Modeling seedling emergence ☆

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Abstract

Most common approaches to predicting or documenting seedling emergence are imprecise. Mechanistic models that simulate seed dormancy and germination and seedling elongation as functions of measured or estimated environmental variables seem to be the most promising approach to the problem, but they also are the most difficult models to develop. These models will need to integrate soil water potential and soil temperature (hydrothermal time), diurnal soil temperature fluctuations, oxygen deficiency, light quality, and seed burial depth to better describe the direct and interactive effects on and among seed dormancy alleviation and induction, seed germination, and seedling elongation. In the meantime, creation and use of simpler empirical models, which also employ microclimate and soil factors for predictions, may provide sufficiently accurate predictions of seedling emergence until better mechanistic models are developed. Published by Elsevier Science B.V.

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1. Introduction

1.1. The importance of emergence pattern

Seedling emergence probably is the single most important phenological event that influences the success of an annual plant. Emergence represents the point in time when a seedling is weaned from dependence upon nonrenewable seed reserves originally produced by its parent, and when photosynthetic autotrophism begins. Timing of emergence often determines whether a plant competes successfully with its neighbors, is consumed by herbivores, infected with diseases, and whether it flowers, reproduces, and matures properly by the end of the growing season.

With so many important plant processes at stake, a thorough understanding of seedling emergence seems warranted. Surprisingly, emergence has not been studied in sufficient detail to permit reliable predictions for even our most common and important annual species. To a large extent, plant scientists have been content with enumerating, estimating, or predicting the initiation of seedling emergence (E_i) or the point in time at which 50% emergence (E_{50}) is reached. Such imprecise indices may be appropriate for some purposes, but are prone to error in many other applications. The problem is that emergence is a complex and
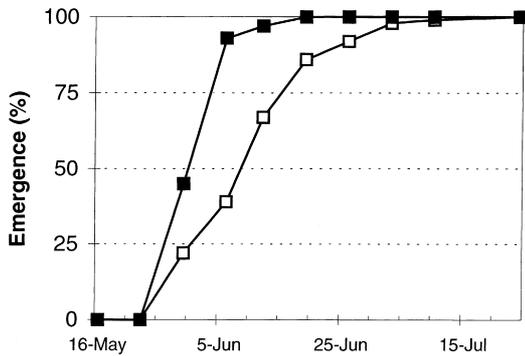

Fig. 1. Emergence of spring wheat (*T. aestivum* cv. Sharp, solid symbols) and *S. viridis* f. *robusta-purpurea* (open symbols) at Morris, MN, USA, during 1996. Wheat was sown on 16 May at 5-cm depth in plowed, disked, and harrowed clay loam soil. Note that neither E_i nor E_{50} would characterize emergence of these species adequately.
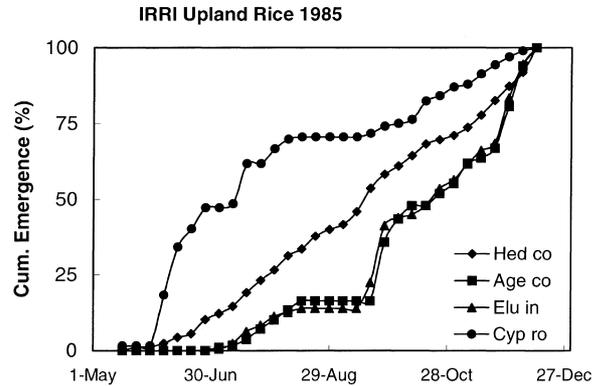

Fig. 2. Emergence of four weed species (*H. corymbosa*, *A. conyzoides*, *E. indica*, and *C. rotundus*) at Los Banos, Phillipines, during 1985. Adapted from Zimdahl et al. (1988).

continuous function that cannot be characterized easily by a simple index. This holds true for both annual crops and weeds.

Crop growth models and crop–weed competition models may be especially sensitive to errors associated with misrepresentations of seedling emergence. For example, complete emergence of neither spring wheat (*Triticum aestivum*) nor the weed, *Setaria viridis*, occurs immediately following E_i (Fig. 1). Furthermore, emergence is not normally distributed around E_{50}, especially for weeds. Instead, emergence can occur over an extended period of time (Spandl et al., 1998), often lasting two weeks to several months, and this occurs in both temperate and tropical environments (Fig. 2). Note also in these examples that emergence of two species, *S. viridis* and *Cyperus rotundus*, extends for a much longer time after E_{50} than before it. In contrast, emergence of other species, including *Ageratum conyzoides* and *Elusine indica*, continues for considerably longer time before E_{50} than after it. Emergence of only one species in the examples displayed in Fig. 2, *Hedyotis corymbosa*, seems distributed evenly around E_{50}. The importance of this asymmetry of emergence is that it indicates that E_{50} does not represent early and late emerging individuals equally for many weed species.

To capture the important features of seedling emergence, a better representation of its full cycle and timing is necessary. Such representations almost

certainly require a dynamic modeling approach. Accordingly, models of seedling emergence are being developed actively worldwide for both crops and weeds. In this report, we attempt to review certain basic components of emergence, describe the main environmental and management factors that affect it, review previously described emergence models, and present a description of a tentative universally applicable emergence model.

2. Components of seedling emergence

2.1. Dormancy

Seed dormancy is a classic feature of weed species from environments with conditions that are adverse for plant growth and reproduction during some portion of the year. However, seeds of some species never experience dormancy. Although lack of dormancy may be more common in plants from the wet tropics than elsewhere, even in tropical environments, especially those with cyclic wet and dry seasons, seed dormancy is common (Garwood, 1989). Not only is seed dormancy a common feature of weed seeds, but it probably also is the most important of a series of components and processes that affect seedling emergence. The paper on seed dormancy included in this issue (Benech Arnold et al., 2000) is devoted largely to describing how dormancy is affected by various environmental factors. Here, we shall list briefly some

factors that affect dormancy as a basis for commenting on the few existing attempts that have been made to model seed dormancy changes.

Normally, seedling emergence of a particular weed in the field occurs when the dormancy level of the population is at its minimum (Probert, 1992). Thus, for the construction of dynamic models that predict seedling emergence on a daily basis, we need to understand and model not only the way that environment modulates germination rate within the "time window" of minimum dormancy, but also the way that environment determines when that "time window" will occur.

Environmental factors that affect dormancy of seed populations can be divided in two categories (Benech Arnold et al., 2000): (a) those that modify the dormancy level of the populations (namely, those such as temperature and soil water content that widen or narrow the range of environmental conditions that permit germination); (b) those that terminate dormancy or remove the ultimate constraint for germination once the degree of dormancy is at its minimum (i.e. light flux density and quality, fluctuating temperatures, nitrate concentration).

For seeds of annual species, dormancy is either released or lowered during the season preceding the period with favorable conditions for seedling development and plant growth. In contrast, dormancy is induced in a period preceding the season with environmental conditions unsuitable for plant survival (Karssen et al., 1988). Although reality is more complex and diverse, changes in dormancy of a seed population in response to temperature are thought to proceed according to any one of the following patterns (Probert, 1992; Benech Arnold and Sánchez, 1994). (a) Seeds from summer annual species, which are dispersed with a high dormancy level at the end of the summer, are released from dormancy by low winter temperatures. High summer temperatures may induce entrance of these same seeds into dormancy again, which is referred to as secondary dormancy. (b) Seeds from winter annuals, which are dispersed during mid-spring to early summer, are released from dormancy by high summer temperatures. In contrast, low winter temperatures induce their entrance into secondary dormancy. Cycles of dormancy and nondormancy can persist within a single seed population for several years.

