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

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Summary

Fundamental features, achievements, and special problems of plant/crop growth and development in the emergence phase are reviewed to provide a base for modelling, which will be reviewed in part VIb.

Key words. Emergence – germination – soil (medium) properties – soil moisture – sowing technique – temperature

Introduction

In the emergence phase basic preconditions of crop establishment are provided, such as timing, crop architecture, crop vigour and if so crop development. Therefore, this phase is an important module of modelling crop growth, particularly as the plants are weak and especially sensitive to environmental influences, including production techniques. In this part the fundamental physiological and physical background for modelling (presented in part b) is reviewed.

Basics

The general morphological and physiological basics of germination and subsequent heterotrophic growth are outlined by Taylor (1997) and others (Toole et al. 1956; Heydecker 1973; Kigel and Galili 1995) and shall not be repeated in this paper. Only important features for modelling will be summarised.

The emergence phase is defined as a process initiated by sowing non-endodormant seeds into a moist substrate, which corresponds to the beginning of water uptake; it ends when a defined percentage of seeds (mostly 50 % or e.g. 80 %) have visibly penetrated the substrate surface. The rates of 50 or 80 % of sown seeds shall eliminate variation by extreme, mostly weak and late emerging germs. With low germination rates the number of emerged seeds may be related to the seeds which finally germinated. Some authors define the emergence phase to be finished when e.g. 50 % of the cotyledons has expanded (e.g. Bierhuizen and Feddes 1973). Due to the speed of opening the cotyledons and the final angle of opening, however, this stage is more difficult to determine. Harrington (1962) defined the development to "normal" seedlings. Wagenvoort et al. (1981) discussed the problems of comparing these experimental values to conditions in practice, where the spread (scatter) of germination is also an important item.

The emergence phase consists of at least two mayor processes: germination, considered to start with imbibition and being completed at the time when the radicle pierces the coat (details see Harrington 1962) and followed by the phase of heterotrophic growth. Blacklow (1973) determined the critical level of rehydration for starting radicle length growth with the seed water content of about 70 % water content of the seed and shoot (about 85 %) of corn. More detailed subdivisions are: soaking > mobilisation of reserves > differentiation > growth of the embryo (Sorauer 1891); phases as e.g. soaking and respiration (Taylor 1997); phases related to water uptake: Initial rapid increase in water content > period with little change in water content > increase in water content when the radicle emerges from the seed coat > growth (Finch-Savage and Phelps 1993). In modelling the emergence of a *poaceae* (spring wheat) Jame and Cutforth (2004) subdivide the emergence phase into germination > coleoptile elongation after crown establishment > subcrown internode elongation. For scheduling horticultural production it proved reasonable to pool these processes, at least at the present stage of modelling (see part VIb).

Concerning plant production three criteria are of special interest: The maximum fraction of sown seeds able to emerge (emergence %, EA), the rate of emerging seeds per unit of time (ER) and therewith emergence duration (ED). The values of these criteria depend on the genotype and the provenience of the seeds (Krug 1964; Thompson and Fox 1976, see also Gray 1975, 1979) and on storage conditions and storage duration on the one hand; on the environmental conditions during emergence on the other hand, such as medium moisture and aeration, salinity, temperature, requirement of light, pathogen content and activity, as well as structural properties of the medium, such as resistance to seedling penetration, e.g. by liability to crusting or on sowing technique, such as sowing depth. In commercial greenhouse production temperature is the most important factor and most studied one, due to tim-

ing and energy cost. In open fields soil moisture and salinity may also be of major importance. FINCH-SAVAGE and PHELPS (1993) stated: "... seedlings' emergence patterns in the field" (Wellesbourne, UK) "are largely generated by the influence of soil water potential on a critical event (i.e. the initiation of radicle growth) ...". Particularities of determining ED in open fields are discussed by BIERHUIZEN and FEDDES (1973).

