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Modelling Production Subsystems at High Abstraction Level – A Review. VIb. Emergence Phase – Modelling (Focussed on Vegetable Crops)

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Summary

A better understanding and quantification of the interdependent relationships within the system crop production serves as a base for production planning and control in research, advice and commercial practice. Since the last decades a new tool was developed, designated by the item modelling, enabling to integrate the numerous factors and relationships involved in decision support and optimisation. Especially at the beginning, scores of approaches and programs nowadays outdated were used, aggravating the use and integration of older files and parameters. Therefore the authors tried to review the modelling research done as a base for future upgrading and application.

Concerning crop growth the reviews are restricted to the models elaborated in their institute (parts I and II). Concerning crop development the reviews are based on international literature for vernalisation (III), photoperiodism (IV), endodormancy (V) and emergence (VIa, b). These reviews recognise the general physiological and modelling basics, the application, however, is focused on vegetable production.

In this last review, the basics of crop emergence are presented (VIa) and approaches to model seed germination and subsequent heterotrophic growth, combined defined as emergence, are outlined as a function of temperature, soil/medium moisture, physical seedling emergence forces, sowing operations and soil properties. Criteria are emergence ability as well as emergence rate, the last resulting in the duration of the emergence phase. Parameters related to vegetable production are compiled, economic aspects are considered and conclusions on horticultural relevance are derived.

Key words. emergence – emergence forces – germination – modelling – soil (medium) properties – soil moisture – sowing technique – temperature

Introduction

A comprehensive physiological, physical background, as reviewed in part VIa, facilitates modelling biological systems, in this case emergence of seeds in soils. Here modelling the emergence phase is reviewed, parameters related to vegetable emergence are compiled, economic aspects are considered and conclusions for commercial practise are drawn.

Modelling

Modelling the emergence phase can be based on descriptive approaches (at high abstraction level) or on more or less mechanistic, physiologically and physically based approaches (at lower abstraction level), such as the models of Blacklow (1973) or Vleeshouwers and Kropff (2000). Both types of approaches offer advantages and suffer disadvantages. The models at low abstraction level may provide the most promising and more universal applicable models in the future, but until now the complexity provokes the risk of over-parameterisation and associated error. This could make simulations unworkable on a practical level (Grundy 2003). Therefore the more simply, descriptive models dominate clearly in the literature of this field. Most emphasis on modelling the emergence phase is done in weed research, such as Mohler (1993), Benech-Arnold and Sanchez (1995), Grundy (2003), Colbach et al. (2005), Ekeleme et al. (2005), Qiu et al. (2006), Martinson et al. (2007). A review on general aspects of modelling the emergence phase is presented by Grundy (2003).

As a **pre-modelling** approach, Kotowski (1926) labelled the rate of reaction of germination to increasing temperature by the Van't Hoff temperature coefficient Q_{10} and found a relation to the chemical composition of the seeds: Proteinaceous seeds (garden and lima bean) showed low Q_{10} values (2.2), seeds rich in fats (lettuce, radish, cucumber, melon) showed high Q_{10} values (2.7–3.4), and starchy and fatty seeds (spinach, beet cauliflower, onion, tomato, eggplant) showed intermediate Q_{10} values (2.3–2.5).

Blacklow (1972a, b, 1973) modelled the emergence phase at **medium abstraction level** by calculating the

hourly rate of imbibition ($dW * dt^{-1}$), which is proportional (k) to the difference between the water capacity of the seed (f(t)) and its water content (W) in the exponential phase of imbibition and a constant rate of imbibition (kr) for the linear phase of imbibition during embryo growth by:

$$dW \bullet dt^{-1} = k \bullet (f(t) - W) + kr \quad (44)$$

The initiation of radicle and shoot growth as well as axis elongation and therewith emergence were determined as a function of fluctuating temperatures (10–32 °C). The model gave good predictions under fluctuating temperatures in controlled environments and in the field.

High abstraction level

Time course of the emergence rate. The time course of the emergence percentage (Y(t)) of seeds generally follows a sigmoid pattern. The ER(t) is frequently skewed to the right (WAGENVOORT et al. 1981). Concerning ER and EA, SCHIMPF et al. (1977) demonstrated the fitting of the logistic function to the germination progress data by simple linear regression. They concluded that the rate appears to be more sensitive to environmental conditions during germination than the final percentage.

WAGENVOORT et al. (1981) derived optimal temperatures by subjective interpolation and calculated the 'spread of germination', the increase of germinated seeds with time, by a logistic function (not skewed) of MILTHORPE and MOORBY (1974):

$$Y(t) = EA \bullet [1 - \exp(-k(t - t_0))] \quad (45)$$

assuming that:

$$ER(t) = k \bullet (EA - p) \quad (46)$$

A high value of k indicates that the rate of germinating seeds per unit time is high and the spread from the first seed to germinate to maximum germination is small. Thus optimal temperature can be defined by high k values (their table 2). The optimal temperatures derived by the time spread of germination were lower than those for germination percentage.

For modelling GAN et al. (1996) checked three non-linear regression equations to fit data of cumulative percent emergence by time of spring wheat grown in growth rooms under widely spread water potentials (−20 to −14.500 hPa). Their 'Weibull function':

$$Y(t) = EA \bullet \left[1 - \exp\left(-((t - a) \bullet b^{-1})^{C}\right)\right] \quad (47)$$

did not provide satisfactory results. Both, the 'Logistic function' and the 'Gompertz function', performed equally well, the first one somewhat better at very low water potentials, the second one at very high water potentials. The authors recommend the 'Gompertz function', which provided the most appropriate characterisation of emergence in the field, such as inflection time [$t = \ln(b) * k^{-1}$]; maximum emergence rate ($Y_{max} = k * EA * e^{-1}$) and medium response time. The 'Gompertz function' reads:

$$Y(t) = EA \bullet \exp[-b \exp(-k \bullet t)] \quad (48)$$

QIU et al. (2006) calculated germination time for each subpopulation of *Dactylis glomerata* L., based on the sigmoid 'Chapman-Richards growth function' (RICHARDS 1959):

$$Y(t) = m \bullet [1 - \exp(-n \bullet t_{(Y)})]^{p} \quad (49)$$

Emergence as a function of temperature and water potential.
Temperature: In greenhouse production with normally high quality seeds, with favourable media and moisture, the energy crisis in 1973 caused special attention to modelling ED as a function of temperature. LEDERLE et al. (1984) tested the adjustment of different approaches to describe $ED_{(50\,\%)}$ or $ED^{-1}_{(50\,\%)}$ as a function of temperature on the basis of an extensive data set of lambs lettuce, produced in boxes with graded temperatures (Fig. 16):

1) TSC (equ. 25, 26), used by FEDDES (1971), HEGARTY (1973a), BIERHUIZEN and FEDDES (1973), BIERHUIZEN and WAGENVOORT (1974), WAGENVOORT and BIERHUIZEN (1977) and others.
2) polynomial 5th order preferred to TSC by THOMPSON and FOX (1976)
3) polynomial 3rd order – ROEGGEN (1981)
4) linearised exponential function – KRUG (1975)
5) Arrhenius plot – SIMON et al. (1976).

