distribution. *Indian Botanical Society Journal*, **44**, 365–80.

Kelley, A. D., & Bruns, V. F. (1975). Dissemination of weed seeds by irrigation water. *Weed Science*, **23**, 486–93.

Kegode, G. O., Forcella, F., & Durgan, B. R. (1999). Limiting green and yellow foxtail (*Setaria viridis* and *S. glauca*) seed production following spring wheat (*Triticum aestivum*) harvest. *Weed Technology*, **13**, 43–7.

Kigel, J. (1994). Development and ecophysiology of Amaranths. In *Amaranth: Biology, Chemistry, and Technology*, ed. O. Paredes-López, pp. 39–73. Ann Arbor, MI: CRC Press.

Kigel, J., & Koller, D. (1985). Asexual reproduction of weeds. In *Weed Physiology*, vol. 1: *Reproduction and Ecophysiology*, ed. S. O. Duke, pp. 65–100. Boca Raton, FL: CRC Press.

King, T. J. (1975). Inhibition of seed germination under leaf canopies in *Arenaria serpyllifolia*, *Veronica arvensis* and *Cerastum* (sic) *holosteoides*. *New Phytologist*, **75**, 87–90.

Kingsbury, J. M. (1964). *Poisonous Plants of the United States and Canada*. Englewood Cliffs, NJ: Prentice-Hall.

Kirk, J., & Courtney, A. D. (1972). A study of the survival of wild oats (*Avena fatua*) seeds buried in farm yard manure and fed to bullocks. In *Proceedings of the 11th British Weed Control Conference*, pp. 226–33. London: British Crop Protection Council.

Knake, E. L. (1972). Effect of shade on giant foxtail. *Weed Science*, **20**, 588–92.

Knezevic, S. Z., & Horak, M. J. (1998). Influence of emergence time and density on redroot pigweed (*Amaranthus retroflexus*). *Weed Science*, **46**, 665–72.

Kremer, R. J., & Spencer, N. R. (1989*a*). Impact of a seed-feeding insect and microorganisms on velvetleaf (*Abutilon theophrasti*) seed viability. *Weed Science*, **37**, 211–16.

Kremer, R. J., & Spencer, N. R. (1989*b*). Interaction of insects, fungi, and burial on velvetleaf (*Abutilon theophrasti*) seed viability. *Weed Technology*, **3**, 322–8.

LaCroix, L. J., & Staniforth, D. W. (1964). Seed dormancy in velvetleaf. *Weeds*, **12**, 171–4.

Lambers, H., & H. Poorter. (1992). Inherent variation in growth rate between higher plants: a search for physiological causes and ecological consequences. *Advances in Ecological Research*, **23**, 187–261.

Lapham, J. (1985). Unrestricted growth, tuber formation and spread of *Cyperus esculentus* L. in Zimbabwe. *Weed Research*, **25**, 323–9.

Lapointe, A.-M., Deschênes, J.-M., Gervai, P., & Lemieux, C. (1984). Biologie du chénopode blanc (*Chenopodium album*): influence du travail du sol sur la levée et de la densité du peuplement sur la croissance. *Canadian Journal of Botany*, **62**, 2587–93.

Law, R., Bradshaw, A. D., & Putwain, P. D. (1977). Life-history variation in *Poa annua*. *Evolution*, **31**, 233–46.

Lawson, H. M., & Wiseman, J. S. (1979). Competition between weeds and transplanted spring cabbage: effects of nitrogen top-dressing. *Horticultural Research*, **19**, 25–34.

Lawson, H. M., Waister, P. D., & Stephens, R. J. (1974). Patterns of emergence of several important arable weed species. *British Crop Protection Conference Monographs*, **9**, 121–35.

Légère, A., & Schreiber, M. M. (1989). Competition and canopy architecture as affected by soybean (*Glycine max*) row width and density of redroot pigweed (*Amaranthus retroflexus*). *Weed Science*, **37**, 84–92.

Lieth, H. (1960). Patterns of change within grassland communities. In *The Biology of Weeds*, ed. J. L. Harper, pp. 27–39. Oxford,UK: Blackwell.

