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Modelling Production Subsystems at High Abstraction Level – A Review. V. Development – Endodormancy (Focussed on Vegetable Crops)

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Summary

Basic features, achievements and special problems of modelling plant/crop development, in this part the impacts of photoperiodism and temperature on endodormancy, are reviewed, extended and applications in vegetable production are discussed.

Key words. crop production – development – dormancy – modelling – photoperiodism – temperature

Introduction

After discussing crop growth modelling in parts I and II (Krug 2008a, b) and the basics and meaning of the developmental processes vernalisation in part III (Krug and Kahlen 2008a) as well as photoperiodism in part IV (Krug and Kahlen 2008b), in this chapter basics, achievements and potentials of modelling endodormancy and its impacts on vegetable production are outlined.

Basics of dormancy

"Dormancy is a temporary suspension of visible growth of any plant structure containing a meristem" (Lang et al. 1987). Recently this definition has been criticised by Rohde and Bhalerao (2007), but it remains adequate for applied research. According to Lang et al. (1987) dormancy comprises different processes, which can be classified as

ecodormancy, "... including all cases of dormancy due to one or more unsuitable environmental factors, which are generally nonspecific in their effect on overall plant metabolism". In other words: Low activity forced by unfavourable growth factors.

paradormancy, e.g. "... the inhibition of visible growth of lateral bud meristem by morphogenic factors produced by nearby organs". According to Rohde and Bhalerao (2007) this is presumably the evolutionarily oldest and original form of (endo)dormancy.

endodormancy, "... when the initial reaction leading to growth control is a specific perception of an environmental or endogenous signal within the affected structure alone" (also defined as "rest period").

All three processes can complement and/or overlap and do not exclude active physiological and molecular changes. In winter cold climates endodormancy often is succeeded by ecodormancy. This article deals only with the phenology of *endodormancy*, a process of adaptation to survive seasonal recurring stress periods, such as drought or cold, as far as associated with vegetable production. Reviews on dormancy are presented among others by Lieth 1974; Osborne 1981; Lang et al. 1987; Lang 1989; van der Schoot 1996, on a molecular genetic basis by Rohde and Bhalerao (2007) and on impacts on vegetable production by Krug (2002).

Endodormancy influences many processes in the life cycle of plants, such as seed germination, bud activity, flowering (all not discussed here) and vegetative growth. It generally starts with the increased shifting of assimilates into storing organs, such as rhizomes, tubers, bulbs, roots or/and stems; cessation of cell division; the leaves drop, the metabolism slows down and the plants become more and more insensitive to growth-promoting signals. The horticulturist says "plants retract". Roots frequently stay active. The mechanisms of establishing and maintaining endodormancy are still not understood (Rohde and Bhalerao 2007).

Endodormancy is **induced** by external signals, primarily temperature and day length, but other factors such as light quality, water potential, nutrient status, irradiance and others may also play a role. Day length actions are frequently connected with special temperature ranges, other species such as asparagus react to low and decreasing temperatures only (see modelling paragraph). In some species endogenous rhythms may also control activity. Lang (1989) states "... for plants obviously evolved dormancy mechanism(s) in concert with the overall environment".

The **transition** phase is not a uniform state, but the "depth" of endodormancy changes according to an inclined bell shaped curve: A weak phase is followed by a phase of deep endodormancy and this is followed by a phase of gradual abating. This process, as with vernalisa-

tion, is primarily connected with the completion of temperature demands, corresponding with the climatic cycles of the sites of origin. According to the "Heat Units" of Reaumear (1735), "Chill Units" (CU) are introduced. One CU was defined as one hour at the optimum chilling temperature and non-optimal temperatures were assigned fractional CU values. For many species these temperatures range from the freezing point of the cell sap, simplified about 0 °C, to about 15 °C and are needed for 11–42 d to overcome endodormancy. Once the essential chilling requirement has been accumulated, a certain amount of exposure to warm temperatures is required for morphogenic expression (e.g. bud break, Lang 1989).