With the data used and for the rate of emergence, neither the polynomial regression of the 5th order, nor the double logarithmic function, nor the Arrhenius plot showed any advantages that warrant preferential treatment. The same will be true for the polynomial 2nd order (R^2 = 0.82), which is used by ODABAS and MUT (2007). Therefore, the polynomial 4th order was considered to provide the best fitting (Fig. 16 and Table 15), especially for a wide range of temperatures. The linear approach (TSC), however, also causes an almost equal fitting.

The deviations from the ascending linear regression line in Fig. 16 agree with results of HEGARTY 1973b, THOMPSON and FOX (1976, lettuce and carrot) and JAME and CUTFORTH (2004, spring wheat) and have to be assumed as realistic ones. Therefore JAME and CUTFORTH (2004) recommend the 'Beta-function' for the subphase emergence of wheat:

$$ER(T) = \exp(\mu) \bullet (T - T_{min})^{\alpha} \bullet (T_{max} - T)^{\beta} \quad (50)$$

This equation covers the total temperature range (here 0 to 42°C) and it allows to calculate T_{opt} and the respective ER:

$$T_{opt} = (\alpha \bullet T_{max} + \beta \bullet T_{min}) \bullet (\alpha + \beta)^{-1} \quad (51)$$

$$ER(T_{opt}) = \exp(\mu)\alpha^{\alpha}\beta^{\beta}((T_{max} - T_{min}) \bullet (\alpha + \beta)^{-1})^{\alpha + \beta} \quad (52)$$

The authors of this review tested the suitability of the 'Beta-function' (50) for the data set of lambs lettuce (LEDERLE et al. 1984, Fig. 16). The cardinal points and R^2 are compiled in Table 15. The T_{min} and T_{max} were almost identical. T_{opt} was somewhat lower with the 'Beta-function'. The R^2 decrease in the ranking: polynomial – TSC – Beta-function, but the differences are small.

SOLTANI et al. (2006) calculated the ER as a function of temperature by:

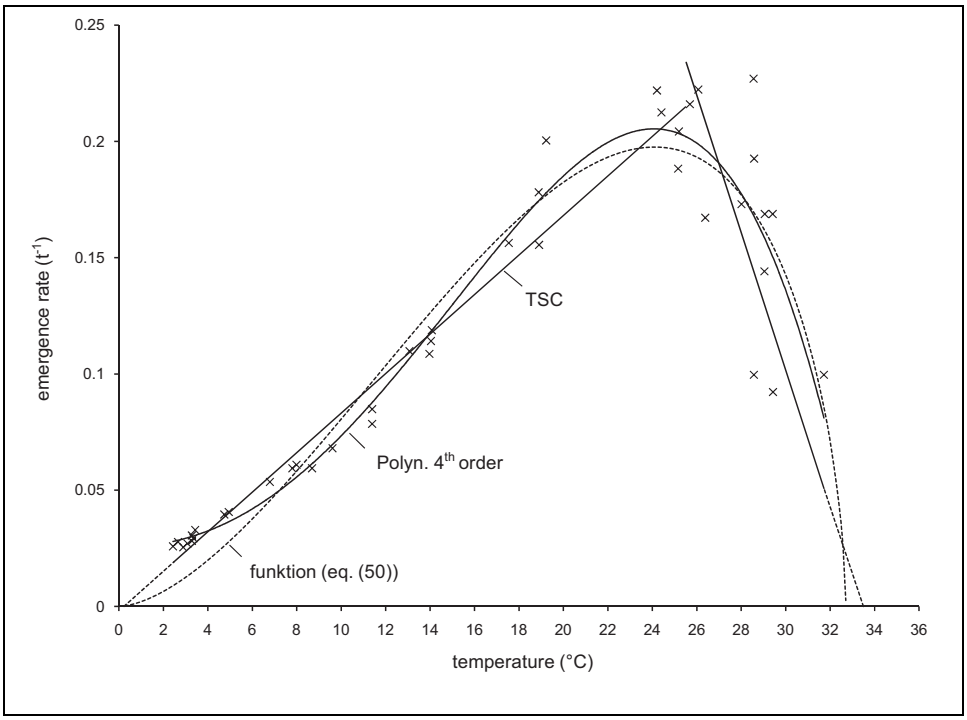


Fig. 16. Emergence rates (t^{-1}) of lambs lettuce as a function of temperature, calculated with the TSC (equ. 25 and 26), and a polynomial 4th order (Lederle et al. 1984), supplemented by the 'Beta-function' (equ. 50). Cardinal points and R^2 see Table 15.

$$ER_{(50\,\%)} = f(T) \bullet ER_{max} \quad (53)$$

using different equations for f(T): Quadratic, cubic, curvilinear, ascendant and descendant linear regressions, 'Beta-function', 'Plateau model' (his 'Dent-like function'). In field experiments, the best fitting was obtained with the 'Beta-function' (acc. Yin et al. 1995). In the pot experiment at controlled temperature, however, the 'Plateau model' was preferred:

$$f(T) = (T - T_{min}) * (T_{opt} - T_{min})^{-1} \quad \text{if } T_{min} < T < T_{opt\,1} \quad (54)$$

$$f(T) = (T_{max} - T) * (T_{max} - T_{opt\,2})^{-1} \quad \text{if } T_{opt\,2} < T < T_{max} \quad (55)$$
$$f(T) = 1 \quad \text{if } T_{opt\,1} \le T \le T_{opt\,2}$$
$$f(T) = 0 \quad \text{if } T \le T_{min} \text{ or } T \ge T_{max}$$

Sowing depth was integrated in this model (see respective paragraph below).

On the basis of these investigations the equations based on the TSC (equ. 22–26 in Krug and Kahlen 2008), temperature related to the reciprocal value of time, are recommended as the first approach:

Ascendant range: $t^{-1} = (T - T_{min}) * S^{-1}$ (25)

Descending range, emanating from T_{max}: (26)
$t^{-1} = (T_{max} - T_{(< Tmax)}) * S^{-1}$

Response surfaces with wide optima should be described by a 'Plateau model', as already recommended in Krug and Kahlen (2008, Fig. 6) for vernalisation.