Lindquist, J. L., Maxwell, B. D., Buhler, D. D., & Gunsolus, J. L. (1995). Velvetleaf (*Abutilon theophrasti*) recruitment, survival, seed production, and interference in soybean (*Glycine max*). *Weed Science*, **43**, 226–32.

Loomis, R. S., & Connor, D. J. (1992). *Crop Ecology*. Cambridge, UK: Cambridge University Press.

Lovely, W. G., Weber, C. R., & Staniforth, D. W. (1958). Effectiveness of the rotary hoe for weed control in soybeans. *Agronomy Journal*, **50**, 621–5.

Lovett Doust, L., MacKinnon, A., & Lovett Doust, J. (1985). Biology of Canadian weeds. 71. *Oxalis stricta* L., *O. corniculata* L., *O. dillenii* Jacq. ssp. *dillenii* and *O. dillenii* Jacq. ssp. *filipes* (Small) Eiten. *Canadian Journal of Plant Science*, **65**, 691–709.

Lueschen, W. E., & Andersen, R. N. (1980). Longevity of velvetleaf (*Abutilon theophrasti*) seeds in soil under agricultural practices. *Weed Science*, **28**, 341–6.

Mack, R. N. (1981). Invasion of *Bromus tectorum* L. into western North America: an ecological chronicle. *Agro-Ecosystems*, **7**, 145–65.

Mack, R. N., & Pyke, D. A. (1983). The demography of *Bromus tectorum*: variation in time and space. *Journal of Ecology*, **71**, 69–93.

Marshall, E. J. P. (1989). Distribution patterns of plants associated with arable field edges. *Journal of Applied Ecology*, **26**, 247–57.

Maxwell, B, D., & Ghersa, C. (1992). The influence of weed seed dispersion versus the effect of competition on crop yield. *Weed Technology*, **6**, 196–204.

Mayer, F., Albrecht, H., & Pfadenhauer, J. (1998). The transport of seeds by soil-working implements. In *Weed Seedbanks: Determination, Dynamics and Manipulation*, ed. G. T. Champion, A. C. Grundy, N. E. Jones, E. J. P. Marshall & R. J. Froud-Williams, pp. 83–9. Wellesbourne, UK: Association of Applied Biologists.

McCanny, S. J., & Cavers, P. B. (1988). Spread of proso millet (*Panicum miliaceum* L.) in Ontario, Canada. II. Dispersal by combines. *Weed Research*, **28**, 67–72.

McCanny, S. J., Baugh, M., & Cavers, P. B. (1988). Spread of proso millet (*Panicum miliaceum* L.) in Ontario, Canada. I. Rate of spread and crop susceptibility. *Weed Research*, **28**, 59–65.

McEvoy, P. B., Rudd, N. T., Cox, C. S., & Huso, M. (1993). Disturbance, competition, and herbivory effects on ragwort *Senecio jacobaea* populations. *Ecological Monographs*, **63**, 55–75.

McLachlan, S. M., Tollenaar, M., Swanton, C. J., & Weise, S. F. (1993). Effect of corn-induced shading on dry matter accumulation, distribution, and architecture of redroot pigweed (*Amaranthus retroflexus*). *Weed Science*, **41**, 568–73.

McWilliams, E. L., Landers, R. Q., & Mahlstede, J. P. (1968). Variation in seed weight and germination in populations of *Amaranthus retroflexus* L. *Ecology*, **49**, 290–6.

Michaux, B. (1989). Reproductive and vegetative biology of *Cirsium vulgare* (Savi) Ten. (Compositae: Cynareae). *New Zealand Journal of Botany*, **27**, 401–14.

Mohler, C. L. (1991). Effects of tillage and mulch on weed biomass and sweet corn yield. *Weed Technology*, **5**, 545–52.

Mohler, C. L. (1993). A model of the effects of tillage on emergence of weed seedlings. *Ecological Applications*, **3**, 53–73.

Mohler, C. L. (1995). A living mulch (white clover) / dead mulch (compost) weed control system for winter squash. *Proceedings of the Northeastern Weed Science Society*, **49**, 5–10.

Mohler, C. L. (1996). Ecological bases for the cultural control of annual weeds. *Journal of Production Agriculture*, **9**, 468–74.