In contrast to the gradual transition of endodormancy, controlled by accumulation of CUs, **breaking** of endodormancy can be released by a variety of physical and chemical treatments as a trigger action (for temperature shown by Sun and Nishimoto 1997), such as non-inductive day lengths (LD), non-inductive, especially extreme temperatures, watering, hypoxia and hyperoxia as well as wounding on the one hand and gibberellins, cytokines, ethylene, chlorohydrins on the other hand.

More detailed investigations than on endodormancy of storage organs were carried out with endodormancy of tree buds, at least for endodormancy transition. Here many parallels to vernalisation become obvious, such as a negation of the effect of previously accumulated chilling temperatures (analogous to devernalisation), varying chilling demands during development and similar response surfaces. According to Seeley (1996) and Metzger (1996), however, in contrast to vernalisation the temperature optimum of endodormancy should remain constant. Endodormancy is no inevitable phase in the life cycle of plants and can be avoided or released.

Concerning **vegetable production**, endodormancy is a major factor in controlling the life cycle of plants, such as germination of seeds and tubers (e.g. potatoes), frost hardening and hibernation or drought resistance of crops (e.g. potato, rhubarb, chives, onion, garlic) and activity for forcing (e.g. rhubarb, chives, onion). In asparagus it helps to explain and avoid unwanted reactions, such as low spear growth, due to induction of endodormancy after decreasing soil temperature with cold weather periods during harvesting or after stopping soil heating. Endodormancy is especially important for storage and long-term food supply. A survey on the reaction of vegetable species is presented in Table 13.

Modelling

Due to the complex, dynamic, multifaceted physiological process, the development of mechanistic models is unimaginable until now (Schoot 1996; Seeley 1996). Therefore empirical phenological models have been preferred, focussed on endodormancy of seeds (e.g. Breadford 1996; Hilhorst et al. 1996) and on endodormancy of buds and flowering in forestry and fruit science (e.g. Lang 1989; Seeley 1996). For example a two-step chilling model, incorporating the effects of cycling temperatures on chilling, degradation and conversion of an unstable precursor to an active factor is elaborated by Fishman et al. 1987a, b, cited and discussed by Lang 1989, his Fig. 7.2).

For modelling it would be preferable to subdivide endodormancy into induction, transition and termination, the latter one normally characterises the end of transition. Since the induction phase is believed to pass fluently over into the transition phase, both phases are difficult to demarcate, especially in open fields. Hence the subdivision has been mostly avoided. Moreover, the existing investigations of crop science are performed to elaborate methods for manipulations in commercial practice and to understand causal relationships and not to work out any specifics for modelling. Therefore this review had to be based on data available for the particular species, always excluding seeds.

Vegetable species adapted to winter cold climates:

Rhubarb (*Rheum rhaponticum* x *rhabarbarum*), outlive with a perennial rhizome:

In growth chamber experiments endodormancy was induced by SD (12 h) of ≤4 weeks (the shortest duration tested) with a temperature optimum around 14 °C (Fig. 11). At higher and lower temperatures SD is less effective; in LD no endodormancy was induced. The induction rate and varying influences, such as fluctuating temperatures, were not tested (details in Krug 1991, Fig. 2).

Duration and depth of endodormancy was tested with an early and a late cultivar by successive transfers of field grown rhizomes to a dark room at 20 °C, where the leaves (≥30 cm length) were successively harvested (Fig. 1 in Krug 1991). Accumulated leaf weight dropped from late July to the end of October and then increased up to the last digging in December. This demonstrates a period of weak endodormancy from August to November-De-

Table 13. Induction of endodormancy in vegetable species

Species (organ)	Photoperiod	Temperature (°C)	References
Onion (bulbs)	LD	≥24	i. a. Brewster 1997
Garlic (cloves)	LD	high	Kamenetsky et al. 2004
Rhubarb (rhizome)	SD	8–14–18	i. a. Krug 1991
Asparagus (ferns)	–		Krug 1998, 1999
(corms)		opt. 5–12	
		opt. 15	
Potato (tubers)	SD	<≈20 °C	i. a. Burton 1963

Other vegetables: Tubers of yams (*Dioscorea* ssp.) as well as corms of taro (*Colocasia esculenta*) also show endodormancy; no endodormancy is shown in bulbous thickened roots of sweet potato (*Ipomoea batatas*) (Suttle 1996).