The statistical T_{min} value in equation (25) is a linear extrapolation of the linear range and differs from the physiological temperature minimum which may be higher or lower (see also Roeggen (1981). It varies with the criterion of emergence with the general tendency that T_{min} decreases with an increase in germination percentage depending on time (e.g. 10 % → 90 % emerged seedlings) (Wagenvoort et al. 1981, their fig. 1). Moreover it is correlated with S: A lower T_{min} is related to a higher S and vice versa. The authors concluded: "... not too much emphasis should therefore be given to the variation of T_{min}". Arnold (1959) optimised T_{min} by calculating the lowest coefficient of variance for ED. Madakadze et al. (2001) discussed the variability of T_{min} of warm season grasses depending on the method of estimation.

Corresponding features will apply for T_{max}, but few investigations are available. Problems arising when temperatures temporarily exceed T_{max} are discussed by

Table 15. Cardinal points and R^2-values of three model approaches to a data set of lambs lettuce [data and TSC Lederle et al. (1984)].

	T_{min}	T_{opt}	T_{max}	R^2 ascending	R^2 descending
TSC	0	26	33.5	0.97	0.52
Beta-equation	0	23	32.7	0.96	0.48
Polynominal 4th order		25	33.5	0.98 (in all)	

Weaich et al. (1996). The intercept point of equations (25) and (26) represents the optimum temperature for the emergence phase (Lederle et al. 1984).

The slopes of the regression lines represent the reciprocal Temperature Sums (S^{-1}). S increases almost linearly with an advanced germination rate (Wagenvoort et al. 1981, their fig. 2). The same authors state that S is not affected by the germination percentage when the time spread (see below) of germination is narrow, but it is strongly affected by germination percentage with a large time spread of germination.

The use of **mean temperatures** provokes the question, whether the temperature reaction remains constant during the germination phase. It was generally assumed that the soaking phase is a physical process, independent of temperature. Blacklow (1973), however, claimed a minor reaction to temperature. Moreover, for a set of cultivated species a relatively short and limited period of increased cold sensitivity has been proved and cold induced injuries are claimed to be more or less irreversible, even in subsequent optimal growing conditions. Among others this has been shown with bean and pea seeds (Reuther 1970).

Another aspect is the effect of **diurnal fluctuating temperatures**, widespread in natural environments. Blacklow (1973) postulated from his experiments with mayze "... that the germinating seed and its elongating axes respond to prevailing temperatures with no adaptation to preceding conditions and that the system responds within minutes to changes in temperature ...", when stress conditions are excluded.

Thompson (1974a, b) reviewed the literature on the effects of fluctuating temperature on germination and stated: "... the germination responses of many species are improved by treatments which include fluctuating temperatures. These may range from an absolute, or almost absolute requirement ... to relatively minor increments in germination ... ". Very often the expression of such responses is dependent on interactions between temperature and light, moisture tension or by endogenous factors in the seed, such as its degree of maturity and post harvest history (Thompson 1974b). The accelerating effect of fluctuating temperature on ER of dormant orchardgrass seeds is clearly shown by Qiu et al. (2006) and calculated by a thermal time model.

Hegarty (1975) demonstrated a clear promoting effect of fluctuating temperature on ER of carrot and calabrese (*Brassica oleracea* L., presumably Broccoli) seeds subjected to severe water stress. He attributed this effect, however, to water availability in the soil. With optimal water supply diurnal temperature fluctuations tended to reduce T_{min} by about 1 °C and to increase S by approximately 30 °Cd of 17 vegetable species, but these results were not significant (Wagenvoort and Bierhuizen 1977).

Harrington (1962), testing 13 vegetable species, and Wagenvoort and Bierhuizen (1977), testing 17 vegetable species, did not find any affect of diurnal fluctuating temperatures when seeds are non-endodormant. With conditional endodormant seeds of *Dactylis glomerata* L., fluctuating temperatures (0–15 °C amplitudes) decreased T_{min} and increased ER as well as EA (Qiu et al. 2006).

Another form of varying temperatures is a steady increase (spring) or decrease (autumn) of temperature. Zhang et al. (2007) found a promotion of germination with three of four wild species in China when sub-optimal temperatures increase compared to decreasing temperatures. The author discusses possible explanations.

Temperatures changing from day to day did not affect ED of radish (*R. sativus*, Krug et al. 1985). A summarising discussion on the effects of fluctuating temperature on germination is presented by Toole et al. (1956, p. 311) and Thompson (1974b). Concluding, with vegetables, at conditions prevailing in horticultural practice, it is considered to be justified to relate EA and ED to mean temperatures, unless light requirement or endodormancy are involved.

TSC-parameters available for the ascending range are presented in Table 16. As already mentioned differences in the overall pattern of response between varieties and cultivars are mostly relatively small (Harrington 1962; Dragland 1972; Thompson and Fox 1976; Wagenvoort

Table 16. Statistic cardinal values of temperature reaction (°C) of emergence duration of vegetable species (compiled from relevant authors).

Species	T_{min} (°C)	S (°Cd)	Range tested
Asparagus	5.0	210	8 – 26
Broad bean	0.4	148	3 – 17
Brussels sprouts	1.1	108	3 – 17
Carrot	1.3	170	3 – 17
Cauliflower	1.3	112	3 – 17
Celeriac	4.6	237	9 – 17
Chicory	5.3	85	9 – 25
Chinese cabbage	2.4	46	5 – 25
Chives	3.0	166	3 – 17
Common bean	7.7	130	13 – 25
Corn salad	0.0	161	3 – 25
Cucumber	12.7	69	15 – 25
Eggplant	12.1	93	3 – 25
Endive	2.2	93	3 – 25
Garden cress	1.0	64	3 – 17
Garden pea[1)]	0.5 – 3.2	69 – 109	3 – 25
Kale	1.2	103	3 – 17
Kohlrabi	3.5	92	3 – 17
Leek	0.0	222	3 – 17
Lettuce	3.5	71	6 – 21
Melon	12.2	108	15 – 25
Onion	1.4	219	3 – 17
Parsley	0.0	268	3 – 17
Radish	1.9	71	3 – 30
Radish (var. *niger*)	0.5	94	3 – 17
Red beet	2.1	119	3 – 17
Red cabbage	1.3	104	3 – 17
Scorzonera	2.0	90	3 – 17
Spinach	0.1	111	3 – 17
Sweet corn	9.0	46	11 – 31
Sweet pepper	10.0	137	15 – 25
Tomato	8.7 [7.9[1)]]	88	13 – 25
Turnip	1.4	97	3 – 17
White cabbage	1.0	106	3 – 17

[1)]cold tolerant genotypes (Bradfort et al. 1993)

and BIERHUIZEN 1977; SOLTANI et al. 2006), but exceptions are accounted for e.g. celery (THOMPSON 1974a), onions, *Brassica oleracea* species (THOMPSON and FOX 1976), pepper (GERSON and HONMA 1978) and peas (KRUG 2002a). GRAY (1975) tested 22 varieties and cultivars of lettuce and found low variability in temperature reaction, except T_{min}. ROEGGEN (1987) demonstrated differences in T_{min} in cucumber, tomato and bean cultivars. Seed dormancy and germination of weed seeds are modelled and discussed by e.g. BENECH-ARNOLD and SANCHEZ (1995), GRUNDY (2003) and QIU et al. (2006).