Mohler, C. L., & Callaway, M. B. (1992). Effects of tillage and mulch on the emergence and survival of weeds in sweet corn. *Journal of Applied Ecology*, **29**, 21–34.

Mohler, C. L., & Callaway, M. B. (1995). Effects of tillage and mulch on weed seed production and seed banks in sweet corn. *Journal of Applied Ecology*, **32**, 627–39.

Mohler, C. L., & Galford, A. E. (1997). Weed seedling emergence and seed survival: separating the effects of seed position and soil modification by tillage. *Weed Research*, **37**, 147–55.

Mortensen, D. A., Johnson, G. A., & Young, L. J. (1993). Weed distribution in agricultural fields. In *Soil Specific Crop Management*, ed. P. C. Robert, R. H. Rust & W. F. Larson, pp. 113–24. Madison, WI: American Society of Agronomy.

Mortimer, A. M. (1976). Aspects of the seed population dynamics of *Dactylis glomerata* L., *Holcus lanatus* L., *Plantago lanceolata* L., and *Poa annua* L. In *Proceedings of the 1976 British Crop Protection Conference – Weeds*, pp. 687–94. Croydon, UK: British Crop Protection Council.

Morton, C. T., & Buchele, W. F. (1960). Emergence energy of plant seedlings. *Agricultural Engineering*, **41**, 428–31, 453–5.

Moss, S. R. (1983). The production and shedding of *Alopecurus myosuroides* Huds. seeds in winter cereals crops. *Weed Research*, **23**, 45–51.

Mt. Pleasant, J., & Schlather, K. J. (1994). Incidence of weed seed in cow (*Bos* sp.) manure and its importance as a weed source for cropland. *Weed Technology*, **8**, 304–10.

Mulugeta, D., & Stoltenberg, D. E. (1997). Increased weed emergence and seed bank depletion by soil disturbance in a no-tillage system. *Weed Science*, **45**, 234–41.

Musselman, L. J., (ed.) (1987). *Parasitic Weeds in Agriculture*, vol. 1, Striga. Boca Raton, FL: CRC Press.

Naylor, R. E. L. (1972). Aspects of the population dynamics of the weed *Alopecurus myosuroides* Huds. in winter cereal crops. *Journal of Applied Ecology*, **9**, 127–39.

Naylor, J. M. (1983). Studies on the genetic control of some physiological processes in seeds. *Canadian Journal of Botany*, **61**, 3561–7.

New York Agricultural Statistics Service (1994). *New York Agricultural Statistics 1993–1994*. Albany, NY: New York State Department of Agriculture and Markets, Division of Statistics.

Nichols, M. L., & Reed, I. F. (1934). Soil dynamics. VI. Physical reactions of soil to moldboard surfaces. *Agricultural Engineering*, **15**, 187–90.

Norris, R. F. (1992). Case history for weed competition/population ecology: barnyardgrass (*Echinochloa crus-galli*) in sugarbeets (*Beta vulgaris*). *Weed Technology*, **6**, 220–7.

Odum, S. (1965). Germination of ancient seeds: floristical observations and experiments with archaeologically dated soil samples. *Dansk Botanisk Arkiv*, **24**, 1–70.

Osborne, D. J. (1980). Senescence in seeds. In *Senescence in Plants*, ed. K. V. Thimann, pp. 13–37. Boca Raton, FL: CRC Press.

Özer, Z. (1979). Über die Beeinflussung der Keimfähigkeit der Samen mancher Gründlandpflanzen beim Durchgang durch den Verdauungstrakt des Schafes und nach Mistgärung. *Weed Research*, **19**, 247–54.

Pemberton, R. W., & Irving, D. W. (1990). Elaiosomes on weed seeds and the potential for myrmecochory in naturalized plants. *Weed Science*, **38**, 615–19.

Philippi, T. (1993). Bet-hedging germination of desert annuals: beyond the first year. *American Naturalist*, **142**, 474–87.

Pieterse, A. H., Verkleij, J. A. C., & ter Borg, S. J. (eds) (1994). *Biology and Management of* Orobanche: *Proceedings of the 3rd International Workshop on* Orobanche *and Related* Striga *Research*. Amsterdam, The Netherlands: Royal Tropical Institute.