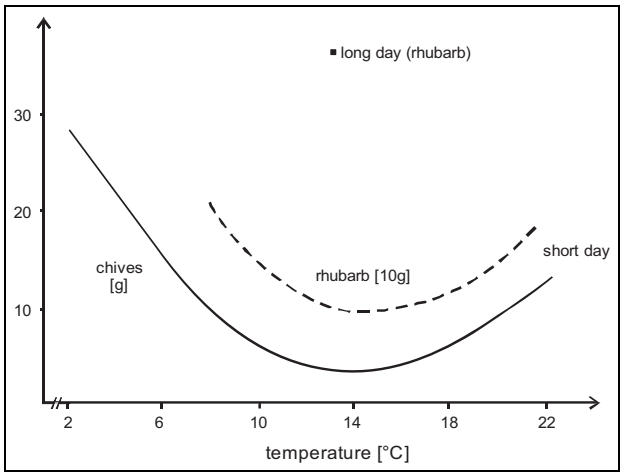


Fig. 11. Endodormancy of rhubarb and chives as a function of temperature and photoperiod. Rhubarb: Cumulative leaf weight (dag plant^{-1}) as means of a 4–8 weeks induction period (KRUG 1991); chives: Leaf fresh weight (g cluster^{-1}) after 20 d at 20–22 °C as means of a 6–8 week induction period (KRUG and FÖLSTER 1976).

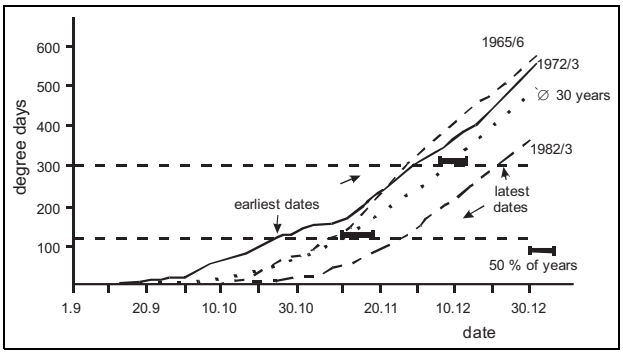


Fig. 12. Simulation of the earliest and latest sprouting ability of rhubarb rhizomes of cultivars with different cold requirements for overcoming endodormancy as a function of mean and extreme cold sums of 30 years in Hannover [°C days with –2 to 10 °C soil temperature at 7 o'clock in 10 cm depth (KRUG 1991)].

cember, including a short period of absolute endodormancy end of October. That the decreasing shooting is not only a consequence of insufficient cold is underlined by the curves of the early cultivar, where no absolute endodormancy is reached. According to LOUGHTON (1965) the increase of leaf weight follows the Temperature Sum Concept (eq. 22–24) with cultivar specific CUs (°C days) in the range of –2 to 10 °C:

$$S = CU = \sum_{1}^{n} T_{(-2 \text{ to } 10°C)} \quad (38)$$

This model allowed to simulate the earliest and latest harvest dates of forcing as a function of soil temperatures (30 years mean) with cultivar specific CU-requirements (Fig. 12).

Chives (*Allium schoenoprasum* L.), outlive with small bulbs, generated annually as side buds:

Endodormancy of chives follows a similar reaction pattern as rhubarb (Fig. 11): Induction in SD with temperatures of about 14 °C with increasing effects up to the duration of 6 weeks. Changing day/night temperatures act approximately like the constant mean of the 24 h-temperatures, but the action was slightly promoted by very high amplitudes within the range of 6–22 °C. In temperatures ≥20 °C plants remained active, but distinct higher activity was observed at ≤6 °C, demonstrating the impact of cold. The critical day length was about 13 h with a stronger reaction with higher light intensity for day lengthening. Dryness retarded activity; older plants showed a more pronounced reaction (KRUG and FÖLSTER 1976).

Field grown chives in Hannover, dug out and forced in 20 °C greenhouses in winter SD, showed via leaf weight that induction of endodormancy started at the end of September, endodormancy was released from November to mid December (FÖLSTER 1967). Diving into water of 42 °C for 1–3 h or a big tank with water of 40 °C at the beginning broke endodormancy fractionally.