Concerning a prediction of field germination HEGARTY (1973b) found a linear relation between field emergence and laboratory germination for carrots:

$$\text{Emergence}(\%) = 0.8 \bullet \text{germination at } 10\ ^\circ\text{C}(\%) \quad (56)$$

Soil temperature in trays upon tables in greenhouses approximates the level of the ambient air temperature (modelling see KRUG et al. 2007a). Temperature of the ground soil in greenhouses showed a positive linear correlation to irradiance and can be computed in the summer season according to equation ((4) in KRUG et al. 2007a with explanations for two equations); in the winter season air temperature also plays an important role, resulting in equation (5) in KRUG et al. (2007a).

To check the impacts of these relations, seeds of parsley were sown in trays on tables and into the ground of greenhouses (Fig. 17). Depending on the season and the set points for heating temperature differences up to 2.5 °C were measured. Especially in the cold season, with low set points for heating, the higher temperatures in the ground shortened ED. With high set points ED was shortened in the trays, but less and only during the coldest season (KRUG et al. 1985). Soil temperatures in open fields are discussed by FEDDES (1969).

Water potential and temperature: Soil water potential is more difficult to model due to problems in measuring soil moisture gradients and fluctuations in the upper soil layers (BIERHUIZEN and FEDDES 1973). These authors, experimenting with vegetable species, state: "... the TSC can also be used in the field when soil moisture content is between 2.0 and 2.7 pF (−100 to −500 hPa)". Above −5004hPa S increases almost linearly with increasing pF, but with great variability.

GUMMERSON (1986), working with sugar beets, developed the concept of "hydro-thermal time" (HTT) for germination, a combination of the TSC (equ. 25) and water potential (Ψ, here of moistened filter paper) above a base potential (Ψ_{min}) and time. The equation for individual seeds reads:

$$HTT = [\Psi - \Psi_{min}(G)] \bullet (T - T_{min}) \bullet t(G) \quad (57)$$

and to consider the distribution of individual seeds in a population:

$$\text{probit}(G \bullet 100 \bullet G_m^{-1}) = 1 \bullet \sigma_{\Psi min}^{-1} \bullet [\Psi - HTT \bullet (T - T_{min})^{-1} \bullet t(G)^{-1}] + 5 - \overline{\Psi min} \bullet (\sigma_{\Psi min})^{-1} \quad (58)$$

For most of the seed populations HTT was a constant. The T_{min} of the seeds were similar, but the Ψ_{min} varied between seeds, but were normally distributed. Equation (57) can be used to predict the time course of germination over a wide range of temperatures and water potentials [details see GUMMERSON (1986)].

A similar approach has also been used and amplified by BRADFORD (1990) for lettuce and by DAHAL and BRADFORD (1990) and BRADFORD et al. (1993) for tomato. According to the last cited authors the population based

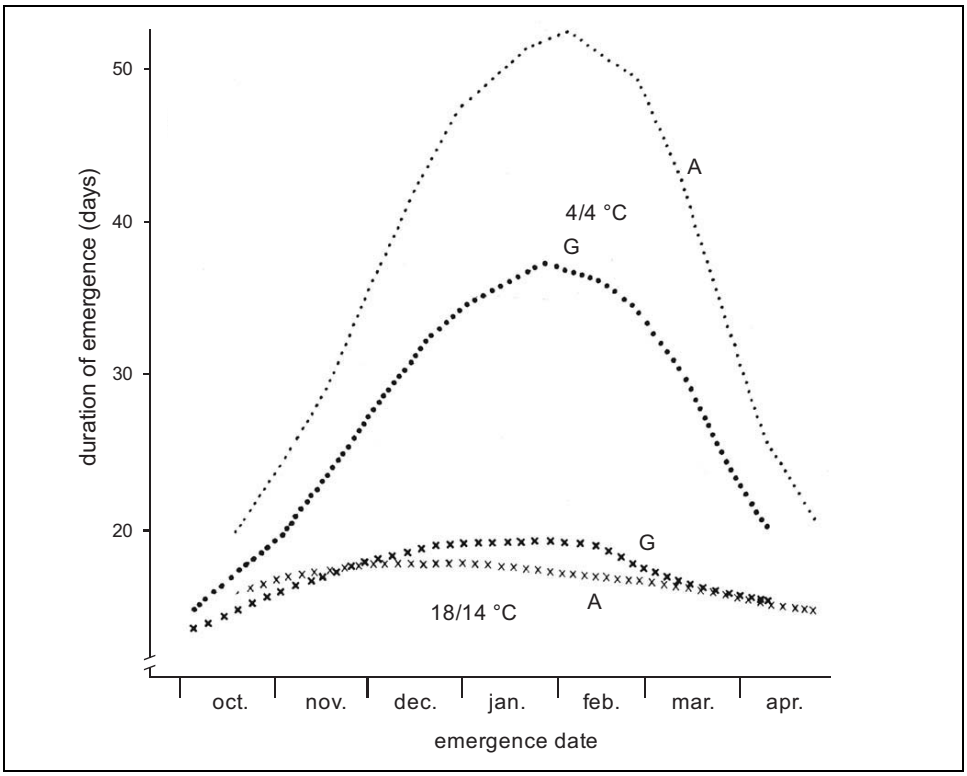


Fig. 17. Duration of the emergence phase of parsley with ground (G) and tray sowings upon tables (air temperature, A) depending on season and set point for heating the air (climate: long term means of irradiance and temperature in Hannover, KRUG et al. 1985).

threshold model can also describe germination responses to the hormones ABA and GA. BRADFORD (1990) characterises the relationship of seed germination rates to Ψ using only three parameters: 'hydrotime constant' (θ_H), the mean and the standard deviation in minimum or Ψ_{min} among seeds in the population. A summarising survey including seed dormancy and applications is given by BREADFORD (2002).

HEGARTY (1976) found a linear relationship between the time to half final emergence of onions and Ψ. Extrapolation gives an estimated Ψ_{min} of −11.000 hPa (pF about 4) for the median of the population.