Temperature

Temperature acts in terms of an asymmetric, right skewed optimum curve with a more or less expanded optimum range. According to SACHS (1860) this curve can be defined by three cardinal points: Temperature minimum, temperature maximum (both × for y = 0) and temperature optimum (Fig. 16 in part VIb). An optimum range can be defined by two cardinal points, leading to four cardinal points altogether. These can be defined for ED, EA or ER. Early compilations of cardinal points are presented by HABERLANDT (1874, cit. by GRAFE 1914) and KOTOWSKI (1926), others by BIERHUIZEN and WAGENVOORT (1974) and KRUG (2002a). According to TOOLE et al. (1956, p. 310) these cardinal points may depend on seed age, presumably caused by endodormancy effects. Moreover, KRETSCHMER (1982) showed an effect of the phytochrome on the temperature reaction of lettuce seeds.

Cardinal points.

Temperature minima, the lowest temperatures enabling emergence, have to be appointed experimentally (physiological minimum) or can be estimated statistically (see paragraph modelling). At constant temperatures the physiological temperature minima, compiled in Table 14 for vegetable species, vary from 0 to 18 °C, the statistically calculated ones listed in Table 16 (see part VIb) range from 0 to 13 °C. Limiting is especially the growth of the hypocotyls, less the growth of the radicles (KOTOWSKI 1926). In practice, however, temperature mostly is not constant, plant reactions depend on several factors, such as storages conditions (e.g. muskmelon, WELBAUM and BRADFORD 1991), time and adaptation to low temperature (see below) and/or pathogen attack. Temperature minima for emergence in commercial vegetable production are derived in KRUG 2002a, b (a in table 4.7-4 and b in table 5-2). Chilling injuries are not discussed here (see WOLK et al. 1982; TAYLOR 1997).

Physiological temperature maxima are the highest temperatures allowing germination, ranging from about 25 °C (25 °C leek, 20–30 °C celery) to < 45 °C (Table 14). With high temperature the percentage of "normal seedlings" dropped much faster than radicle emergence percentages (HARRINGTON 1962).

Optimal temperatures can be defined as the highest ER, the shortest ED, or the highest EA. Concerning EA, Table 14 presents values of 7 to 35 °C with distinctly higher optima for warm season crops (18–35 °C) than for cold season crops (7–35 °C). Concerning ED the range varies from about 20 to 35 °C with a conspicuous optimum at 25 °C. With these data certain effects of remains of endodormancy cannot be excluded. Less data are available concerning optima ranges.

Since the optima for ED in many cases are higher than for EA, a compromise has to be found in production. HARRINGTON (1962) states: "... the optimum germination temperature could be considered to be the highest temperature of the optimum temperature range for total germination". WAGENVOORT et al. (1981, their tables 1 and 2) defined the optimum temperature range by maximum germination percentage and the germination percentage, which is 10 % lower. They also consider the "spread of germination", a parameter of increase of germination rate with time (see part VIb – modelling). Optimum temperatures for germination of the vegetables tested, derived by the time spread, ranged over about 13 °C, varying from 7 °C (gherkin, eggplant) to 17 °C (radish, lettuce). KRUG (2002b) claims an optimisation of temperature control on the basis of complete rotations; this means to include the consequences of emergence duration on all the crops grown in that year. However, this may be a future task.

Variation in temperature response of **cultivars** and their relation to wild ancestors was investigated by HEGARTY (1973) and THOMPSON (1973). HEGARTY (1973) concluded that strains of cultivated species "... do not posses a generalised germination response, produced, perhaps adaptively, by selection for particular qualities imposed by the special features of cultivation by man. Nor is there any suggestion that strains of vegetables selected for sowing in different seasons in the open ground or in any artificially heated environment, such as glasshouse, are likely to differ from one another in major respects. Thus, the germination responses found from one cultivar to another one of a particular crop plant were notably similar, though not necessarily the same, ...". This should even be true for different forms of e.g. *Brassica*, originated from one ancestor. The geographical origin of the ancestors is the primary reason.