Pitelli, R. A., Charudattan, R., & Devalerio, J. T. (1998). Effect of *Alternaria cassiae, Pseudocercospora nigricans*, and soybean (*Glycine max*) planting density on the biological control of sicklepod (*Senna obtusifolia*). *Weed Technology*, **12**, 37–40.

Plummer, G. L., & Keever, C. (1963). Autumnal daylight weather and camphor-weed dispersal in the Georgia Piedmont region. *Botanical Gazette*, **124**, 283–9.

Pons, T. L. (1989). Breaking of seed dormancy by nitrate as a gap detection mechanism. *Annals of Botany*, **63**, 139–43.

Popay, A. I., & Roberts, E. H. (1970). Factors involved in the dormancy and germination of *Capsella bursa-pastoris* (L.) Medik. and *Senecio vulgaris* L. *Journal of Ecology*, **58**, 103–22.

Popay, I., & Field, R. (1996). Grazing animals as weed control agents. *Weed Technology*, **10**, 217–31.

Povilaitis, B. (1956). Dormancy studies with seeds of various weed species. *Proceedings of the International Seed Testing Association*, **21**, 88–111.

Proctor, V. W. (1968). Long-distance dispersal of seeds by retention in digestive tract of birds. *Science*, **160**, 321–2.

Qasem, J. R. (1992). Nutrient accumulation by weeds and their associated vegetable crops. *Journal of Horticultural Science*, **67**, 189–95.

Qi, M., Upadhyaya, M. K., & Turkington, R. (1996). Dynamics of seed bank and survivorship of meadow salsify (*Tragopogon pratensis*) populations. *Weed Science*, **44**, 100–8.

Rao, A. N., & Moody, K. (1990). Weed seed contamination in rice seed. *Seed Science and Technology*, **18**, 139–46.

Regnier, E. E., & Harrison, S. K. (1993). Compensatory responses of common cocklebur (*Xanthium strumarium*) and velvetleaf (*Abutilon theophrasti*) to partial shading. *Weed Science*, **41**, 541–7.

Regnier, E. E., & Stoller, E. W. (1989). The effects of soybean (*Glycine max*) interference on the canopy architecture of common cocklebur (*Xanthium strumarium*), jimsonweed (*Datura stramonium*), and velvetleaf (*Abutilon theophrasti*). *Weed Science*, **37**, 187–95.

Rew, L. J., & Cussans, G. W. (1997). Horizontal movement of seeds following tine and plough cultivation: implications of spatial dynamics of weed infestations. *Weed Research*, **37**, 247–56.

Rew, L. J., Froud-Williams, R. J., & Boatman, N. D. (1996). Dispersal of *Bromus sterilis* and *Anthriscus sylvestris* seed within arable field margins. *Agriculture, Ecosystems and Environment*, **59**, 107–14.

Roberts, E. H. (1972). Dormancy: a factor affecting seed survival in the soil. In *Viability of Seeds*, ed. E. H. Roberts, pp. 321–59. Syracuse, NY: Syracuse University Press.

Roberts, E. H. (1988). Seed aging: the genome and its expression. In *Senescence and Aging in Plants*, ed. L. D. Noodén & A. C. Leopold, pp. 465–98. San Diego, CA: Academic Press.

Roberts, H. A. (1984). Crop and weed emergence patterns in relation to time of cultivation and rainfall. *Annals of Applied Biology*, **105**, 263–75.

Roberts, H. A. (1986). Persistence of seeds of some grass species in cultivated soil. *Grass and Forage Science*, **41**, 273–6.

Roberts, H. A., & Benjamin, S. K. (1979). The interaction of light, nitrate and alternating temperature on the germination of *Chenopodium album*, *Capsella bursa-pastoris* and *Poa annua* before and after chilling. *Seed Science and Technology*, **7**, 379–92.

Roberts, H. A., & Dawkins, P. A. (1967). Effect of cultivation on the numbers of viable weed seeds in soil. *Weed Research*, **7**, 290–301.