FINCH-SAVAGE and PHELPS (1993) developed a 'temperature * seed-water-potential model' for onions, using the TSC, where temperature summation was stopped when $\Psi \leq \Psi_{min}$ (−11.100 hPa). They state: "The model accurately predicted the onset of seedling emergence and the occurrence and timing of subsequent seedling flushes in a wide range of seed bed conditions" (in spring in the UK).

Later on FINCH-SAVAGE et al. (1998) transform equation (57) of Gummerson to

$$t^{-1}(G) = [(T - T_{min}) \bullet (\Psi - \Psi_{min}) \bullet (G)] \bullet HTT^{-1} \quad (59)$$

(G) regards the variability of Ψ_{min}. Since the seeds, once imbibed, progress towards germination, unaffected by Ψ, provided it remained above Ψ_{min}, equation (59) becomes:

$$t^{-1}(G) = [(T - T_{min}) \bullet (-\Psi_{min}(G))] \bullet HTT^{-1} \quad (60)$$

These equations fitted well the data measured in constant conditions and are supposed to fit in well-cultured horticultural crops. Deviations occurred under variable field conditions. FINCH-SAVAGE et al. (1998) expected that below Ψ_{min} metabolic processes follow other reaction patterns which have to be incorporated into the hydrothermal-time-theory.

In summary the authors concluded that delays in seedling emergence occur largely in the germination phase, which can be adequately predicted using a modified threshold model, but seedling losses and variation in the spread of seedling emergence times within the population occur largely during the post-germination growth phase.

To predict the pattern of cumulative wild oat seedling emergence MARTINSON et al. (2007) compared measured values for the TSC and/or HTT under field conditions using a 'Weibull function' (compared to equation (47) k = $(b^{-1})^c$ and z = a):

$$ER = EA \bullet [1 - \exp(-k \bullet ((TSC \text{ or } HTT) - z)^c)] \quad (61)$$

Seedling emergence was correlated with TSC (R^2 = 0.93) and HTT (R^2 = 0.92).

Physical forces. **Physical seedling emergence forces** of leguminous species in darkness and 23 °C are parameterised by INOUYE et al. (1979):

$$EA = EF \bullet Ch \bullet Sp \quad (62)$$

EA is a function of the elongation force of the seedling (EF), of the physiological and morphological characteristics of the seedlings (Ch), such as the shape of the seedling and the amount of guttation fluid from the tip moistening the soil (Sp) and it is a measure of the speed of elongation of the seedling in darkness. The maximum EF differed significantly among species and among cultivars within species and was positively correlated with seed weight. Soil physical variables were also parameterised by EKELEME et al. (2005) using a model for seed emergence based on HTT. Basic data for modelling growth force of carrot seedlings as a function of seed weight, sowing depth and temperature are published by TAMET et al. (1995).

Sowing operations and soil properties. **Sowing depth** primarily determines soil temperature, soil moisture/oxygen and the forces required to penetrate the overlying soil layer. FINCH-SAVAGE et al. (1998) state: "... delays in seedling emergence occur largely in the germination phase, but that seedling losses and variation in the spread of seedling emergence times within a population occur largely during the post-germination growth phase". This means that in fields sowing depth affects the emergence criteria greatly in the post-germination growth phase. This applies all so more, the greater the variability in seed depth, thus more with weeds, distributed over the total cultivation depth than for well-drilled crops.

DRAGLAND (1972) found emergence speed of leek seeds to be linearly correlated with sowing depth (0.5 to 2 cm). He found an increase of S by 39 °Cd at 11 °C and by 27 °Cd at 20 °C per cm sowing depth with leek. According to ITABARI et al. (1993) increasing planting depth of mays by 1 cm increases S required for emergence by 2.8 °Cd and decreasing water content by 1 % increased S for emergence by 3.2 °Cd. In student experiments in Hannover no distinct effect of sowing depth resulted in the range of 0.5–2.0 cm, but a considerable decrease of ER with 4 cm sowing depth with lambs lettuce (Krug unpubl.). In contrast WAGENVOORT and BIERHUIZEN (1977) found no considerable effect on the T_{min} and S values of 8 tested vegetable species in the range of sowing depths used in practice. ITABARI et al. (1993) pointed out the problems in modelling effects of sowing depth evolving by the interference of sowing depth and soil moisture in field experiments.

PROSTKO et al. (1997) parameterised the percentage of emergence of weed species as a function of burial depth (b), considering soil moisture and soil texture (by variation of the parameters only), by the three parameters of the 'Fermi-Dirac distribution function', an equivalent to the standard logistic function (compare to part III equ. (27):

$$Y(b) = EA \bullet [1 + \exp(\alpha \bullet (b - b_{1/2}))]^{-1} \quad (63)$$

α is calculated by:

$$-\alpha = -4(slope) \bullet (EA)^{-1} \quad (64)$$

An example of the effects of soil texture, calculated by the 'Fermi-Dirac function' is presented in Fig. 18. This equation assumes that seed distribution is uniform throughout the soil profile and does not yet account for the effects of variable temperature. It is considered a module for prospective more mechanistic models.

The model 'SIMPLE' for simulation of sugar beet emergence (length of seedling path and EA) considering temperature and soil structure (number, size and distribution of clods), sowing depth and temperature, emitting soil

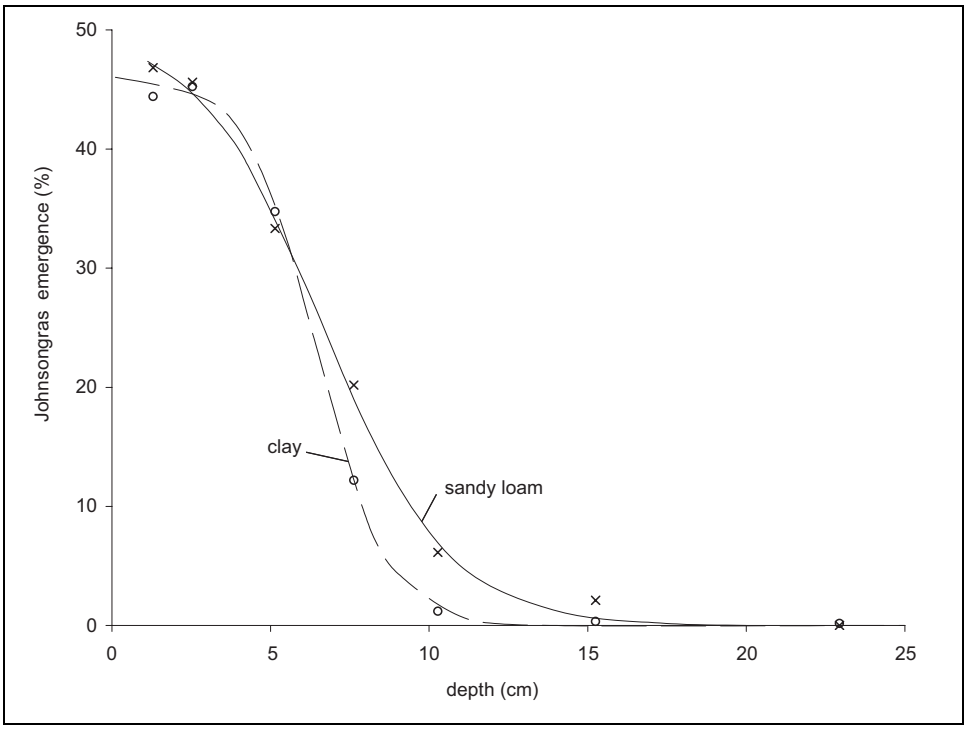


Fig. 18. Field emergence percentage of johnsongrass, observed and modelled (equ. 63) as a function of soil type (| very fine sandy loam, --- sharkey clay soil, changed after PROSTKO et al. 1997).