Although the classic paper for cyclic induction into secondary dormancy was by Courtney (1968) for *Polygonum aviculare*, probably the first model to consider changes in dormancy level regulated by soil temperature was that proposed by Bouwmeester and Karssen (1992). Those authors produced a model that succesfully predicted changes in dormancy of the summer annual *Polygonum persicaria* as a function of the thermal conditions while seeds were buried. The model was based on the hypothesis by Totterdell and Roberts (1979) for other species within the Polygonaceae that changes in dormancy in these summer annuals result from two processes: (a) relief of primary dormancy as a result of exposure to temperatures <15°C; (b) induction of secondary dormancy with a rate that rises with higher prevailing temperatures. The model by Bouwmeester and Karssen (1992), therefore, considers the level of dormancy (*D*) as a function of cold (*C*) and heat (*H*) unit sums:

$$D = f(C, H) \qquad (1)$$

The value of *C* is raised by an arbitrary value of 1 unit for each period of 10 days that the mean soil temperature is below the critical value of 15°C. *H* is calculated by summing the mean soil temperature of each successive 10-day period. The degree of dormancy was related to the width of the thermal range permissive for germination (i.e., the lower the dormancy level, the wider the permissive thermal range). Hence, for a given date when seeds were exhumed for testing, the germination percentage (G_t) at various temperatures could be described by a quadratic function of the test temperature (T_g):

$$G_t = aT_g^2 + bT_g + c \qquad (2)$$

The values of the coefficients *a*, *b* and *c* are proposed to be functions of *D*:

$$a, b, c = f(C, H) \qquad (3)$$

Thus, the model allows estimation of the width of the thermal range permissive for germination (namely, minimum and maximum temperatures permitting germination) for seeds that have been buried for differing periods of time and exposed to variable thermal environments. For instance, Vleeshouwers (1997) plotted changes in germination temperature range for *P. persicaria* with soil temperature (Fig. 3). Germination periods during the year for this species can
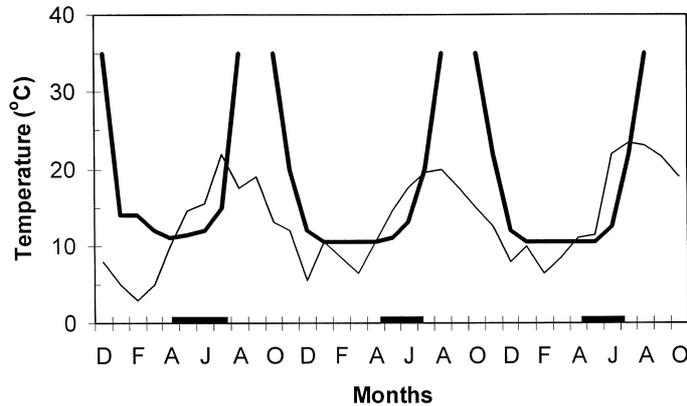
Fig. 3. Overlap of soil temperature and the seasonally variable temperature response of seeds of *P. persicaria* for dormancy relief and germination. Thick lines represent minimum and maximum temperatures that elicit 50% germination. Thin lines represent soil temperature at 10-cm depth. Shaded areas on *x*-axis depict periods of overlap of field temperature and germination temperature, and represent the times when germination may be expected to occur. Figure adapted from Vleeshouwers (1997).

be inferred from this plot as the periods when field temperature overlaps the temperature range for germination as indicated by the heavy bars on the *x*-axis of Fig. 3.

Seeds of the winter-annual grass, *Bromus tectorum*, lose primary dormancy through dry "afterripening" during the summer and are then capable of germinating when sufficient moisture is present (Bauer et al., 1998). Bauer et al. (1998) derived a simulation model to predict dormancy loss from seeds of this species. The model is based on the assumption of a thermal time requirement for afterripening. The model considers accumulation of temperature above a base temperature according to the following equation:

$$TT_{ar} = (T_s - T_1)t_{ar} \qquad (4)$$

where TT_{ar} is the thermal time requirement for afterripening, T_s the temperature of storage, T_1 the lowest or base temperature (at or below which afterripening does not occur), and t_{ar} the time required for afterripening.

The model also accounts for dormancy loss during afterripening through changes in the base water potential of the seeds' environment that permits 50% germination ($\Psi_{b(50)}$) (Bradford, 1995), which is allowed to vary with incubation temperature as well as afterripening status. Laboratory studies confirmed that $\Psi_{b(50)}$ did become more negative as seeds afterripened

(Christensen et al., 1996). Hence the model assumes that the rate of change in $\Psi_{b(50)}$ is a linear function of TT_{ar}. Therefore, assuming TT_{ar} as the thermal time required for $\Psi_{b(50)}$ to change from its initial value (the value for recently harvested seeds) to its final value (the value for fully afterripened seeds), the decrement in $\Psi_{b(50)}$ per degree-hour (or degree-day) can be expressed as

$$\Psi_{b(50)\,decrement} = \frac{\Psi_{b(50)\,initial} - \Psi_{b(50)\,final}}{TT_{ar}} \qquad (5)$$

This relationship can be used directly in the field simulation model of dormancy loss. The decrease in $\Psi_{b(50)}$ in any interval of time is expressed as

$$\Psi_{b(50)\,decrease} = (\Psi_{b(50)\,decrement})((T_s - T_1)t) \qquad (6)$$

In the model by Christensen et al. (1996), the seed-zone soil temperatures recorded at 1-h time steps are input for T_s, a value of 1 is input for time, and constant values for $\Psi_{b(50)\,decrement}$ and T_1 are input for a particular collection and incubation temperature. Therefore, for each h increment, the model then calculates $\Psi_{b(50)}$ decrease for a specific seed collection at each incubation temperature, using the corresponding thermal afterripening time parameters. If estimated seed-zone water potential during that hour is considered low enough for afterripening to proceed (below approximately -4 MPa), the $\Psi_{b(50)}$ value of the population is decreased by the change in $\Psi_{b(50)}$ due to afterripening

during that hour. The $\Psi_{b(50)}$ value is saved as the $\Psi_{b(50)}$ value of the population, and serves as the initial value for the next time step. The process continues until the $\Psi_{b(50)}$ value of fully afterripened seeds is reached. To our knowledge this is the only model to consider dormancy changes, not only in relation to the thermal environment, but also as a function of the soil water status.

In some seed populations, once a low level of dormancy has been attained, dormancy may be terminated entirely by the effect of light, nitrate, or fluctuating temperatures, to allow the germination process to proceed. In those cases, changes in degree of dormancy not only comprise changes in temperature requirements for germination, but also in sensitivity to the effects of dormancy-terminating factors. A model that considers changes in sensitivity to light as a result of changes in dormancy level, for example, would be useful since it could be employed for predicting the time of the year at which maximum sensitivity to light is attained (i.e., very low influence-type of response). If this maximum sensitivity to light coincides with the period of overlap between field temperature and the temperature range over which germination can proceed, this should be the time during which maximum emergence could be expected after previously buried seeds are exposed to light through soil disturbance. Indeed, soil disturbance would expose a fraction of the seed population to daylight with a spectral composition that would have the same effect on dormancy release as red light.

