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Modelling Production Subsystems at High Abstraction Level – A Review. III. Development – Vernalisation

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Summary

Basic features and special problems of modelling plant/crop development, in this part vernalisation, are reviewed, extended and utilisations in vegetable production are shown.

Key words. crop production – development – modelling – photoperiodism – vernalisation

Introduction

Growth is the primarily considered process in vegetable production and can be described rather precisely at high abstraction level (part I and II). In numbers of processes, however, growth is closely connected with or even dominated by developmental processes. Therefore, modelling development often is a precondition of understanding and modelling growth and with both approaches more comprehensive submodels of the entire production process are afforded. After providing essential definitions and approaches to understand development, in this part basics and modelling vernalisation are reviewed.

[In part II, page 138, unfortunately a misprint has been incorporated. It should read: Radish (*Raphanus sativus* L. var. *sativus* (Table 2) and *Raphanus sativus* L. var. *niger* (Table 3).]

Definitions and Approaches

Abbreviations

c_{max} = 1 h^{-1}; c_{min} = 0.01 h^{-1}; cv = cultivar; d = days; D_b = basic (shortest) duration of DTF; DR = Differentiation rate; DTF = days to flowering; ER = Development rate; f (–) to customise model parameters; LD = long day; μ ($°C^{-1}$) to customise model parameters; n = number of ... ; NTF = nodes to flowering; N_b' = the fewest primordia produced when there is no vernalisation gene activity; S = temperature sum (°Cd, slope of the regression equation); SD = short day; S_v = sensitivity to the low-temperature treatment; T= temperature and mean temperature of the phase, respectively; t = time in days; T_{bv} = base temperature for activity of the vernalisation gene(s); T_{max} = maximal temperature (x for y=0, ER=0); Tmin = basis temperature (x for y=0, ER=0); v = duration in days of the low-temperature treatment;

V_{req} = duration of that low-temperature required to cause expression of the N_b'; VR = Vernalisation rate.

Development means the characterisation of ontogenesis and its control by the gene * environment interaction, the latter offering an adaptation to the growing conditions, e.g. to climate cycles. Main adaptation processes are the control of flowering, of vegetative reproduction and of activity by entering a rest period of plants or organs. Signals are temperature levels (especially vernalisation), maybe temperature gradients and day lengths (photoperiodism) and to some extent dryness.

Development expresses itself by the manner and chronological sequence of differentiation and by the activity of physiological processes involved, both connected interactively with metabolism and growth. This may concern the entire plant, particular organs or special processes only. Due to the manifold processes development cannot be measured by just one criterion, as e.g. weight for growth, but the following criteria are established:

– The rate of differentiation (**Differentiation rate**, DR):

$$DR = n * t^{-1} \quad (20)$$

This criterion is used in phases with dominating processes of measurable differentiation (e.g. leaf number, differentiation of the growing point)

– The minimum number of differentiated organs (e.g. leaves, weight of onion sets) before entering the next phase (e.g. **Juvenile phase**)
– When differentiation is difficult to measure, the duration of the respective process (e.g. emergence phase) is a useful criterion. The reciprocal value of time provides the **Development rate** (ER). It is a relative parameter and presents the fraction of progress per unit of time (t, e.g. days) related to the total time of the respective phase.

$$ER = t^{-1} \text{ or in \% } ER = 100 * t^{-1} \quad (21)$$

The ER has the advantage that – in a range to be defined – it is frequently linear proportional to the cumulated quantum of growth factors, especially temperature. This is the basis for the **Temperature sum concept** (Reaumur 1735; Feddes 1971). Main equations are:

$$\text{Temperature sum}(^{\circ}\text{Cd}): S = \sum_{i=1}^{n} (T_i - T_{min}) \quad (22)$$

Mean temperature (°C): $T = T_{min} + S * n^{-1}$ (23)

Duration of the phase (d): $n = S * (T - T_{min})^{-1}$ (24)

The manner of coaction of these different processes of development on species/cultivars behaviour is manifold; an example is shown with pea cultivars by Krug (2002, p. 78).

Due to these special features modelling of development differs from modelling of growth. On the one hand it deals not with one definite criterion as weight, but with a multiplicity of criteria. On the other hand adaptation reactions are controlled mostly only by one or two dominating factors compared to the multiplicity of factors affecting growth. This may facilitate to build mechanistic models, when the underlying processes are understood. Apart from these characteristics the procedure of modelling development is similar to modelling growth.