moisture, has been developed by AUBERTOT et al. (1999) and extended and evaluated by DÜRR et al. (2001). The simulated values were not statistically different from those measured in seedbeds in the field experiments. ED depended mainly on the sowing depth and soil temperature, but finally ER was altered by clods. The model is claimed to be useful for testing sowing techniques and the effects of seed characteristics.

With 'SIMPLE', now including soil water potential, DORSAINVIL et al. (2005) simulated the emergence of white mustard to sowing conditions (varied soils and climates, sowing strategies). EA was well predicted at all sites but predicted progress of emergence was slightly earlier than observed in most cases. Coarse seed beds and large quantities of straw were not as important as soil water content, temperature, and sowing depth in explaining variations in emergence.

MOREAU-VALANCOGNE et al. (2008) used 'SIMPLE' to predict ER and ED of seed characteristics and sowing conditions of beans. The model accurately predicted ER, while ED predictions could be improved by including a correction factor that decreased the elongation rate.

SOLTANI et al. (2006) varied sowing depth (2.5–14.0 cm) in a pot experiment at 21 °C and found a linear relationship of sowing depth to the physiological days requirement (t_{min} = 0.8 + 0.88 d). Including the field experiments they preferred a normalised form for a sowing depth of 5 cm:

$$t_{min} = (0.169\ b + 0.154) \bullet 6 \qquad (65)$$

t_{min} for chickpea emergence was 6 days (S = 94 °Cd) at a sowing depth of 5 cm and increased by 0.9 physiological days per cm increase of sowing depth.

Fertilisation: According to experimental data and model calculations of HEGARTY (1976) nitrogen, phosphate and potassium fertilisers did cause delays in crop emergence (calabrese, carrot, onion, red beet), but only nitrogen caused a reduction in EA in field experiments. In pot experiments equivalents to 0–500 kg ha^{-1} nitrogen and low soil moisture resulted in reduced EA. Carrot was most sensitive; calabrese was least sensitive to moisture stress. The rate of EA in carrot and onion was linearly related to water potential.

Economic aspects. Economic aspects are manifold and difficult to model, but regarding energy cost and ground area use efficiency in greenhouse production they are of particular interest. A most simple approach is to minimise energy demand or energy cost of the emergence phase. Examples for vegetables are presented by KRUG et al. (1985) and KRUG (2002b). Recommendations on the basis of modelling, including physiological and phytopathological aspects, are presented in KRUG 2002b, table 5-2. Calculation of energy demand and energy cost as a function of ambient climate, greenhouse type, size and arming as well as heating strategy is outlined in KRUG et al. (2007a, b). Incorporation into models on economic optimisation of single crops or even of rotations is generally possible, but for rotations until now data are insufficient.

Conclusions

In the emergence phase basic prerequisites for crop establishment have to be provided. In open field production more or less manipulable factors will dominate, such as soil moisture and physical soil conditions (pathogens are not considered here), focussed on EA. In all–season greenhouse production with well–conditioned soils and water supply, the factor temperature is of main interest, affecting EA, ER as well as ED. Since production area in greenhouses is much more valuable than that in open fields and since temperature control can be expensive, economic aspects play a major role than in field production and complicate

the decisions. In both production fields, however, multifaceted systems are engaged, which can only be integrated by modelling, to assure substantiated arrangements.

This review tries to provide a survey of the actual situation in understanding and modelling seed emergence. Modelling temperature reactions is rather advanced in general, but parameters for species and particularly cultivars are fragmentary, also the dependence of affecting factors, such as proveniences and the effects of pathogens are lacking. Concerning soil moisture and physical soil factors including tillage and sowing technique, important features are published, but much has still to be done. Modelling, however, has deepened our knowledge, encouraged physiological understanding and already now provides important decision supports for production and genetic selections, which have to be integrated with other insights and empirical knowledge.

Abbreviations

(To relievable understanding and comparisons the original short cuts are altered for unification)

a, b, c, k (in equ. 45 for a time spread, in equ. 58 rate of increase), α, β, μ = coefficients, b = depth (cm) of the seed, $b_{1/2}$ = depth (cm), at which Y_b is half of EA, Ch = characteristics of seedlings, d = days, EA = emergence ability, maximum germination percentage (in equ. 58 the asymptote, in equ. 61 and 62 the theoretical % at the soil surface?), ED = duration of the emergence phase, EF = vertical elongation force, ER = rate of emerged seeds (speed of emergence), ER_{max} = maximal rate of emerged seeds, f(T) = temperature function ranging between 0 and 1, G = each seed can be assigned a value of G, which is the fraction of the population at which it germinates, G_m = proportion of live seeds, H_g = hydrothermal time to germinate, HTT = hydrothermal time, kr = constant rate of imbibition, m = asymptote parameter, n = number of ..., p = germination percentage at any time t, in equa. (48) shape parameter, pF = logarithm of cm water column, PWP = permanent wilting point, q = shape parameter,S = temperature sum (°Cd, 1/S = slope of the regression equation), Sp = speed of elongation of a seedling or the time to reach maximum force, t = time (mostly in days), t_{min} = the minimum number of days for emergence at optimal temperature (physiological day requirement for emergence), t_0 = time for the first seed to germinate, T= temperature and mean temperature of a phase, respectively, T_{min} = minimal temperature for germination/emergence, basis temperature (x for y=0, ED = 0), T_{max} = maximal temperature for germination/emergence (x for y = 0, ED = 0), T_{opt} = temperature optimum for germination/emergence, TSC = Temperature Sum Concept, W = water content of seeds, Y = cumulative percent emergence by time (t), in equ. (63) by burial depth, z = lag phase, α = slope ?, Ψ = water potential, Ψ_{min} = base of water potential of the seed for germination/emergence, $\overline{\Psi_{min}}$= mean of Ψ_{min} within a population of seeds, θ_H = hydrotime constant.