Vleeshouwers (1997) proposed a simulation model that uses the amount of a hypothetical membrane-located phytochrome receptor, protein X (Hilhorst, 1993), as a measure for the degree of dormancy. The dormancy model simulates seasonal changes in the amount of the receptor X in buried seeds, driven by seasonal changes in dormancy. Because the hypothetical receptor X cannot be measured, its status must be inferred indirectly from germination tests conducted over a range of conditions. The dormancy model is coupled to a germination model that calculates germination percentages of seed samples that are irradiated with red light and tested for germination at different temperatures. Conceptually, this model is a good starting point for the formulation of similar models, though other factors such as soil water status during afterripening should be considered as involved

in the modeling of changes in light sensitivity. Indeed, there is evidence indicating that some seeds would require several cycles of imbibition–dehydration to acquire extreme sensitivity to far-red light (Hilhorst et al., 1996).

A thorough understanding of dormancy mechanisms, especially of the roles of microclimate in the relief of primary dormancy and induction of (secondary) dormancy will be essential in the development of useful seedling emergence models.

2.2. Germination

Assuming seeds are nondormant, germination is the key component of seedling emergence. Although germination is a continuous process commencing with various physiological activities within seeds, it typically is considered from a practical point of view. That is, germination is represented by the first visual appearance of the radicle from the outermost structure enveloping the embryo.

Seed germination is perhaps the most thoroughly examined aspect of plant development. It has been studied extensively in controlled environments, but only rarely in natural soil environments. Nevertheless, the primary factors governing seed germination in arable soils are: temperature, water potential, and air quality. These factors, and others, have been reviewed extensively elsewhere (Roberts, 1988; Roberts and Ellis, 1989) and will be discussed in the following section on environmental effects on emergence.

Before leaving this topic, however, the role of seed populations must be noted in reference to germination (Bradford, 1995). That is, germination is only rarely an instantaneous phenomenon. Each individual seed within a population has a unique genotype, and this genotype may affect the seed's response to environmental stimuli. Accordingly, when germination percentages or germination rates (i.e., speed or velocity) are plotted against standard environmental variables, the result is often skewed bell-shaped curves, even in the absence of dormancy. The tails of such curves provide indirect evidence for intrapopulation variability for seed germination. Methods for analyzing differing seed populations have advanced quickly in recent years (Garcia-Huidobro et al., 1982; Ellis et al., 1986; Bradford, 1995).

2.3. Pre-emergence seedling elongation

Seeds are distributed in the soil profile at differing depths. Burial in arable soils is largely due to tillage implements. However, even in no-till (direct-drilled) systems, burial may result from sowing implements, wheel traffic, animal traffic, soil shrinking, swelling and sloughing, and self-burial via structural characteristics of seeds (such as hydroscopic awns).

Seed burial has both positive and negative consequences for seedling emergence. The most obvious negative consequence is burial so deep that seed germination is prevented. Germination sometimes occurs with deep burial but seed reserves may be exhausted before the seedling reaches the soil surface, which leads to seedling death. As might be expected, deep burial is more detrimental to small-seeded than to large-seeded species. Unfortunately, quantitative data on this topic is scarce (King and Oliver, 1994).

Burial also places a downward physical force on seedlings which acts as an impediment to emergence. This is especially true after intense rainfall on a freshly prepared seedbed. Here, a soil crust forms that can be impenetrable by some seedlings. However, some species may have evolved seedling structures that facilitate emergence through crusted soils. For example, as a seedling of *Amaranthus retroflexus* extends towards the soil surface, its cotyledons are reflexed, and their bases form a pointed apex at the top of the hypocotyl. This seems to allow seedlings of this species to elongate even through compacted soil. Similarly, sharp-pointed coleoptiles of some grass seedlings enable elongation through densely packed soils.

The benefits of burial are reduced exposure to air, where even 99% relative humidity of air is equal to a water potential of about -1.5 MPa. Soil overlying very young seedlings creates a mulch that maintains high humidity at or near 100% and allows growth to proceed relatively rapidly. Moreover, soil burial also provides protection of seeds and seedlings from abnormally low and high air temperatures as well as granivores and herbivores that dwell on or near the soil surface.

2.4. Emergence

Like germination of a seed, emergence of a seedling can be defined by the observer. For instance, Benech

Arnold et al. (1990b) defined emergence of *Sorghum halepense* as the time when the first leaf of a seedling was fully expanded. A stricter, but equally arbitrary definition of emergence might be the first appearance of a seedling at the soil surface. For small-seeded species, that definition would demand close and repeated inspection of the soil surface. First appearance of emerged seedlings in field settings can be quantified reliably only if researchers are willing to spend substantial time on hands and knees, often in cold, damp, and muddy conditions. Data emanating from casual visual estimates of E_i or E_{50}, which are encountered frequently in the literature, may be useful, but should be interpreted cautiously.

3. Environmental effects on emergence

Soil temperature, soil water, soil air quality, and light quality are the main environmental factors affecting seedling emergence. In the absence of irrigation, these factors tend to be "natural," in the sense that they are influenced mainly by radiation, rainfall, and other weather variables over which humans have no control. However, these factors can be manipulated indirectly through management. Other factors, such as soil fertility, salinity, compaction, tillage, and surface residue also influence emergence, and these can be manipulated more directly through management. Although these factors will be discussed individually below, interactions among them are in plenty.

3.1. Soil temperature

In temperate regions, soil temperature is probably the most distinct and recognizable factor governing emergence. The literature describing temperature effects on germination is voluminous, whereas descriptions of temperature effects on initial seedling elongation and emergence are less abundant. Nevertheless, in most instances where a sufficiently broad temperature range was examined, variously shaped parabolic relationships exist between germination, elongation, or emergence and temperature (Carberry and Campbell, 1989; Fyfield and Gregory, 1989). In many instances where fluctuating temperatures appear to enhance germination or emergence beyond that measured for comparable uniform temperatures, the

direct effect was through the breaking of seed dormancy rather than enhancing seed germination, per se (Benech Arnold et al., 1990a).

From an emergence-modeling perspective, the uniform temperatures of growth cabinets, or the geometric averages in experiments with fluctuating temperatures, correspond theoretically and in practice with average daily soil temperatures in the field. For example, germination of *Abutilon theophrasti* and *Chenopodium album* in growth cabinets, which were set at various constant and fluctuating temperatures, permitted development of successful simulation models that used average daily soil temperature at 5-cm depth as the primary input variable to predict emergence of these species in field settings (Forcella, 1993; Harvey and Forcella, 1993). In these cases, germination data had to be transformed into units (germination rate index) that accounted for both the extent and speed of germination at each temperature setting. This allowed creation of equations that simulated effects of average daily soil temperature on germination response. After addition of an appropriate time lag, which accounted for hypocotyl elongation, emergence could be predicted with some assurance.

Soil temperature can be used directly as a predictor of seedling emergence, or it can be converted to soil thermal time (TT), i.e. growing-degree days. TT has been used in crop growth models with some success (Angus et al., 1981). This probably occurred because crop seeds are relatively homogeneous genetically, and they typically are sown directly into moist soil at precise soil depths. In contrast, genetically diverse weed seeds are distributed unevenly at various soil depths where they experience varying levels of soil moisture and TT. Consequently, early attempts at TT-based models for predicting E_i and E_{50} of weeds were disappointing (Boydston, 1989).