Basics of vernalisation

In the traditional view vernalisation is a response to adapt development and growth to season and habitat by blocking the turnover from the vegetative to the reproductive stage, which has to be overcome by a cold period. This shall ensure sufficient time for formation and ripening of the reproductive organs. The receptive organs are the dividing cells of the growing point. The changeover is indicated by differentiation of inflorescence and flower buds, respectively, at the growing point. Vernalisation may be an indispensable precondition of initiation of the organ to be harvested (qualitative reaction, e.g. cauliflower, many biennials) or it may only accelerate the initiation of flower buds (quantitative reaction, e.g. lettuce, many winter annuals) with different vernalisation sensitivity in growth phases and in required cold quantity of species or culivars. Vernalisation has to be avoided, whenever a vegetative organ shall be harvested (e.g. kohlrabi, spinach, lettuce). In some cases, vernalisation can be replaced or supported by SD during the vernalisation period and more often development is accelerated by LD after vernalisation. With other species (spinach, lettuce, endive, peas) the photoperiodic reaction is dominant and vernalisation has a modifying effect only.

General reviews are presented by Rees 1987; Wiebe 1989b; 1990b; especially with kinetic and mathematical aspects by Roberts and Summerfield 1987; Roberts et al. 1991 and with molecular genetic and mathematical aspects by Yan and Wallace 1996. Concerning crop production, secondary effects on morphology (e.g. form of tubers or leaves, bolting) or just marketable yield may also be used as criteria (particulars in Habegger 1985; Wiebe 1989b; Krug 2002). Therefore, the vernalisation requirement can be an important characteristic of earliness and yielding.

Basic data preferably have to be elaborated in controlled environments. Plants are subjected to a graduation of – initially constant – temperatures, to test sensitivity during ontogenetic development, such as the embryonic phase of the seed at the mother plant, emergence phase and stages during autotrophic growth, which can be characterised by leaf number or/and apex stage (differentiation of the inflorescence bud or flower buds). Here, an essential reaction in vernalisation is the existence of a juvenile phase. During the juvenile phase the plants are insen-

Table 11. Key data for vernalisation of vegetable species (Wiebe 1989b, actualised in Krug 2002).

Species	Cold requirement[1], start of sensitivity[2] (leaf number > 2 cm, juvenile phase)					Inductive temperature range[3] (°C)	Exposure time[4] (weeks)	Devernalisation and antivernalisation[5] (°C)		Photo-period[6]
Cauliflower	o	–	–	–	P (4–12)	0 – 10 – 16/30	1 – 6	De low		
Chicory	o	E	S	K	P	(0) – 5 – 12	4 – 8	De		LD
Chinese cabbage	o	–	S	K	P	0 – 5/8 – 20	1 – 4	Anti	>20 °C	LD
Endive	f	E	S	K	P	(0) – 4 – 17	3 – 4	Anti	>20 °C	LD
Kohlrabi	o	–	–	–	P (>2)	(0) – 5 – 12	4 – 8	De strong	>16 °C	
Cabbage	o	–	–	–	P (4–15)	0 – 4/7 – 12	4 – 20	De strong	>16 °C	(LD)
Lettuce	f	E	S	K	P	0 – 2/5 – 12	2 – 3	De		LD
Carrot	o	–	–	–	P (>8)	0 – 2/6 – 10	5 – 12	De	>20 °C	SD/LD
Parsley	o	–	–	–	P (>5)	(0) – 2/6 – (10)	5 – 8			
Leek	o	–	–	–	P (>5)	0 – 5/8 – 18	3 – 6			SD/LD
Radicchio	o f	E	S	K	P	0 – 5/10 – 15	2 – 3	Anti low	>15 °C	LD
Radish (niger)	o f	–	–	K	P	0 – 5/8 – 15	1 – 4	De	>20 °C	LD
Red beet	o	E	S	K	P	(0) – 5/9 – 18	3 – 5	De strong	>18 °C	LD
Scorzonera	o	–	S	K	P	(0) – 2	3			
Celeriac	o	–	–	–	P (4–6)	0 – 5/8 – 14	2 – 5	De + Anti	>20 °C	SD/LD
Onion	o	–	–	–	P (4–6)	2 – 9/13 – 18	4 – 12	De + Anti	>20 °C	LD