In other investigations also little differences of cultivar reaction within many species have been verified, but for cultivars of some species considerable differences have been proved (e.g. table beet (*Beta vulgaris* L.), rutabaga, carrot, onion – Torfason and Nonnecke 1961, carrot – Hegarty 1973, celery – Thompson 1974, pea – KRUG 2002c...). HEGARTY (1973) stated: "significant differences of response between the cultivars of each crop type used...". On the other hand GULLIVER and HEYDECKER (1973) pointed out: " ... differences in responses between seed lots of one cultivar can be more important than differences between cultivars and possibly even species." These differences may occur as tolerances to high and low temperatures (HEGARTY 1973). In other investigations cultivar differences were detected mainly at low temperatures (e.g. JAME and CUTFORTH (2004) with spring wheat). CRAUFURD et al. (1996) provided evidence for substantial genotypic variation in seed germination of cowpea cultivars from different habitats and latitudes, concerning Tmin and Topt, not for Tmax. Estimates of Tmin were highest in genotypes originating from locations close to the equator.

For sowings in the cold season, the **tolerance of soaked seeds** to initial low temperature periods may be important. KOTOWSKI (1926) stated the ability to survive for rutabaga and garden cress (3–4 months at 0 °C, cit. by ULOTH (1875) or at 4 °C for cabbage, cauliflower, carrot and beet. TORFASON and NONNECKE (1961) tested the reaction of vegetable species to varied periods (1, 8, 15, 22 days) of low temperature (at 1.7, 4.4, 7.2, 10 °C), by counting the percentage of healthy seedlings, developed in a 21 °C room. Germination of table beets and onions was not appreciably reduced by initial temperatures be-

Table 14. Experimentally derived physiological cardinal points of temperature reaction (°C) during the emergence phase of vegetable species (ER, underlined for ED, bold for ER and ED, b = between. Indexes indicate authors. The values of minimum and maximum of ER and ED should be almost identical, but are listened separately when derived from different experiments). No claim for completeness.

Species	Minimum	Optimum	Maximum
Asparagus	b **5–10**[2)]	**25**[2)]	b **35–40**[2)]
Bean	b 11–18[1], b **10–15**[2)], 10[3)], b 7–10[4)], 11–12[5)]	25–≥ 30[1)], 15–25[2)], 30–35[2)], 32[3)]	> 30[1)], b **35–40**[2)], 37[3)]
Brussels sprouts	< 5[8)]	7–35[8)]	> 42[8)]
Cabbage	b 4–8[1)]	8[1)]	> 30[1)]
Carrot	b 4–8[1)], b **0–5**[2)], 4–5[3)], < 5[8)]	18[1)],10–30[2)], 20–30[2)], 25[3)], 10–33[8)]	> 30[1], b **35–40**[2)], 30[3)], 40[8)]
Cauliflower	b 4–8[1)]	11–25[1)]	> 30[1)]
Celeriac, celery	b 5–10[6)]	10–15[6)]	b 20–30[6)]
Corn	10[2)], b 8–10[3)]	32–35[3)], 34[9)]	40–44[3)], 43[9)]
Cucumber	b11–18[1)], b **10–15**[2)], 12[3)], b 12–15[4)], 11–12[5)]	25–30[1)], 15–35[2)], 30–35[2)], 32–35[3)]	> 30[1)], **40**[2)], 40[3)]
Cucurbit	12[3)]	33–34[3)]	40[3)]
Eggplant	b 11–18[1)]	25–≥ 30[1)]	> 30[1)]
Garden pea	< 4[1)], 1–2[3)]	18[1)], 30[3)]	35[3)]
Leek	< 5[8]	10–18[8]	25[8]
Lettuce	< 4[1)], < **0**[2)], ≤ 0[8)]	4–25[1)], 0–25[2)], 20–25[2)], 5–25[8)]	b 25–30[1)], b 30–35[2)], 25[2)], 35[8)]
Melon	b 11–18[1)], 12–15[3)]	25–≥ 30[1)], 35[3)]	> 30[1)], 40[3)]
Okra	b **10–15**[2)]	20–30[2)], 30–40[2)]	b **40–45**[2)]
Onion	b 4–8[1)], **< 0**[2)], 1[7)]	18[1)], 5–25[2)], 25–30[2)]	**>** 30[1)], **40**[2)]
Parsley	b 4–8[1)], 0[2)]	11–25[1)]	> 30[1)]
Parsnip	**< 0**[2)]	15–20[2)], 20–25[2)]	**35**[2)]
Pea	**<** 4[1)]	4–25[1)]	b 25–30[1)]
Radish	< 4[1)], 1[7)]	11–> 30[1)]	> 30[1)]
Red beet	b 4–8[1)]	11–25[1)]	> 30[1)]
Rutabaga	1[7)]		
Spinach	< 4[1)], **< 0**[2)]	5–10[2)], 25[2)]	> 30[1)]**, < 35**[2)]
Sweet corn	b **5–10**[2)]	15–25[2)], 25–35[2)], 34[9)]	**40**[2)], 43[9)]
Sweet pepper	b 11–18[1)], b **10–15**[2)]	18–30[1)], 20–30[2)], 25–35[2)]	> 30[1)], b **35–40**[2)]
Tomato	b 8–11[1)], b **5–10**[2)], 8–11[4)]	18–30[1)], 15–25[2)], 25–30[2)]	> 30[1)], b **35–40**[2)]
Turnip	0[2)], b 5–10[2)]	15–35[2)], 20–35[2)]	b 40–45[2)], 40[2)]
All species tested	< 0–15[3)]		(25) **30–43**