Use of TT in emergence models became successful with the realization that emergence can be represented by a simple continuous cumulative sigmoidal curve, but only if the upper few centimeters of field soil remained continuously moist, either through irrigation or natural rainfall. Gompertz, Weibull, Richards, and logistic functions (Brown and Mayer, 1988), in which soil TT serves as the independent variable, can represent such a curve. These functions considerably improved prediction of cumulative relative seedling emergence (CRE) of some weed species.

The Gompertz function, in its simplest form, is as follows:

$$CRE = 100 \exp\{-a \exp(-bTT)\} \qquad (7)$$

Some researchers have used complicated extensions of these functions, such as the double Gompertz curve (Kremer and Lotz, 1998). For the simple Gompertz equation, the coefficients are easily interpreted, with *a* representing a TT lag before emergence commences, and *b* representing the rate of increase of emergence once it is initiated. Examples of use of TT in CRE predictions for weeds include *Digitaria ischmaeum* (Fidanza et al., 1996), *S. halepense* (Benech Arnold et al., 1990b), and 15 other species in computer software called WeedCast (Forcella, 1998).

Some researchers have used calendar days as the time variable in CRE models (e.g., Cussans et al., 1996; Vleeshouwers, 1997). In these models the effects of temperature on emergence are included as rather complex mathematical expressions that replace the *a* or *b* coefficients. Where calendar days have been used as the time variable, results have not been as impressive as those with TT.

Temperature-based emergence models can be divided into two categories: mechanistic and empirical. Mechanistic models probably have the greatest chance of success in the long-term because they are based on known and experimentally quantified environmental effects on seed dormancy, imbibition, and germination, and seedling elongation. Vleeshouwers' (1997) synthesis of information on *C. album*, *P. persicaria*, and *Spergula arvensis* plus the recent simulations by Roman et al. (2000), also on *C. album*, probably represent the best displays to date of mechanistic emergence models. These models entail equations that were developed from data derived from experiments conducted under controlled conditions. In those types of experiments, temperatures of incubators or growth chambers are thought to be surrogates for temperatures in the seed-bearing zone of soils. The resulting data may be analyzed to determine rates of seed germination at specific temperatures or temperature ranges (e.g., Carberry and Campbell, 1989). Such temperature-sensitive germination rates (often called speeds or velocities) then can be inserted into models in which soil temperature (or sometimes air temperature) is the main driving variable (e.g., Alm et al., 1993;

Harvey and Forcella, 1993; King and Oliver, 1994; Oryokot et al., 1997; Vleeshouwers, 1997).

Despite the wealth of laboratory studies of germination and initial seedling growth, there are relatively few mechanistic seedling emergence models. Fewer still is the number of reports that compare model simulations with actual observations of emergence in field settings. Nevertheless, existing mechanistic models have met with some success (Benech Arnold et al., 1990b; Forcella, 1993; Vleeshouwers, 1997; Roman et al., 2000).

Mechanistic models may be highly sensitive to the idiosyncrasies of the seed accession that was used to generate the temperature-sensitive germination rates. For example, base temperatures (T_b) and thermal times necessary for 50% seed germination (TT_{50}) of *S. viridis* varied according to the site at which the seed accession was obtained (Fig. 4). Among seed accessions from the states (USA) of Iowa, Kansas, Minnesota (three accessions), Nebraska, and South Dakota, T_b ranged from 3.5°C (Nebraska) to 11.5°C (Minnesota #2), and TT_{50} ranged from 20°C day (Minnesota #2) to 59°C day (South Dakota). Because all seed accessions were treated with gibberillic acid (GA_3) prior to testing, differential dormancy among the accessions should not have been a factor influencing these results.

In addition to TT_{50}, values for TT_{10}, TT_{30}, TT_{70}, and TT_{90} also were calculated for *S. viridis* and are plotted in Fig. 4, along with best-fit (least-squares) Gompertz equations, for each seed accession. These equations represent $TT_{germination}$ models for *S. viridis*. Although individual models appeared similar for Minnesota #2 and Kansas seed accessions, as well as for the Minnesota #1 and Minnesota #3 accessions, there were large differences between these two groups and among the remaining accessions in how their seeds responded to thermal time. Thus, substantial heterogeneity exists within this species with regard to the effects of TT on seed germination rate.

T_b has been reported as a stable trait within crop cultivars (Bradford, 1995). However, for noncrop species, such as *S. viridis*, neither T_b, TT_{50}, nor $TT_{germination}$ appeared stable. This may not be surprising as *S. viridis* has distinct genetic variability (Wang et al., 1995) that is relatively small but still larger than that found within a crop cultivar. Moreover, if maternal environments during seed maturation are less
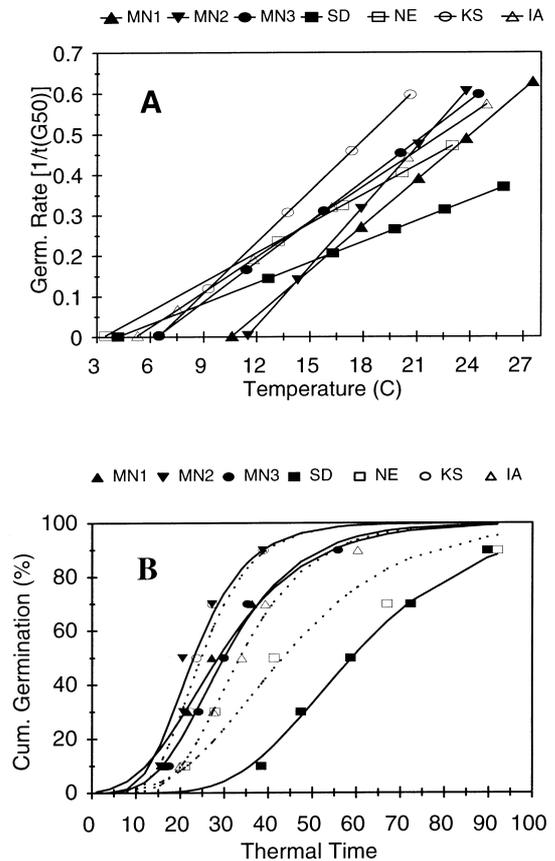

Fig. 4. (A) Relationships between incubation temperatures and germination rates are linear for seven seed accessions of *S. viridis*. Regression lines all had r^2 values >0.98 (unpublished data). Seeds were collected from at least 20 plants at each location in August 1991 and subjected to constant temperatures on a thermogradient bar during March 1992. Base temperatures (T_b) for germination can be represented by the points where the lines intercept the temperature axis. The inverse of the slope of each line represents the thermal time (TT) required for 50% germination (TT_{50}). (B) Thermal times to 10, 30, 50, 70, and 90% germination (TT_{10}–TT_{90}, symbols) and curves from Gompertz-type equations representing these relationships for the same seven populations as in (A).

uniform for noncrop species than for crops, then more heterogeneous seed responses to temperature might be expected for noncrop species.

Both T_b and $TT_{germination}$ (TT_{10}–TT_{90}) can be used as bases for successful emergence models (Benech Arnold et al., 1990b). To do so, however, clearly assumes constancy of these seed characteristics within the modeled species. Appreciable variability of these

characteristics would necessitate development of multiple models, possibly as many as the number of seed accessions examined. In fact, preliminary emergence models were made for the seven *S. viridis* accessions, and their predictions were compared to field observations of seedling emergence in Minnesota and Iowa. Unfortunately, Minnesota- and Iowa-based models did not always predict emergence in these locations as well as Nebraska- and Kansas-based models (data not shown).