Roberts, H. A., & Feast, P. M. (1972). Fate of seeds of some annual weeds in different depths of cultivated and undisturbed soil. *Weed Research*, **12**, 316–24.

Roberts, H. A., & Feast, P. M. (1973). Changes in the numbers of viable weed seeds in soil under different regimes. *Weed Research*, **13**, 298–303.

Roberts, H. A., & Lockett, P. M. (1975). Germination of buried and dry-stored seeds of *Stellaria media*. *Weed Research*, **15**, 199–204.

Roberts, H. A., & Neilson, J. E. (1980). Seed survival and periodicity of seedling emergence in some species of *Atriplex*, *Chenopodium*, *Polygonum* and *Rumex*. *Annals of Applied Biology*, **94**, 111–120.

Roberts, H. A., & Potter, M. E. (1980). Emergence patterns of weed seedlings in relation to cultivation and rainfall. *Weed Research*, **20**, 377–86.

Root, R. (1973). Organization of a plant–arthropod association in simple and diverse habitats: the fauna of collards (*Brassica oleracea*). *Ecological Monographs*, **42**, 95–124.

Sagar, G. R., & Mortimer, A. M. (1976). An approach to the study of the population dynamics of plants with special reference to weeds. *Applied Biology*, **1**, 1–43.

Salisbury, E. J. (1942). *The Reproductive Capacity of Plants*. London: Bell.

ed Science, **44**,

ice and

ocklebur
hading. *Weed*

ference on the
msonweed
, 37, 187–95.
ine and
ations. *Weed*

sterilis and
ystems and

n *Viability of*
sity Press.
ce and Aging in
A: Academic

of cultivation

d soil. *Grass and*

d alternating
ursa-pastoris and
79–92.
s of viable weed

different depths

d seeds in soil

ed seeds of

lling emergence
nnals of Applied

ıgs in relation to

and diverse
raphs, **42**, 95–124.
pulation
gy, **1**, 1–43.

Salisbury, E. J. (1961). *Weeds and Aliens*. London: Collins.

Šarapatka, B., Holub, M., & Lhotská, M. (1993). The effect of farmyard manure anaerobic treatment on weed seed viability. *Biological Agriculture and Horticulture*, **10**, 1–8.

Sauer, J., & Struik, G. (1964). A possible ecological relation between soil disturbance, light-flash, and seed germination. *Ecology*, **45**, 884–6.

Schafer, D. E., & Chilcote, D. O. (1970). Factors influencing persistence and depletion in buried seed populations. II. The effects of soil temperature and moisture. *Crop Science*, **10**, 342–5.

Schippers, P., Ter Borg, S. J., Van Groenendael, J. M., & Habekotte, B. (1993). What makes *Cyperus esculentus* (yellow nutsedge) an invasive species? – A spatial model approach. In *Brighton Crop Protection Conference – Weeds*, pp. 495–504. Farnham, UK: British Crop Protection Council.

Schläpfer, B., & Ryser, P. (1996). Leaf and root turnover of three ecologically contrasting grass species in relation to their performance along a productivity gradient. *Oikos*, **75**, 398–406.

Schmidt, W. (1989). Plant dispersal by motor cars. *Vegetatio*, **80**, 147–52.

Scopel, A. L., Ballaré, C. L., & Sánchez, R. A. (1991). Induction of extreme light sensitivity in buried weed seeds and its role in the perception of soil cultivations. *Plant, Cell and Environment*, **14**, 501–8.

Seibert, A. C., & Pearce, R. B. (1993). Growth analysis of weed and crop species with reference to seed weight. *Weed Science*, **41**, 52–6.

Selleck, G. W. (1958). Life history of leafy spurge. In *Proceedings of the 15th Annual Meeting, North Central Weed Control Conference*, pp. 16–17.

Sharrow, S. H., & Mosher, W. D. (1982). Sheep as a biological control agent for tansy ragwort. *Journal of Range Management*, **35**, 480–2.

Silvertown, J. (1980). Leaf-canopy-induced seed dormancy in a grassland flora. *New Phytologist*, **85**, 109–18.

Slagell Gossen, R. R., Tyrl, R. J., Hauhouot, M., Peeper, T. F., Claypool, P. L., & Solie, J. B. (1998). Effects of mechanical damage on cheat (*Bromus secalinus*) caryopsis anatomy and germination. *Weed Science*, **46**, 249–57.