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References

Arnold, C.Y. 1959: The determination and significance of the base temperature in a linear heat unit system. Proc. Amer. Soc. Hort. Sci. **74**, 430–445.

Aubertot, J.N., C. Dürr, G. Richard and P. Dubrulle 1999: Simple: A model for simulation of plant e emergence. Proc. Intern.. Symp. Modelling Cropping Systems, Lleida, Spain.

Benech-Arnold, R.A.L.R. and A. Sanchez 1995: Modelling weed seed germination. In: Kigel, J. and G. Galili (eds.): Seed development and germination. Marcel Dekker, Inc. New York.

Bierhuizen, J.F. and R.A. Fedds 1973: Use of temperature and short wave radiation to predict the rate of seedling emergence and the harvest date. Acta Hort. **27**, 269–278.

Bierhuizen, J.F. and W.A. Wagenvoort 1974: Some aspects of seed germination in vegetables. I. The determination of heat sums and minimum temperature for germination. Sci. Hort. **2**, 213–219.

Blacklow, W.M. 1972a: Mathematical description of the influence of temperature and seed quality on imbibition by seeds of corn (*Zea mays* L.). Crop Sci. **12**, 643–646.

Blacklow, W.M. 1972b: Influence of temperature on germination and elongation of the radicle and shoot of corn (*Zea mays* L.). Crop Sci. **12**, 647–650.

Blacklow, W.M. 1973: Simulation model to predict germination and emergence of corn (*Zea mays* L.) in an environment of changing temperature. Crop Sci. **13**, 604–608.

Bradford, K.J. 1990: A water relation analysis of seed germination rates. Plant Physiol. **94**, 840–849.

Bradford, K.J., P. Dahal and B.-R. Ni 1993: Quantitative models describing germination responses to temperature, water potential and growth regulators. In: Come, D. and F. Corbineau (eds.): 4th Intern. Workshop on Seeds, Angers, France, 1992, 239–248.

Bradford, K.J. 2002: Application of hydrothermal time to quantifying and modeling seed germination and dormancy. Weed Sci. **50**, 248–260.

Colbach, N., C. Dürr, J. Roger-Estrade and L. Caneill 2005: How to model the effects of farming practices on weed emergence. Weed-Research, Oxford **45**, 2–17.

Dahal, P.K. and J. Bradford 1990: Effects of priming and endosperm integrity on seed germination rates of tomato genotypes. II. Germination at reduced water potential. J. Exp. Bot. **41**, 1441–1453.

Dorsainvil, F., C. Dürr, E. Justes and A. Carrera 2005: Characterisation and modelling of white mustard (*Sinapis alba* L.) emergence under several sowing conditions. Eur. J. Agron. **23**, 146–158.

Dragland, S. 1972: Germination of leek seed at different temperatures. Meldinger fra Norges Landbrukhogeskole **51** (Nr. 20), 1–10.

Dürr, C., J.N. Aubertot, G. Richard, P. Dubrulle, Y. Duval and J. Boiffin 2001: SIMPLE: A model for SIMulating of PLant Emergence predicting the effects of soil tillage and sowing operations. Soil Sci. Soc. Am. J. **65**, 414–423.

Ekeleme, F., F. Forcella, D.W. Archer, I.O. Akobundu and D. Chicoye 2005: Seedling emergence model for tropic ageratum (*Ageratum conyzoides*). Weed Sci. **53**, 55–61.

Fedds, R.A. 1969: Some physical aspects of heat transfer in soil. Acta Hort. **27**, 189–196.

Fedds, R.A. 1971: Effects of water and heat on seed emergence and crop production. Water, heat and crop growth. Meded. Landbouw Hogeschool Wageningen **71**, 1–184.

Finch-Savage, W. and E.K. Phelps 1993: Onion (*Allium cepa* L.) seedling emergence patterns can be explained by the influence of soil temperature and water potential on seed germination. J. Exp. Bot. **44**, 407–414.

Finch-Savage, W., J.R.A. Steckel and E.K. Phelps 1998: Germination and post-germination growth to carrot seedling emergence: predictive threshold models and sources of variation between sowing occasions. New Phytol. **139**, 505–516.

Gan, Y.E., H. Stobbe and C. Njue 1996: Evaluation of selected nonlinear regression models in quantifying seedling emergence rate of spring wheat. Crop Sci. **36**, 165–169.

Gerson, R. and S. Honma 1978: Emergence response of the pepper at low soil temperature. Euphytica **27**, 151–156.

Gray, D. 1975: Effects of tem0perature on germination and emergence of lettuce (*Lactuca sativa* L.) varieties. J. Hort. Sci. **50**, 349–361.

Grundy, A.C. 2003: Predicting weed emergence: a review of approaches and future challenges. Weed-Research-Oxford **43**, 1–11.