[1]o = obligatory, f = facultative; [2]E = embryo at mother plant, S = seeds after soaking, K = emergence of root, P = plants of specific size, – = no requirement; [3]values in ( ) estimated, mean value = optimal value, 5/8 presents a range; [4]first value = shortest duration for optimal vernalisation temperature, second for late cultivars in weeks; [5]DE = devernalisation, Anti = antivernalisation; [6]SD = short day during and LD = long day after vernalisation.

sitive to vernalising temperatures. It is an important characteristic of many cultivars. Most early cultivars have a shorter juvenile phase than the later ones.

When the sensitive phase(s) is/are determined, the interaction of temperature with the duration of exposure on the vernalisation process has to be worked out to determine the cold quantity required. Thereafter, the effects of fluctuating diurnal temperatures as well as interruptions by higher temperature periods have to be checked to appoint the forces of devernalisation (high temperature after or during vernalisation, but only in an early stage of flower bud development) and antivernalisation (high temperature before vernalisation), which can delay or even erase the successive vernalisation effect (Chinese cabbage, celeriac, endive, onion). Moreover, photoperiodic effects have to be considered, which may accelerate vernalisation. In general, SDs promote development during vernalisation and LDs promote development thereafter (Chinese cabbage: KRUG and KLING 1982, radish (var. *niger*): WIEBE 1985, leek: WIEBE 1994). Irradiance levels before vernalisation had no effect on vernalisation of cauliflower, while decreasing irradiance during vernalisation increased the number of leaves (WIEBE 1974). Other environmental factors, such as nitrogen availability, plant water potential or soil density (HAHN 1995), soil temperature (RIETZE and WIEBE 1988) did not influence vernalisation effects significantly. Main characteristics for vegetable species are summarised by WIEBE 1989a, b (updated in Table 11; for major field crops see ROBERTS and SUMMERFIELD 1987, their table 2.1).

According to HABEGGER (1985) each species and possibly each cultivar has a specific response surface of vernalisation, mostly an asymmetric optimum curve with potential ranges from negative temperatures ('Petkus' winter rye −5 °C, most species, however, about 0 to >20 °C, e.g. tropical cauliflower cvs.). The duration of a cold treatment varies from a few days to about 60 days. These reaction curves are varied by effects of diurnal fluctuation, by high temperature interruptions and by devernalisation, potentially also antivernalisation and photoperiodic effects (Fig. 5). The effect of (de)vernalisation, moreover, may be varied by the continuity of vernalising temperatures. ALT and WIEBE (2001) stated for experiments with celeriac "not the maximum vernalisation value but the continuous existence of a positive vernalisation sum yields the best bolting prediction". Moreover, morphological aspects (kohlrabi tuber form and degree of bolting: HABEGGER 1985) have to be considered.

Modelling vernalisation requires adequate functions to describe the response surfaces to calculate the respective **parameters** in order to enable the simulation of the vernalisation process. The efficiency of temperature for vernalisation generally follows an optimum curve. In smaller ranges, however, the relationship can be described more or less as to be linear, especially when the VR is applied. Linear approaches have the advantage that every degree temperature (°C) has the same effect and, according to the Temperature Sum Concept (eq. 21–23), the degrees just have to be added. Two approaches are offered for the ascending range of the VR, emanating from T_{min}:

$$t^{-1} = VR = (T - T_{min}) * S^{-1} \quad (25)$$

and for the descending range, emanating from T_{max}:

$$t^{-1} = VR = (T_{max} - T_{(<Tmax)}) * S^{-1} \quad (26)$$

For Chinese cabbage in Japan, e.g., T_{max} reads 13 °C and S = 87 °Cd (NAKAMURA 1977).

If linearity is provided in sections only, these sections have to be demarcated, the VRs for each section calculated and summed up. A first approach for modelling vernalisation of onion cultivars, but without indicating demarcation of the boundary values, is published by BREWSTER (1987, his Fig. 13.3). A plateau model by means of four cardinal temperatures is used by KAGE and STÜTZEL (1999) to calculate the VR of cauliflower as a function of temperature (Fig. 6, curve a, more about plateau models see KUZYAKOV et al. 1997).