Smith, C. J., Elston, J., & Bunting, A. H. (1971). The effects of cutting and fertilizer treatments on the yield and botanical composition of chalk turf. *Journal of the British Grassland Society*, **26**, 213–19.

Smith, J. E., & Jordan, P. W. (1993). Sicklepod (*Cassia obtusifolia*) shoot structure as affected by soybean (*Glycine max*) interference. *Weed Science*, **41**, 75–81.

Smith, L. M., & Kok, L. T. (1984). Dispersal of musk thistle (*Carduus nutans*) seeds. *Weed Science*, **32**, 120–5.

Spitters, C. J. T., & Kramer, T. (1985). Changes in relative growth rate with plant ontogeny in spring wheat genotypes grown as isolated plants. *Euphytica*, **34**, 833–47.

Staver, C. (1991). The role of weeds in the productivity of Amazonian bush fallow agriculture. *Experimental Agriculture*, **27**, 287–304.

Steinbauer, G. P., & Grigsby, B. (1957*a*). Interaction of temperature, light, and moistening agent in the germination of weed seeds. *Weeds*, **3**, 175–82.

Steinbauer, G. P., & Grigsby, B. (1957*b*). Dormancy and germination characteristics of the seeds of four species of *Plantago*. *Proceedings of the Association of Official Seed Analysts of North America*, **47**, 158–64.

Stevens, O. A. (1932). The number and weight of seeds produced by weeds. *American Journal of Botany*, **19**, 784–94.

Stoller, E. W., & Wax, L. M. (1974). Dormancy changes and fate of some annual weed seeds in the soil. *Weed Science*, **22**, 151–5.

Takabayashi, M., Kubota, T., & Abe, H. (1979). Dissemination of weed seeds through cow feces. *Japan Agricultural Research Quarterly*, **13**, 204–7.

Tanji, A., Zimdahl, R. L., & Westra, P. (1997). The competitive ability of wheat (*Triticum aestivum*) compared to rigid ryegrass (*Lolium rigidum*) and cowcockle (*Vaccaria hispanica*). *Weed Science*, **45**, 481–7.

Tasrif, A., Sahid, I. B., Sastroutomo, S. S., & Latiff, A. (1991). Purity study of imported leguminous cover crops. *Plant Protection Quarterly*, **6**, 190–3.

Taylorson, R. B. (1970). Changes in dormancy and viability of weed seeds in soils. *Weed Science*, **18**, 265–9.

Taylorson, R. B. (1972). Phytochrome controlled changes in dormancy and germination of buried weed seeds. *Weed Science*, **20**, 417–22.

Taylorson, R. B. (1979). Response of weed seeds to ethylene and related hydrocarbons. *Weed Science*, **27**, 7–10.

Taylorson, R. B. (1987). Environmental and chemical manipulation of weed seed dormancy. *Reviews of Weed Science*, **3**, 135–54.

Teasdale, J. R. (1998). Cover crops, smother plants, and weed management. In *Integrated Weed and Soil Management*, ed. J. L. Hatfield, D. D. Buhler & B. A. Stewart, pp. 247–70. Chelsea, MI: Ann Arbor Press.

Thompson, K., Band, S. R., & Hodgson, J. G. (1993). Seed size and shape predict persistence in soil. *Functional Ecology*, **7**, 236–41.

Thompson, K., Bakker, J. P., Bekker, R. M., & Hodgson, J. G. (1998). Ecological correlates of seed persistence in soil in the north-west European flora. *Journal of Ecology*, **86**, 163–9.

Thurston, J. M. (1960). Dormancy in weed seeds. In *The Biology of Weeds*, British Ecological Society Symposium no. 1, ed. J. L. Harper, pp. 69–82. Oxford, UK: Blackwell.

Thurston, J. M. (1966). Survival of seeds of wild oats (*Avena fatua* L. and *Avena ludoviciana* Dur.) and charlock (*Sinapis arvensis* L.) in soil under leys. *Weed Research*, **6**, 67–80.