Gummerson, R.J. 1986: The effect of constant temperatures and osmotic potentials on the germination of sugar beet. J. Exp. Botany **37**, 729–741.
Harrington, J.F. 1962: The effect of temperature on the germination of several kinds of vegetable seeds. In: XVI. Internat. Hort. Congr. 1962, ed. Duculot, Gembloux, Belgique, 435–441.
Hegarty, T.W. 1973a: Temperature coefficient (Q_{10}), seed germination and other biological processes. Nature **243**, 305–306.
Hegarty, T.W. 1973b: Temperature relations of germination in the field. In Heydecker, W. (ed.): Seed ecology. Butterworth, London, pp. 411–431.
Hegarty, T.W. 1975: Effects of fluctuating temperature on germination and emergence of seeds in different moisture environments. J. Exp. Botany **26**, 203–211.
Hegarty, T.W. 1976: Effects of fertiliser on the seedling emergence of vegetable crops. J. Sci. of Food and Agric. **27**, 962–968.
Inouye, J., S. Tankamaru and K. Hibi 1979: Elongation of seedlings of leguminous crops. Crop Science **19**, 599–602.
Itabari, J.K., P.J. Gregory and R.K. Jones 1993: Effects of temperature, soil water status and depth of planting on germination and emergence of maize (*Zea mays*) adapted to semi-arid Eastern Kenya. Expl. Agric. **29**, 351–364.
Jame, Y.W. and H.W. Cutforth 2004: Simulating the effects of temperature and seeding depth on germination and emergence of spring wheat. Agric. and Meteorol. **124**, 207–218.
Kotowski, F. 1926: Temperature relations to germination of vegetable seed. Proc. Am. Soc. Hort. Sci. **23**, 176–184.
Krug, H. 1975: Gartenbau unter Glas bei hohen Energiepreisen – Anpassung durch Temperaturführung und Kulturprogramm. Tätigkeitsbericht der Fakultät für Gartenbau und Landeskultur, Hannover **3**.
Krug, H., E. Lederle and H.P. Liebig 1985: Modelle zur kultur- und kostengünstigen Temperaturführung während der Auflaufphase. Gartenbauwissenschaft **50**, 54–59.
Krug, H. 2002a: Pflanzenanzucht. In: Krug, H., H. P. Liebig and H. Stützel: Gemüseproduktion. Eugen Ulmer Verlag, Stuttgart, 214–233.
Krug, H. 2002b: Produktionsplanung und -führung. In: Krug, H., H. P. Liebig and H. Stützel: Gemüseproduktion. Eugen Ulmer Verlag, Stuttgart, 214–233.
Krug, H., A. Romey and T. Rath 2007a: Decision support for climate dependent greenhouse production planning, and climate control by modelling. I. Modelling climate. Eur. J. Hort. Sci. **72**, 97–103.
Krug, H., A. Romey and T. Rath 2007b: Decision support for climate dependent greenhouse production planning, and climate control by modelling. II. Modelling plant growth. Eur. J. Hort. Sci. **72**, 145–151.
Krug, H. and K. Kahlen 2008: Modelling production subsystems at high abstraction level – A review. III. Development – Vernalisation. Eur. J. Hort. Sci. **73**, 183–187.
Krug, H. and K. Kahlen 2009: Modelling production subsystems at high abstraction level – A review. VIa Emergence phase – Basics. Eur. J. Hort. Sci. **74**, 124–129.
Lederle, E., H. Krug, H.P. Liebig and W.E. Weber 1984: Funktionen zur Quantifizierung der temperaturabhängigen Auflaufdauer am Beispiel von Feldsalat (*Valerianella locusta* L.). Gartenbauwissenschaft **49**, 262–266.
Madakadze, I.C., B. Prithiviraj, K.A. Stewart, P.R. Peterson, B.E. Coulman and D.L. Smith 2001: Variation in base temperatures for germination of warm season grasses. Seed Sci. and Technology **29**, 31–38.
Martinson, K., B. Durgan, F. Forcella, J. Wiersma, B. Spokas and D. Archer 2007: An emergence model for wild oat (*Avena fatua*). Weed Sci. **55**, 584–591.
Milthorpe, F.L. and J. Moorby 1974: An introduction to crop physiology. Cambridge Univ. Press.
Mohler, C.L. 1993: A model of the effects of tillage on emergence of weed seedlings. Ecological Applications **3**, 53–73.
Moreau-Valancogne, P., F. Coste, Y. Crozat and C. Dürr 2008: Assessing emergence of bean (*Phasesolus vulgaris* L.) seed lots in France: Field observations and simulations. Eur. J. Agron. **28**, 309–320.
Odabas, M.S. and Z. Mut 2007: Modeling the effect of temperature on percentage and duration of seed germination in grain legumes and cereals. Amer. J. Plant Physiology **2**, 303–310.
Prostko, E.P., H.I. Wu, J.M. Chandler and S.A. Senseman 1997: Modelling weed emergence as influenced by burial depth using the Fermi-Dirac distribution function. Weed Sci. **45**, 242–248.
Qiu, J., Y. Bai, B.J. Coulman and T. Romo 2006: Using thermal time models to predict seedling emergence of orchardgrass (*Dactylis glomerata* L.) under altrernating temperature regimes. Seed Sci. Res. **16**, 261–271.
Reuther, G. 1970: Wachstumsphysiologische Untersuchungen temperatursensibler Stadien keimender Samen. Ber. Dt. Bot. Gesellschaft **83**, 151–160.
Richards, F.J. 1959: A flexible growth function for empirical use. J. Exp. Bot. **10**, 290–300.
Roeggen, O. 1981: Different procedures for the calculation of minimum germination temperature in pea (*Pisum sativum*) Acta Hort. **122**, 39–46.
Roeggen, O. 1987: Variation in minimum germination temperature for cultivars of bean (*Phaseolus vulgaris* L.), cucumber (*Cucumis sativus* L.) and tomato (*Lycopersicon esculentum* Mill.). Sci Hort. **33**, 57–65.
Schimpf, D.J., S.D. Flint and L.G. Palmblad 1977: Representation of germination curves with the logistic function. Ann. Bot. **41**, 1357–1360.
Simon, E.W., A. Minchin, M.M. McMenomin and Z.M. Smith 1976: The low temperature limit for seed germination. New Phytology **77**, 301–311.
Soltani, A., M.J. Robertson, B. Torabi, M. Yousefi-Daz and R. Sarparast 2006: Modelling seedling emergence in chickpea as influenced by temperature and sowing depth. Agric. and Forest Meteor. **138**, 156–167.
Tamet, V., N. Souty and C. Rode 1995: Émergence des plantules de carotte (*Daucus carota* L.) sous des obstacles mécaniques superficiels. Agronomie **15**, 109–121.
Thompson, P.A. 1974a: Germination of celery (*Apium graveolens* L.) in response to fluctuating temperatures. J. Exp. Bot. **25**, 156–163.
Thompson, P.A. 1974b: Effect of fluctuating temperatures on germination. J. Exp. Bot. **25**, 164–175.
Thompson, P.A. and J.C. Fox 1976: The germination response of vegetable seeds in relation to their history of cultivation by man. Sci. Hort. **4**, 1–14.
Toole, E.H., S.B. Hendrix, H.A. Borthwick and V.K. Toole 1956: Physiology of seed germination. Ann. Rev. Plant Physiol. **7**, 299–323.
Vleeshouwers, L.M. and M.J. Kropff 2000: Modelling field emergence patterns in arable crops. New Phytologist **148**, 445–457.
Wagenvoort, W.A. and J.F. Bierhuizen 1977: Some aspects of seed germination in vegetables. II. The effect of temperature fluctuation, depth of sowing, seed size and cultivar on heat sum and minimum temperature for germination. Sci. Hort. **6**, 259–270.
Wagenvoort, W.A., A. Boot and J.F. Bierhuizen 1981: Optimum temperature range for germination of vegetable seeds. Gartenbauwissenschaft **46**, 97–101.
Weaich, K., K.L. Bristow and A. Cass 1996: Agronomic models. Modelling preemergent maize shoot growth: I. Physiological temperature conditions. Agron. J. **88**, 391–397.
Yin, X., M.J. Kropff, G. McLaren and R.M. Visperas 1995: A non-linear model for crop development as a function of temperature. Agric. For. Meteorol. **77**, 1–16.
Zhang, H., D. Zhou, P. Wang, T. Wang and Y. Jin 2007: Germination responses of four wild species to diurnal increase or decrease in temperature. Seed Sci & Technol. **35**, 291–302.

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