For non-linear relationships adaptation curves have to be calculated. The response surface of kohlrabi in Fig. 5, e.g., can be parameterised by a polynomial of 4th order. Here, the efficiency of the VR has to be weighted by fractional values. Another approach is a transformed logistic function (ALT and WIEBE 2001, Fig. 6, curve b):

$$VR = (c_{max} - c_{min}) * [(c_{max} * \exp(-\mu T)] * (c_{min} + (c_{max} - c_{min}) * \exp(-\mu T))^{-1} - f \quad (27)$$

According to the functions these equations require at least 3–5 measured values for parameterisation. There-

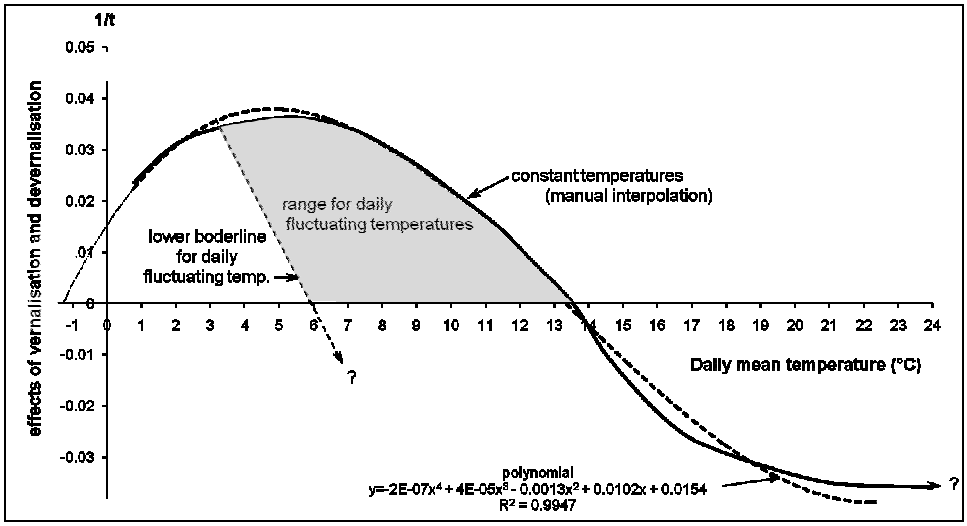


Fig. 5. Schematic presentation of vernalisation and devernalisation effects on kohlrabi (HABEGGER 1985).

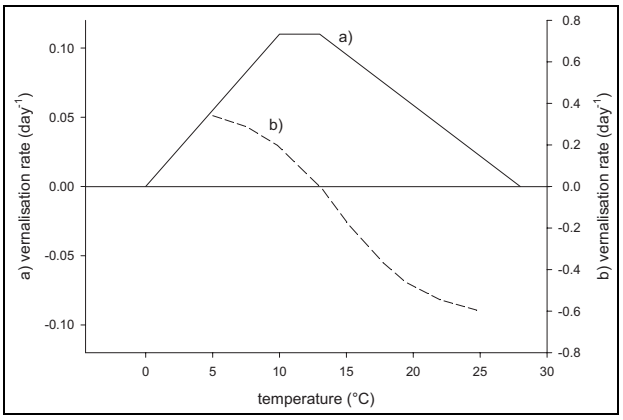


Fig. 6. Response surfaces of vernalisation and devernalisation rates: a) cauliflower in the shape of a plateau model (KAGE and STÜTZEL 1999, based on data of WIEBE 1972b); b) celeriac in the shape of a transversed logistic function (ALT and WIEBE 2001).

with the question arises, whether the three cardinal values, listed in Table 11, permit parameterisation. A proximate approach is a polynomial of 2nd order, but this disregards the asymmetry of the temperature reaction of vernalisation, proved for many species. T. Rath (pers. comm., 2008) proposes a Gauß-function, which allows an adaption to the skewness of the vernalisation reaction:

$$VR = a * \exp(-1 * r^2 * (T_2-T)^2 * [2\,(T_2-b)^2]^{-1}) \quad (28)$$

where a = maximal VR, b = T_1 when $T \leq T_2$, else b = T_3; r = $|T2-b| * \sigma-1$, σ = standard deviation of the normalized Gauß-function, (r = 2 => 95,45 % of the effects are presented with the model, r = 3 => 99,73 % of the effects are presented with the model); T_1 = minimum temperature, T_2 = optimum temperature, T_3 = maximum temperature.