Tilman, D. (1982). *Resource Competition and Community Structure*. Princeton, NJ: Princeton University Press.

Tilman, D., & Wedin, D. (1991*a*). Plant traits and resource reduction for five grasses growing on a nitrogen gradient. *Ecology*, **72**, 685–700.

Tilman, D., & Wedin, D. (1991*b*). Dynamics of nitrogen competition between successional grasses. *Ecology*, **72**, 1038–49.

Tompkins, D. K., Chaw, D., & Abiola, A. T. (1998). Effect of windrow composting on weed seed germination and viability. *Compost Science and Utilization*, **6**, 30–4.

Tonkin, J. H. B. (1982). The presence of seed impurities in samples of cereal seed tested at the official seed testing station, Cambridge in the period of 1978–1981. *Aspects of Applied Biology*, **1**, 163–71.

Totterdell, S., & Roberts, E. H. (1980). Characteristics of alternating temperatures which stimulate loss of dormancy in seeds of *Rumex obtusifolius* L. and *Rumex crispus* L. *Plant, Cell and Environment*, **3**, 3–12.

Tumbleson, M. E., & Kommedahl, T. (1961). Reproductive potential of *Cyperus esculentus* by tubers. *Weeds*, **9**, 646–53.

Turkington, R., & Harper, J. L. (1979). The growth, distribution and neighbour relationships of *Trifolium repens* in a permanent pasture. I. Ordination, pattern and contact. *Journal of Ecology*, **67**, 201–18.

Vengris, J., Colby, W. G., & Drake, M. (1955). Plant nutrient competition between weeds and corn. *Agronomy Journal*, **47**, 213–16.

Vengris, J., Drake, M., Colby, W. G., & Bart, J. (1953). Chemical composition of weeds and accompanying crop plants. *Agronomy Journal*, **45**, 213–18.

Villiers, T. A (1973). Ageing and the longevity of seeds in field conditions. In *Seed Ecology, Proceedings of the 19th Easter School in Agricultural Sciences, University of Nottingham, 1972*, ed. W. Heydecker, pp. 265–88. University Park, PA: Pennsylvania State University Press.

Villiers, T. A. (1980). Ultrastructural changes in seed dormancy and senescence. In *Senescence in Plants*, ed. K. V. Thimann, pp. 39–66. Boca Raton, FL: CRC Press.

Villiers, T. A., & Edgcumbe, D. J. (1975). On the cause of seed deterioration in dry storage. *Seed Science and Technology*, **3**, 761–74.

Vincent, E. M., & Roberts, E. H. (1977). The interaction of light, nitrate and alternating temperature in promoting the germination of dormant seeds of common weed species. *Seed Science and Technology*, **5**, 659–70.

Wareing, P. F., & Foda, H. A. (1957). Growth inhibitors and dormancy in *Xanthium* seed. *Physiologia Plantarum*, **10**, 266–80.

Warnes, D. D., & Andersen, R. N. (1984). Decline of wild mustard (*Brassica kaber*) seeds in soil under various cultural and chemical practices. *Weed Science*, **32**, 214–17.

Warwick, S. I., & Black, L. D. (1988). The biology of Canadian weeds. 90. *Abutilon theophrasti*. *Canadian Journal of Plant Science*, **68**, 1069–85.

Weaver, S. E., & Lechowicz, M. J. (1983). The biology of Canadian weeds. 56. *Xanthium strumarium* L. *Canadian Journal of Plant Science*, **63**, 211–25.

Weaver, S. E., & Riley, W. R. (1982). The biology of Canadian weeds. 53. *Convolvulus arvensis* L. *Canadian Journal of Plant Science*, **62**, 461–72.

Weaver, S. E., & Thomas, A. G. (1986). Germination responses to temperature of atrazine-resistant and -susceptible biotypes of two pigweed (*Amaranthus*) species. *Weed Science*, **34**, 865–70.

Webster, T. M., Cardina, J., & Loux, M. M. (1998). The influence of weed management in wheat (*Triticum aestivum*) stubble on weed control in corn (*Zea mays*). *Weed Technology*, **12**, 522–6.