Causes for the disparities between location-specific models and associated emergence patterns might be explained by a bewildering array of possible effects. These effects may include factors such as maternal and environmental influences on seed physiology during maturation of the seeds that were used for model development, variable genetic structure of the seed accessions, different seed burial depths in soils in the observed populations, and different soil and management characteristics. Equally confusing, however, are the consequences of this problem for emergence modeling. For instance, which seed accessions are best to use for model construction, and should an emergence model for a single species have regional (geographic) subroutines? Are laboratory-generated mechanistic models appropriate for predictions of field emergence? These questions cannot be answered presently with the current information base.

An alternative to a mechanistic model is an empirical model, which can have various levels of empiricism. The most basic empirical model would be a simple representation of emergence over time (calendar days) averaged across years. By including a temperature component to time (i.e., soil TT), such empirical models at once become more mechanistic. A simple representation of such a model is presented in Fig. 5, which is based on field observations of *Digitaria sanguinalis* emergence over two years with two seedbed preparation dates each year (King and Oliver, 1994). In this figure, the finely dotted line represents the least-squares best fit of a Gompertz function with *a* and *b* values of 13 and 0.015, respectively. Clearly, there are striking disparities between the best-fit line and actual observations, justifying past conclusions that TT and emergence are not tightly linked (Boydston, 1989; Forcella, 1993). The disparities most likely are due to the inability of TT to compensate for levels of soil water that are too low to
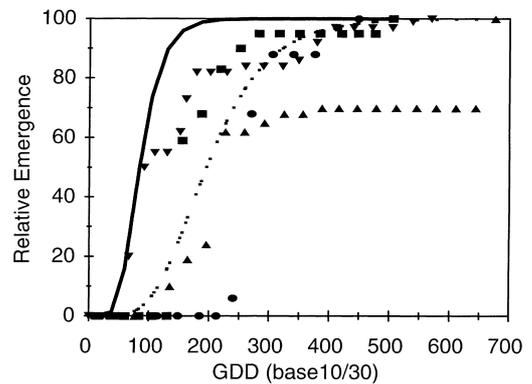

Fig. 5. Observations (symbols) of *D. sanguinalis* emergence (King and Oliver, 1994) for two sowing dates in each of 1991 and 1992 in Arkansas, USA. Emergence is plotted against soil thermal time at 5-cm depth using base and ceiling temperatures of 10 and 30°C, respectively. The dotted line represents a least-squares best fit to the data using a Gompertz equation. The solid line represents the presumed upper boundary of the data.

permit germination, seedling elongation, and emergence (King and Oliver, 1994).

One solution to the lack of integration of the effects of low water potentials in a best-fit TT-emergence relationship is to use an upper boundary approach. This concept is illustrated in Fig. 5 by the solid line, which theoretically represents the true influence of TT on emergence in the absence of confounding effects of other environmental variables, most notably, soil water potential. In this instance, Gompertz coefficients for this curve are 20 and 0.04 for *a* and *b*, respectively. Furthermore, this curve should conform to laboratory data in which only temperature affected seed germination. Indeed, inspection of Fig. 2 in King and Oliver (1994), which depicted CRE at several temperatures against time after sowing in growth chambers under moist experimental conditions (−0.03 MPa) revealed that maximum emergence occurred quickly and within 100°C day (base 10/30°C), much like that in Fig. 5.

3.2. Soil temperature fluctuations

Seed dormancy, seed germination, and seedling emergence are continuous and intimately related processes. Seed dormancy is reviewed elsewhere in this issue (Benech Arnold et al., 2000) and will not be
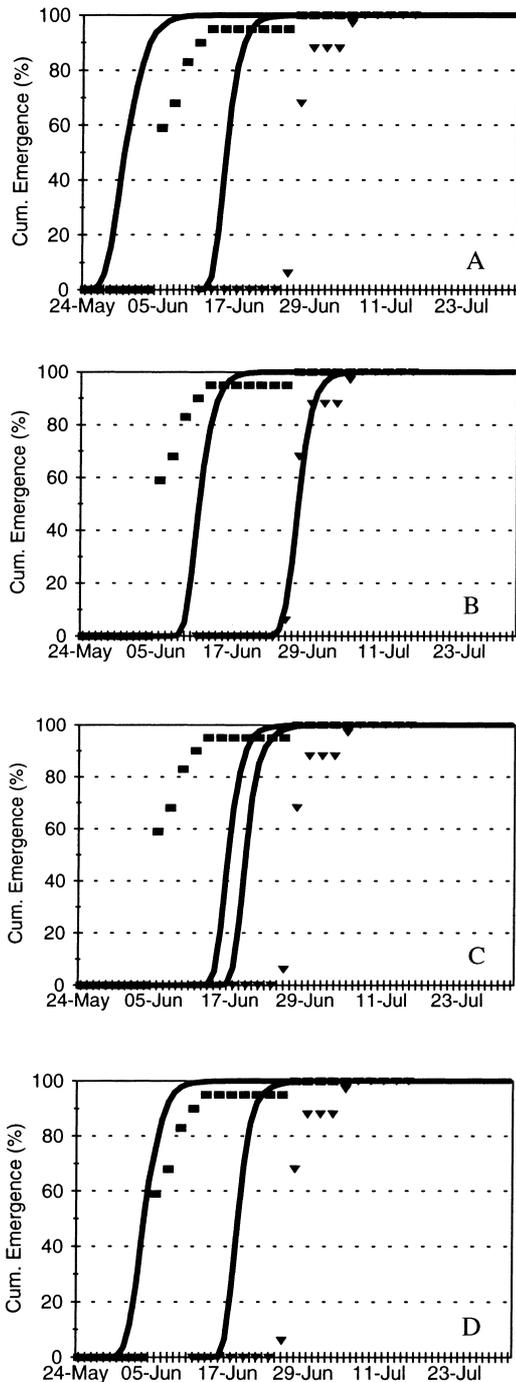
discussed here except to mention that it is strongly influenced by soil temperature. In particular, the extent and number of diurnal soil temperature fluctuations can be critical in lessening seed dormancy of several species (Vleeshouwers, 1997), which thereby allows germination and emergence to continue. For emergence models, this effect is best described and documented for *Sorghum halapense* in Argentina (Benech Arnold et al., 1990a,b). Seeds of this species may remain dormant unless they undergo 1–3 diurnal cycles of soil temperature fluctuations with an amplitude of 15°C. As this requirement is being met, germination of specific seed fractions commences and emergence proceeds according to a typical TT response. Seeds buried deeply by tillage will not be exposed to these temperature fluctuations as frequently or as early in the growing season as seeds buried at shallow soil depths.

The effects of number and amplitude of soil temperature cycles can be reaffirmed in a simplified manner with the *D. sanguinalis* data of King and Oliver (1994). In Fig. 6A, emergence observations from two seedbed preparation dates during 1990 are plotted against time (calendar days), along with predictions based upon the Gompertz model presented in Fig. 5. That is, emergence is dependent solely upon cumulative TT without any other restricting variables. Fig. 6B is an example of adding the "cycles" restriction of Benech Arnold et al. (1990a,b), in this case four cycles of a diurnal amplitude of 12°C. Likewise, Fig. 6C represents the effects of 12 cycles of 6°C diurnal amplitude. Finally, Fig. 6D illustrates the response of the Gompertz model to restrictions of four cycles of 6°C amplitude. Note that when "cycles" restrictions are applied, only in Fig. 6D does simulated emergence consistently overestimate observed emergence. For emergence modeling, overestimation is a desired characteristic when other variables of known importance, such as soil water potential, are missing from the model.