If no satisfactory adaptation equation is found, the graphically hand drawn method, as used by WIEBE (1975), may be an alternative solution. WIEBE (1975) and HABEGGER (1985) presented accordant response surfaces of cauliflower and kohlrabi. The effects of photoperiod on vernalisation will be outlined in part IV of this serial.

When the parameters of the respective response surface are acquired, simulation is a simple process, just adding the VRs, full or fractional values, until the value one = 100 % is reached.

YAN and WALLACE (1996) offered a new interpretation of vernalisation from a molecular genetic point of view. They claimed that vernalisation is not induced by low temperature, but a gene controls repression of the inherent capability of rapid development to flowering with increasing temperature. This means, low-temperature vernalisation prevents the inhibition of vernalisation gene activity. The nodes to flowering (NTF) as a criterion of gene activity is described by:

$$NTF = N_b' + S_v * (T-T_{bv})^2 \quad (29)$$

where $T \geq T_{bv}$ and $P = P_{opt}$ with no photoperiodic repression.

If all parameters are measured in days rather than in number of nodes, an identical equation reads:

$$DTF = D_b + S_v * (v-V'_{req})^2 \quad (30)$$

where $v \leq V_{req}$. When the DTF is controlled by additional genes, a more comprehensive equation is required (see part IV). For a replacement or backing of vernalisation by the photoperiod in this concept consult the original literature. The terms devernalisation and antivernalisation are not mentioned in that paper.

Applications in commercial practice

The vernalisation models are useful tools in horticultural production (cited literature presents examples):

- to understand and consider the character of species and cultivars (cauliflower: WIEBE 1972a, b, c, 1973a, celeriac: WIEBE 1998, 2001, radish var. *niger*: WIEBE 2000)
- to prevent bolting in the field by warm raising of transplants or by damping and analysing, respectively, the effects of cool weather periods in the field during the vernalisation sensitive phase (Chinese cabbage: KRUG and KLING 1982; ELERS and WIEBE 1984; celeriac: WIEBE 1998, 1999; ALT and WIEBE 2001; leek: WIEBE 1990a, 1994, 1995a; lettuce: WIEBE 1986, 1987a; radicchio (*cichorium intybus*): WIEBE 1997, radish (var. *niger*): WIEBE 1984; WIEBE and ALPERS 1983).
- to reverse no desired vernalisation of transplants in greenhouses by devernalisation
- antivernalisation (kiln) of onion sets
- to estimate the causes of bolting for rights of recourses to transplant nurseries
- to produce good qualities and less variability (cauliflower: WIEBE 1973b, 1974)
- to predict time and quality of harvest (cauliflower: WIEBE 1973b, this model was extended by more mechanistic approaches by KAGE and STÜTZEL 1999; BAZLEN et al. 1996, radish, var. *niger*: WIEBE 2000)
- to reduce the energy consumption in greenhouses (kohlrabi: WIEBE et al. 1992; WIEBE 1995b)
- to produce seeds (cabbage: WIEBE 1987b, shallot: TABOR 2004; TABOR et al. 2006)
- to prevent vernalisation effects during seed ripening on the mother plant (chicory, lettuce, spinach WIEBE 1989b)

A comprehensive discussion on the application of vernalisation models is presented by HABEGGER (1985).

Concluding remarks

Vernalisation, besides some photoperiodic effects, primarily is a quasi-mono causal process for entering the generative stage with all the consequences for dry matter distribution and therewith yielding. It is easier to understand and to model than photoperiodic effects, but species and cultivars differ in many responses, which will have to be investigated. For many vegetable species cardinal values are elaborated and equations are offered for parameterisation, which assists to calculate the ER, here called Vernalisation Rate, for modelling vernalisation and devernalisation effects. For a complete description of the miscellaneous processes occurring in crop production, however, more investigations, especially on the effects of fluctuating temperatures, resulting in interactions of vernalisation and devernalisation and photoperiod will have to be done.

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