Weiss, P. W. (1981). Spatial distribution and dynamics of populations of the introduced annual *Emex australis* in south-eastern Australia. *Journal of Applied Ecology*, **18**, 849–64.

Wellington, P. S. (1960). Assessment and control of the dissemination of weeds by crop seeds. In *The Biology of Weeds*, ed. J. L. Harper, pp. 94–107. Oxford, UK: Blackwell.

Wesson, G., & Wareing, P. F. (1969*a*). The induction of light sensitivity in weed seeds by burial. *Journal of Experimental Botany*, **20**, 414–25.

Wesson, G., & Wareing, P. F. (1969*b*). The role of light in the germination of naturally occurring populations of buried seeds. *Journal of Experimental Botany*, **20**, 402–13.

White, J. (1979). The plant as a metapopulation. *Annual Review of Ecology and Systematics*, **10**, 109–45.

Wilcut, J. W., Dute, R. R., Truelove, B., & Davis, D. E. (1988). Factors limiting the distribution of cogongrass, *Imperata cylindrica* and torpedograss, *Panicum repens*. *Weed Science*, **36**, 577–82.

Wiles, L. J., Oliver, G. W., York, A. C., Gold, H. J., & Wilkerson, G. G. (1992). Spatial distribution of broadleaf weeds in North Carolina soybean (*Glycine max*) fields. *Weed Science*, **40**, 554–7.

Williams, J. T., & Harper, J. L. (1965). Seed polymorphism and germination. I. The influence of nitrates and low temperatures on the germination of *Chenopodium album*. *Weed Research*, **5**, 141–50.

Wilson, B. J. (1972). Studies of the fate of *Avena fatua* seeds on cereal stubble as influenced by autumn treatment. In *Proceedings of the 11th British Weed Control Conference*, pp. 242–7. London: British Crop Protection Council.

Wilson, B. J., & Brain, P. (1991). Long-term stability of distribution of *Alopecurus myosuroides* Huds. within cereal fields. *Weed Research*, **31**, 367–73.

Wilson, B. J., & Cussans, G. W. (1972). The effect of autumn cultivations on the emergence of *Avena fatua* seedlings. In *Proceedings of the 11th British Weed Control Conference*, pp. 234–41. London: British Crop Protection Council.

Wilson, B. J., & Lawson, H. M. (1992). Seedbank persistence and seedling emergence of seven weed species in autumn-sown crops following a single year's seeding. *Annals of Applied Biology*, **120**, 105–16.

Wilson, P. J., & Aebischer, N. J. (1995). The distribution of dicotyledonous arable weeds in relation to distance from the field edge. *Journal of Applied Ecology*, **32**, 295–310.

Wilson, R. G. Jr. (1980). Dissemination of weed seeds by surface irrigation water in western Nebraska. *Weed Science*, **28**, 87–92.

Yenish, J. P., Fry, T. A., Durgan, B. R., & Wyse, D. L. (1997). Establishment of common milkweed (*Asclepias syriaca*) in corn, soybean, and wheat. *Weed Science*, **45**, 44–53.

Young, F. L. (1986). Russian thistle (*Salsola iberica*) growth and development in wheat (*Triticum aestivum*). *Weed Science*, **34**, 901–5.

Zahnley, J. W., & Fitch, J. B. (1941). Effect of ensiling on the viability of weed seeds. *Journal of the American Society of Agronomy*, **33**, 816–22.

Zanin, G., & Sattin, M. (1988). Threshold level and seed production of velvetleaf (*Abutilon theophrasti* Medicus) in maize. *Weed Research*, **28**, 347–52.

Zanin, G., Berti, A., & Zuin, M. C. (1989). Estimation du stock semencier d'un sol labouré ou en semis direct. *Weed Research*, **29**, 407–17.

Zorner, P. S., Zimdahl, R. L., & Schweizer, E. E. (1984*a*). Sources of viable seed loss in buried dormant and non-dormant populations of wild oat (*Avena fatua* L.) seed in Colorado. *Weed Research*, **24**, 143–50.

Zorner, P. S., Zimdahl, R. L., & Schweizer, E. E. (1984*b*). Effect of depth and duration of seed burial on kochia (*Kochia scoparia*). *Weed Science*, **32**, 602–7.