Fig. 6. Simulations (lines) and observed data (symbols; King and Oliver, 1994) for emergence of *D. sanguinalis* in Arkansas, USA. (A) Emergence affected only by cumulative GDD. (B) Emergence affected by GDD and the preliminary necessity of four diurnal cycles of 12°C amplitude. (C) Emergence affected by GDD and the preliminary necessity of 12 diurnal cycles of 6°C amplitude. (D) Emergence affected by GDD and the preliminary necessity of four diurnal cycles of 6°C amplitude. Note that in B and C, emergence is under-represented by at least one of the simulations.

3.3. Soil water potential (Ψ)

Among ecologists and modelers there often are debates about the relative importance of soil temperature and soil water in governing plant responses, including emergence. This is a needless debate, however, as both variables are critical. Advocates for soil temperature may have been influenced, at least partially, by the concept of thermal time. This variable has two valuable traits for predicting emergence. First, it has considerable empirical and biologically rational explanatory power, and second, it is simple to measure and calculate. Until recently, soil water potential had no equally simple and inherently logical abstraction. Soil water has been relatively difficult to measure, and its cumulative effects on dormancy, germination, and emergence were difficult to integrate. These difficulties now are being resolved.

Integration of the cumulative effects of water deficits has been encapsulated in the "hydrotime" concept. This idea was first illustrated by Gummerson (1986) and later eloquently explained, examined, and expanded by Bradford (1995). To date it has been used primarily to describe seed germination in laboratory settings rather than seedling emergence in field soils. Nevertheless, the idea of hydrotime, particularly when combined with thermal time and expanded to "hydrothermal time," is so appealing that rapid adoption can be expected by those involved with modeling seedling emergence. In fact, the bases for a hydrothermal time model for *C. album* recently were developed (Roman et al., 1999, 2000). Rapid adoption will be especially true with resolution of the second difficulty surrounding the use of Ψ as a predictive variable, namely the ease of its measurement.

Although various instruments are now available for measuring Ψ, they are often expensive, complicated, or inaccurate. Consequently, Ψ is not measured routinely in the same manner as soil temperature. Luckily, Ψ of the upper 5 cm of soil, where most weed seeds with germination potential reside, can be estimated from other micrometeorological variables.

Several crop growth models provide estimates of Ψ of surface soil layers. These models typically require a complex array of measurements for such estimations, such as soil surface albedo and residue levels; bulk density, infiltration, and percolation characteristics for different soil layers; and above-ground humidity,

radiation, temperature, and wind speed. Thus, these models have been used more for research than for management. However, a rough but simple and relatively reliable system of estimating Ψ of the soil seed zone (upper 5 cm) was devised specifically for seedling emergence modeling (Forcella, 1993). This model is based primarily on two input variables, daily rainfall (and irrigation) and average daily soil temperature at 5 cm, coupled with a single initialization variable, soil textural class. General soil water retention characteristics are assigned to each soil textural class, and soil temperature and time since last rainfall (or irrigation) integrate many variables that otherwise determine soil water evaporation. The result is a relatively robust model with a degree of reliability. For example, Fig. 7 represents simulated daily soil water contents using daily soil temperature and rainfall data supplied by C.A. King (personal communication, 1998) for a site in Arkansas where soil water contents were monitored gravimetrically on alternate days (King and Oliver, 1994). Increases in soil water were always associated with rainfall events, and decreases were related to rainless periods. Simulations underestimated observed soil water contents when soil water was below 9% (-10 MPa) in this silt loam soil. However, this may not have too great an effect on predictions of seedling emergence as seeds do not germinate in soil that dry. Although the robust concepts of hydrotime and hydrothermal time have not yet been used in field emergence
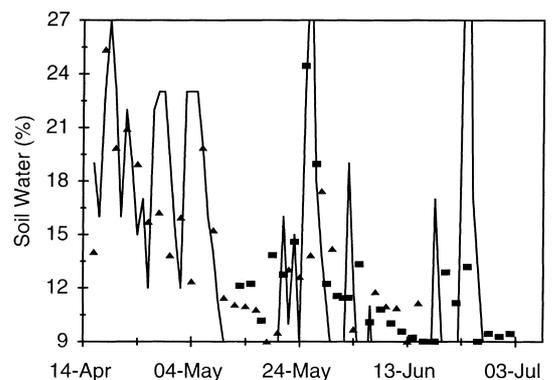

Fig. 7. Daily estimates of soil water percentages (solid line) for Arkansas, USA, seedbeds during 1991 that were prepared early (triangles) or late (squares), as adapted from King and Oliver (1994). Soil water was determined gravimetrically from soil cores sampled on alternate days.

models of either crops or weeds until recently (Roman et al., 2000), the practical ability of easily estimating daily Ψ should aid their implementation.

In the meantime, another modeling strategy that combines soil water potential and soil temperature has met with some success in predicting seedling emergence. A simple, yet insightful, approach that couples soil TT and Ψ can be labeled as the punctuated TT model. In this approach, a threshold soil water potential (Ψ_E) is used to stop the accumulation of TT. An excellent example of this approach is that of onion (*Allium cepa*). On days when $\Psi > \Psi_E$ (-1.1 MPa), TT accumulates and germination and emergence of onion progresses. However, when $\Psi < \Psi_E$, TT accumulation ceases and germination stops until the next rainfall or irrigation event (Finch-Savage and Phelps, 1993). This approach was used to predict field emergence of onion successfully. The relationships between onion germination and TT as well as Ψ_E were derived from laboratory experiments. The same approach has been used for several weed species using data derived entirely from field settings (Forcella, 1998). This approach will be described below in more detail.

The empirically derived relationship between CRE_{max} and TT can be modified according to Ψ by examining the effects of several values of Ψ_E through an iterative process. An example for *D. sanguinalis* is illustrated in Fig. 8. Here, the basic Gompertz equation shown in Figs. 5 and 6, which is unencumbered by the effects of Ψ, is represented by the thin solid line

labeled as -10 MPa in Fig. 8. This line indicates how *D. sanguinalis* would be expected to emerge if TT were the only factor governing emergence. That is, the assumption would be that *D. sanguinalis* has an exceptionally high tolerance to water stress ($\Psi_E < -10$ MPa). Although the observed data (solid circular symbols, adapted from King and Oliver, 1994) agree somewhat with this prediction, clearly some effect other than TT is influencing emergence.

In contrast to assuming a very low Ψ_E (-10 MPa) in the first iteration of determining a threshold water potential, a second iteration can assume high sensitivity to water potential ($\Psi_E = -0.1$ MPa). This assumption also results in a relatively poor fit of the simulation to observed data (Fig. 8). This iterative process continues until the simulation conforms satisfactorily to the observed data. In this example, the best fit appears to occur when $\Psi_E = -0.5$ MPa.

If -0.5 MPa is used as the correct Ψ_E for *D. sanguinalis* in a punctuated TT model, highly satisfactory agreement between simulations and observations occur for data sets not used in the empirical determination of Ψ_E (Fig. 9). Although the purely empirical nature of these models provides some doubt as to their general application, they seem surprisingly robust (Forcella et al., unpublished).