Authors: [1)]Kotowski 1926: Silica sand in flats, 2/4 cm deep, emergence. [2)]Harrington 1962: On blotting paper, ≥ 50 % normal seedlings, max. > 0 %. [3)]Haberland 1874 (cit. by Grafe 1914): Germination. [4)]Roegen 1987: Emergence, minimum is defined as between growth can be observed or not observed. [5)]Simon et al. 1976: 50 % germination (radicles protruding through the testa) on filter paper. Bean = mung bean. [6)]Thompson 1974: The range denotes the values of 5 cultivars, sown in thermo-gradient bars, cardinal values (minimum germination %). [7)]Valovich and Grif 1975: Filter paper in Petri dishes, ≥ 10 % germination and continuing growth. [8)]Thompson 1973: Sown in thermo-gradient bars, germinated seeds (%) reaching zero, read from graphs. [9)]Itabari et al. 1993: Controlled environments in Eastern Kenya.

low 10 °C, but carrot germination was reduced after temperatures < 10 °C (this does not correspond with horticultural experience) and rutabaga germination was significantly reduced after previous exposures to 1.7 °C. The conclusion is that species with high T_{min} values (bean, cucumber) are generally more sensitive to preliminary low temperature impacts, but cold season vegetables also differ in reactions to initial periods of low temperature.

Water potential

A precondition of germination and temperature action is an adequate **water potential** of the seeds, depending on many factors, such as properties of the seeds (e.g. morphology of the testa), soil type and architecture, water status and aeration of the medium (soil/substrate), hydraulic conductivity of the medium (Williams and Shaykewich 1971; Fedtes 1971), contact between medium and seeds, e.g. by pressing the seeds into the surrounding medium by sowing techniques as well as salinity of the ambient soil water and sensitivity of the seeds to salinity. Literature up to about 1970 is discussed by Fedtes (1971).

Due to a high matrix potential the soaking of seeds and germination of some species starts already with very low soil moisture, seeds of cultivars of some species (cabbage, turnip, sunflower, radish) already below the PWP (pF 4.2, ≅ −15.000 hPa). According to Hunter and Erickson (1952, cit. by Fedtes 1971), testing five soil types, germi-

nation/emergence started, with minimum (basic) values of matrix pressures (Ψ_{min}) of −12.700 hPa (corn), −8.000 hPa (rice), −6.700 hPa (soybean), −3.500 hPa (sugar beet). An example of the relation of constant water potential (on paper) to rate of germination in deciles (t^{-1} of the first phase of emergence for deciles) of carrot is presented by FINCH-SAVAGE et al. (1998) and shown in Fig. 14. Ψ_{min} increases with the percentage of germinated seeds and the rate of germination is linear proportional to $\Psi > \Psi_{min}(G)$.