3.4. Soil burial

Most seeds are buried by at least some soil. Consequently, after germination seedlings must elongate to reach the soil surface. Reserves in the seeds provide the only energy source for this activity. If the energy supply does not meet the energy demand for coleoptile or hypocotyl elongation, pre-emergence mortality results. This simple energy balance for seedling emergence is the basis, in part, for soil tillage as a pre-emergence weed management tool. That is, tillage buries some seeds at depths where they germinate but do not emerge.

Several researchers have demonstrated the effect of soil burial on seedling emergence. As a general rule, species with small seeds emerge better from very shallow soil depths than larger-seeded species. In fact, the model developed by Grundy et al. (1996) implicitly assumes maximum emergence potential at the soil surface for all species, which is followed by logarithmic decreases in emergence from seedlings
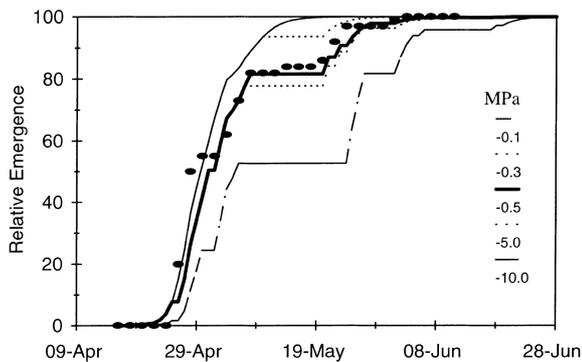

Fig. 8. Iterative procedure for empirically examining the effect of a threshold soil water potential (MPa) for thermal time accumulation on emergence of *D. sanguinalis*. Solid circles are observations from King and Oliver (1994). The heavy line represents the best-fit simulation. It used a water potential threshold of -0.5 MPa.
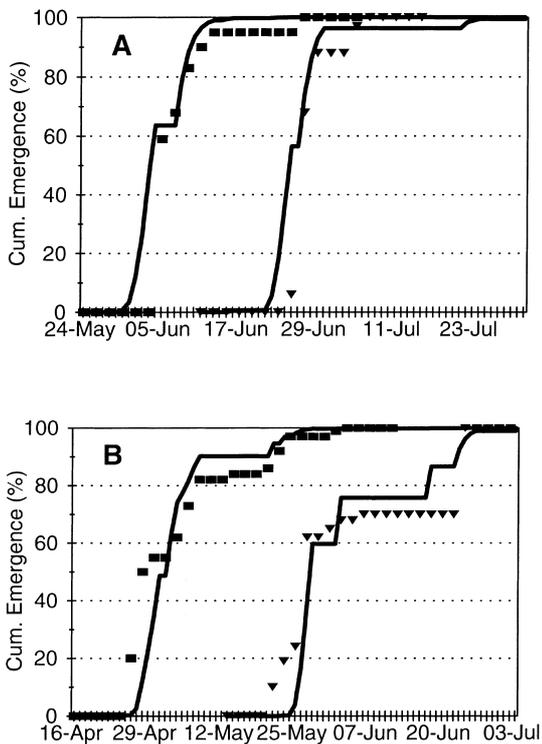
Fig. 9. Observations of *D. sanguinalis* emergence in Arkansas, USA, during (A) 1990 and (B) 1991 as reported by King and Oliver (1994), and predictions using the following coefficients from a punctuated Gompertz model: lag, 20; rate, 0.04; cycles, 4; dT, 6; Ψ_E, −0.5 MPa.

Fig. 10. Relative probabilities of seedling emergence of species with seed sizes ranging from small to large. Mat, *Matricaria ordorata*; Che, *C. album* (adapted from Grundy et al., 1996); Set, *Setaria faberi*; Pol, *Polygonum pensylvanicum*; Abu, *A. theophrasti* (adapted from Buhler, 1995).

whose seeds were buried under more and more soil. Monotonic decline of emergence with soil burial depth does not occur with larger-seeded species (Fig. 10), which appear to require substantially more time to imbibe water prior to germination. Thus, large seeds at the soil surface are exposed to greater risk of dehydration than their buried or smaller-seeded counterparts (Buhler, 1995). Consequently, emergence patterns of some species, especially those with large seeds, exhibit parabolic relationships with soil burial depth (Fig. 10). Unfortunately, differential emergence abilities in response to burial depths have not been incorporated into most emergence models.

Soil tillage is intimately associated with seed burial and is an important, albeit indirect, variable that regulates seedling emergence. Fortunately, in recent years several researchers have documented tillage effects on seed distributions in soil. Indeed, models
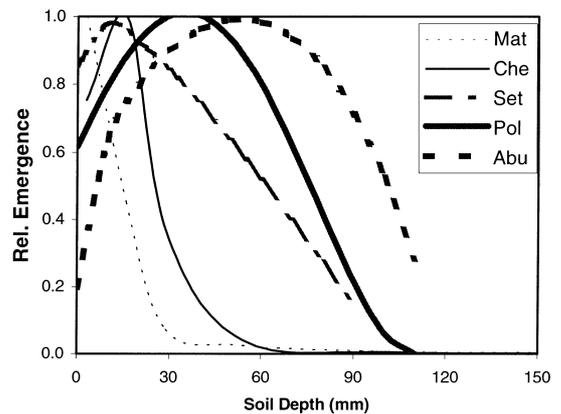
now exist that simulate seed distributions in the soil profile after one or more years of tillage (Cousens and Moss, 1990; Grundy et al., 1996). These types of models can be beneficial for comparative studies, especially when they are combined with "emergence-from-depth" models of small- and large-seeded species (Forcella et al., 1996). However, integration of these types of simple models with the more dynamic, microclimate-driven emergence models remains an important challenge.

3.5. Seedling elongation

From a mechanistic point of view, another critical aspect of emergence modeling that largely is missing from the literature involves seedling elongation prior to emergence. Soil temperature, water potential, impedance, and many other factors govern elongation rates of coleoptiles and hypocotyls prior to emergence. Seedling elongation can be modeled in much the same manner as germination, with base temperatures, thermal times, and so forth. In fact, because cotyledon and hypocotyl lengths are continuous measurements, rather than binary observations (germinated or not germinated) typically quantified by percentages or probabilities, modeling actually is easier for seedling elongation than for seed germination. Indeed, seedling elongation rates (mm per day) often are simple linear

functions of TT, at least within normal soil tempera-
ture ranges (e.g., Carberry and Campbell, 1989;
Fyfield and Gregory, 1989; Oryokot et al., 1997;
Roman et al., 2000). Despite this ease of prediction,
most field-verified mechanistic emergence models
have employed simple nonmechanistic constructs
for seedling elongation, ca. 10 mm per day regardless
of environmental conditions (Benech Arnold et al.,
1990a,b; Forcella, 1993). Thus, although integration
of seedling elongation rates is progressing (Roman et
al., 2000), it mostly remains as another important
future addition to seedling emergence models.

3.6. Light requirements

Seeds of several species require light for germina-
tion. In most instances this light requirement can be
met with fluxes of much less than $1000\ \mu mol\ m^{-2}$.
Under normal daylight conditions, this requirement is
met when seeds are exposed to light for only a fraction
of a second. Consequently, any soil tillage operation
probably provides sufficient light to meet the require-
ments for most seeds. The exception would be night-
tillage (Hartmann and Nezedal, 1990), but even under
this specific management condition emergence of
most light-sensitive species seems quite variable both
among plots within experimental treatments and
among sites and years (Buhler, 1997; Botto et al.,
1998; Gallagher and Cardina, 1998b). Thus, for the
purposes of emergence modeling, light requirements
for seed germination may be relatively unimportant,
but still a largely unexplored area of research. If light
quantity proves to be an important variable for seed-
ling emergence, its coding in models may be nothing
more than a simple qualitative "light switch" (e.g.,
receipt of < or >$100\ \mu mol\ m^{-2}$) that is either on or off.
Of greater modeling difficulty would be the timing of
implementation of this switch, as the sensitivity of
seeds to light changes seasonally. However, Gallagher
and Cardina (1998a) stated that only 10–20% of seeds
within populations of *Amaranthus*, *Ambrosia*, and
Chenopodium might require light during the seasons
when germination and emergence would be expected
to occur. This reinforces the interesting but marginal
role that light might play in emergence models.

In contrast to total irradiance, the quality of light
received by seeds may be more important. Far-red
light (FR, about 735 nm) can inhibit germination
(Ballaré et al., 1992). FR or the ratio of FR to red
light (R, about 645 nm) increases as plant canopies
develop and solar elevation decreases with time after
the summer solstice. As a result, emergence of sensi-
tive species should be inhibited somewhat as a crop
canopy expands or as the summer season progresses.
Thus, emergence of FR-sensitive species might be less
than expected after interrow cultivation within an
established row-crop, fallow tillage in late summer,
or autumn plowing. However, the practical signifi-
cance of FR exposure for emergence in field settings is
not well known. Vleeshouwers (1997) specifically
included light quality effects in models for three weed
species, but mostly in a quasi-quantitative manner.
That is, light quality measurements are not used as
input variables in these models, but after a general
light exposure, hypothetical phytochrome conversions
($P_{FR}\leftrightarrow P_R$) in seeds are modeled in a quantitative and
logical manner. These models are quite interesting, but
not yet tested fully. Ballaré et al. (1992) indicated that
once the light requirement of a light-sensitive species
(*Datura ferox*) is met, less than 10% of this effect can
be reversed by FR exposure. In brief, despite the vast
literature regarding light quality (specifically FR and
R) influences on seed germination, a quantitative
representation of these effects in emergence models
is not yet available.

3.7. Air quality within soil

The three main biologically active gases in soil are
oxygen, carbon dioxide, and water vapor. Ethylene
also is present, but its role in governing seed germina-
tion and seedling emergence is not known (Baskin and
Baskin, 1998). All of these gases affect seeds and
seedlings in various ways. During storage of seeds in
soil, oxygen can have both detrimental and beneficial
effects. Dry seeds maintain viability longer than wet
seeds, especially between about 3–15% seed moisture
(-350 to -14 MPa). Within this range of water con-
tents, oxygen has a negative influence on seed viabi-
lity. Below 3% seed moisture, apparently neither
oxygen nor water has much effect on seed viability.
In contrast, above 15% moisture, seed longevity con-
tinues to decline in anaerobic environments but
increases when oxygen is present (Roberts and Ellis,
1989). Although these facts specifically relate to
storage of crop seeds, they may well be applicable

to noncrop species. Little such information is available for these latter species, however, and therefore none has yet been used in emergence models.

When soils are flooded, the ratio of carbon dioxide to oxygen typically increases and can have detrimental effects on seed germination and seedling emergence. This can occur in addition to the general detrimental effect that long-term high humidity has on seed viability; at least in crop seeds, mortality is positively related to water potential between -350 and -14 MPa (Roberts and Ellis, 1989). Effects of flooding on emergence of aquatic and semiaquatic plants are relatively well documented (Kennedy et al., 1987), as are those for important upland crops such as maize (Martin et al., 1991) and for trees, whereas the literature for upland weeds is scant. Despite this scarcity, flooding has distinct and immediate effects on arable weeds, with reductions in emergence of greater than 50% with only 1 or 2 days of flooding. The close relationship between flooding duration and reduced germination or emergence (Fig. 11) is seemingly universal among susceptible plants (cf. Kennedy et al., 1987; Martin et al., 1991).

Grass seeds germinating under hypoxia or anoxia endure radicle inhibition, but coleoptile elongation still may proceed (Kennedy et al., 1987; Kordan

and Ashraf, 1990; Wijte and Gallagher, 1996). Apparently, shoot elongation into an oxygen-rich aerial environment takes precedence over root growth in oxygen-depleted media. This might explain the common observation in water-saturated petri dishes and thermogradient bars of small proportions of grass seeds germinating via protrusion of their coleoptiles instead of their radicles (e.g., Dekker et al., 1996).

Despite the vast literature on flooding effects on crop, tree, and aquatic plants, there appear to be no emergence models that incorporate these effects. Consequently, soil air quality (specifically low oxygen and high carbon dioxide resulting from flooding) remains a promising area for seedling emergence models.

4. Future directions and needs

In brief, the most critical need for improving models of seedling emergence in the future is mechanistic integration of microclimate and management variables with the rates of dormancy alleviation/induction, germination, and seedling elongation. Equally important is the integration of these latter three components of emergence. Soil microclimate submodels will be critical components of emergence models. Soil temperature and water contents, and other variables, change as continuous functions throughout the seed-bearing zone of soils. Current emergence models use estimates of soil microclimate at only single soil depths (e.g. 5 cm) to make predictions. Finely scaled step functions, or preferably continuous integrated functions, for the upper soil profile are needed to better predict seedling emergence. Without such integration, agronomists, weed scientists, crop consultants, and farmers will continue to manage crops and weeds with less than ideal information.

Good initiations to such mechanistic integration are the emergence modeling studies by Benech Arnold et al. (1990b), Vleeshouwers (1997), and Roman et al. (2000). The model derived from the first study integrates seed dormancy, seed germination, and soil temperature. In the second study, seed dormancy cycling (via light and temperature), seed germination, seedling growth, and soil temperature are meshed. In the third, soil temperature and water potential are combined into hydrothermal time to predict seed germination and thermal time to estimate seedling
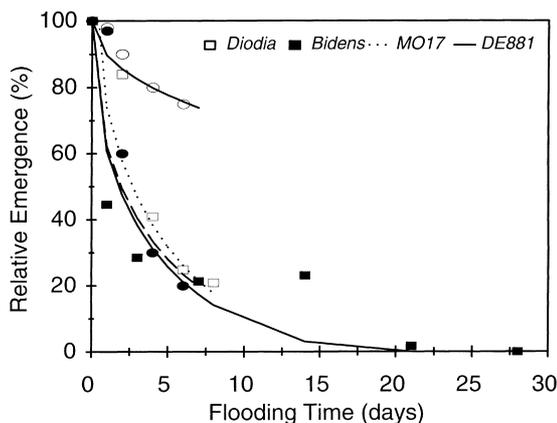

Fig. 11. Effect of flooding duration on the relative emergence of four plants: two weeds of arable soils, *Bidens pilosa* (adapted from Reddy and Singh, 1992) and *Diodia virginiana* (adapted from Baird and Dickens, 1991), and two maize (*Zea mays*) inbreds, flood-sensitive MO17 and flood-intolerant DE881 (Khosravi and Anderson, 1990). The curves are of the form, RE=$(a-bd^{-2})^2$, where RE is relative emergence (%) and d is flooding time in days.

elongation. Although none of these studies reaches perfection, they point in the direction that emergence models must follow. In the meantime, crude but effective empirical models that combine soil temperature and soil water potential (e.g., Finch-Savage and Phelps, 1993) will have to suffice for increasing the information-richness of agronomic management decisions, which have been proven to enhance the timeliness and cost-effectiveness of standard management operations (Forcella, 1998).

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