Using another criterion germination starts with a water content of the seeds of 26–60 %, depending on the properties of the respective seeds. HADAS (1970, cit. by FEDDES 1971) stated that for good germination and emergence relative water uptake around 100 % of the initial seed weight should be necessary.

In the course of emergence, however, the reaction to soil moisture changes. According to FINCH-SAVAGE and PHELPS (1993) and FINCH-SAVAGE et al. (1998) the initiation of radicle growth is the moisture-sensitive, rate-limiting step which determines the base of water potential of the seed for germination and controls the progress towards seedling emergence patterns in a seed bed with variable moisture content as far as $\Psi > \Psi_{min}$. Therefore in fields with changing soil moisture the first five days after sowing were crucial. TAYLOR (1997) also stated: "... In phase III (visible germination) the seed becomes a seedling and also looses its ability to withstand desiccation...., while drying seeds during phase I (imbibition) and II (mobilisation of metabolism) is not injurious to the viability of the seed". HEGARTY (1980/81) found in laboratory experiments that "... the initiation of cell elongation is the process in germination most sensitive to water stress".

In the range above Ψ_{min} no uniform results are published (see FEDDES 1971). Whereas some authors found little effect of decreasing soil water potential on EA, others reported reduced EA with decreasing water potential in the soil and seeds germinated somewhat slower. There was no correlation between soil water potential reaction and seed size (DONEEN and MCGILLIVRAY 1943).

The **upper range of soil matric potential** is limited by oxygen availability, depending on soil architecture and soil water status, according to DASBERG and MENDEL (1971) causing the thickening of the water films around the seeds, which interfere with oxygen supply. The authors found an optimal matric potential for germination of *Oryzopsis holciformis* (*Poaceae*) in coarse sand of −5 hPa and in sandy loam of −500 hPa. KRUG (2002a) concluded: The **optimal soil water content** is a compromise, it is considered to vary between −100 and −400 hPa, with light soils in the upper range and compact soils in the lower one.

Species react different to high soil water potential. Very sensitive to oxygen shortage proved e.g. spinach and pea, relatively insensitive lettuce. Sensitive reaction to dry soils was found in carrot, celery/celeriac, onion, lettuce, beets, pea, lima bean and with constraint 'New Zealand spinach'. Relative insensitive to dry soils are claimed radish and *Brassica* species (details see TAYLOR 1997).

Interaction of temperature reaction and water potential: In an experiment of BIERHUIZEN and FEDDES (1973) with seven sowing dates the Temperature Sum (S, see chapter modelling) for ED of radish, spinach, broad bean and garden beet (*Beta vulgaris* L. var. *vulgaris*) was not noticeably influenced by the water potential of the soil down to about −270 hPa; with lower water potential S increased linearly, more or less independently of soil type (loam and clay) and ground water table (45 and 165 cm). The S of the sowings on sandy loam, however, were lower than those on clay soil and those with 45 cm ground water lower than those with 165 cm ground water. FEDDES (1971) recommends sprinkler irrigation to keep the moisture content between −490 and −98 hPa (pF 2.7–2.0).

An example of action of **soil moisture** and **salinity** on the number of germinated onion seeds is demonstrated by AYERS (1952, Fig. 15). Salt tolerance of vegetable species is compiled by SCHARPF and LIEBIG (2002, table 4.3-29, p. 191) and shall not be discussed here.

Physical forces

The ability to penetrate hardened soils or crusts is higher with seeds of high vigour. This is correlated with high

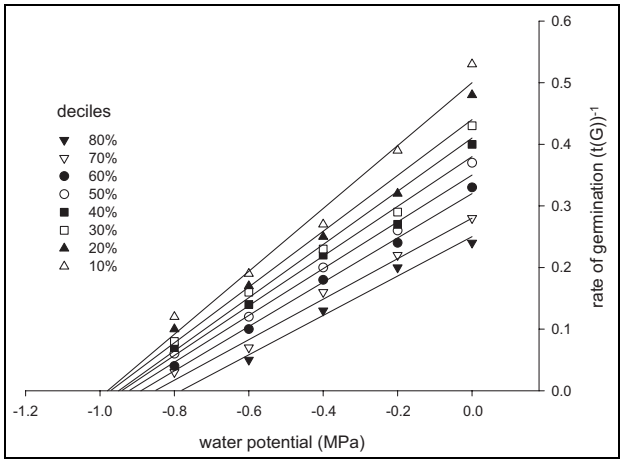


Fig. 14. The effect of constant water potentials (on moist paper) on the basic water potentials (Ψ_{min}) and the rate of germination ($t(G)^{-1}$) for deciles of a carrot seed population at 20 °C (FINCH-SAVAGE et al. 1998).

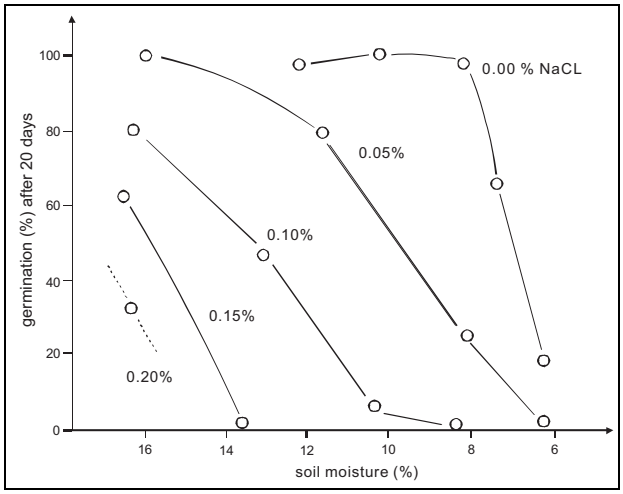


Fig. 15. Germination percentage of onion seeds after 20 days as a function of the water and salt content of the soil (AYERS 1952, cit. by KRUG 2002).

seed weight and high lipid content as an energy source (TAYLOR 1997, his table 11.6), with favourable temperature and with a favourable water status of the seedling. Hypogeal germinating species have a greater ability than epigeal germinating species, which have to push the cotyledons through the soil. TAYLOR and TEN BROECK (1988, their table 1) as well as INOUYE et al. (1979, their table 1) listed respective data for vegetable crops. Total force, percent seedling emergence, force per seedling, pressure exerted, and energy content increased with seed size in a linear trend. Production techniques to prevent unfavourable soil structures for emergence or to improve the physical soil structure are outlined by HENNING (1994).

Sowing technique

Sowing technique determines among others sowing depth and soil compaction around the seeds.

WAGENVOORT and BIERHUIZEN 1977 stated regarding sowing depth and

- EA: Greater sowing depth (1.5–15 cm) can be applied for crops with larger seed size. It seems that with an increase in temperature, the sowing depth can be increased. This reaction was not affected by the fraction of seed weight of radish.
- ED: Increase in sowing depth causes a longer germination period, with a tendency towards greater differences at lower temperatures. In moderate conditions the elaborated values of T_{min} and S can be used, under extreme conditions (deep sowing, low temperature) deviations may occur. Neither S nor T_{min} were affected by seed fraction of radish.

In general: Optimal sowing depth depends on many factors: Water and oxygen availability, soil temperature, physical soil properties, penetration forces of the seeds, timing, stableness of the individual plant and pathogen risk. In dry soils deeper sowing and more compact deposition improve water uptake, but require higher penetration forces and more time. In humid soils shallow sowing reduces penetration forces, duration of the emergence phase and shortage of oxygen, but it increases the risk of drying up. Deep sowing results in a somewhat longer ED, especially with low soil temperature. For shallow sowing, however, equal water availability in the upper soil layers is a precondition.

Conclusions

Conclusions will be presented in part VI b.

Abbreviations

(To relievable understanding and comparisons the original short cuts are unified)

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, ER = rate of emerged seeds (speed of emergence), G = germination fraction of the population at which it germinates, PWP = permanent wilting point, S = temperature sum (°Cd), T_{min} = minimum temperature for germination/emergence, T_{max} = maximum temperature for germination/emergence, T_{opt} = temperature optimum for germination/emergence, Ψ = water potential, Ψ_{min} = base of water potential of the seed for germination/emergence

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