Potato (*Solanum tuberosum* L.), tubers with buds are the perenating organ:

Endodormancy is restricted to the tuber buds. After tuber initiation the buds of growing tubers are dormant, but it is not clear whether by paradormancy, caused by the aerial sprouts, or by endodormancy. Endodormancy should finally start when the aerial sprouts die off. It ceases after weeks to months, depending on cultivars and environmental conditions, especially temperature with an optimum of 19–28 °C and enhanced by a cold period. A cold period (1–4 °C), however, is not an indispensable precondition to terminate endodormancy. There are differences in the depth of endodormancy of cultivars. The termination of dormancy and start of "germination", however, is a creeping metabolic and anatomic process and difficult to determine. Conventionally a visible stage, the appearance of germs (about 0.45 mm length) is used as a practical criterion.

Endodormancy is shorter when the mother plants are grown at high temperature (>20 °C) with LD, high nitrogen supply, conditions favouring haulm growth, and with mature tubers compared to immature ones. In the cold season and cold storage, respectively, it is followed by ecodormancy. When the temperature rises, one to several terminal germs sprout, side buds, however, still stay paradormant, especially when stored at high temperature.

At high summer temperatures endodormancy can already be broken during tuber growth, called second growth, with two types, gemmation and chain tuberisation (repeatedly germ growth and tuberisation). After "ripening" "germination" of the terminal bud as well as that of the side buds (paradormancy) are stimulated by low temperature, wounding (e.g. shaking) or several chemicals, such as rindite (7 parts ethylene chlorohydrin, 3 parts ethylene dichloride, 1 part carbon tetrachloride) or by gibberellins. Summaries on dormancy of the potato are elaborated by BURTON 1963, of other tuberous plants by SUTTLE (1996).

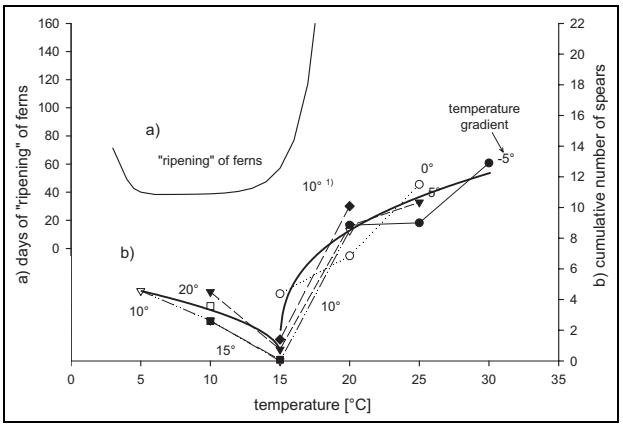


Fig. 13. Response surfaces of asparagus development: (a) fern "ripening" as a function of mean day (24 h) temperature; (b) sprouting ability of asparagus crowns after fern cutting (1) with ferns) related to incubation temperature; the different gradients from growth temperature to incubation temperature are indicated by numbers at symbols (KRUG 1999a.)

Species, presumably originated in the salt steppes of Eastern Europe and the Near East:

Asparagus (*Asparagus officinalis* L.), outlive with a rhizome and storage roots:

Another reaction pattern has been developed by asparagus. Asparagus did not react to day length, but to decreasing temperature (KRUG 1996; 1999a, b, Fig. 13). An intensified drain of carbohydrates into the crowns and therewith yellowing of the ferns was induced by temperatures >2 °C to 15 °C with a wide optimum of 5–12 °C (Fig. 13). Preceding high temperatures (25–30 °C) enforced "ripening", showing that the temperature gradient is also effective.

Endodormancy of the crowns was induced by higher temperatures than for fern "ripening" with a distinct optimum of 15 °C and also enforced by a stronger temperature gradient (KRUG 1996, 1999a). Rest induction by water shortage is less obvious, but comparable effects as with temperature are shown (KRUG 1998).

These relationships, worked out in growth chambers (KRUG 1996, 1999b), are parameterised with the following equations:

a) Fern "ripening": For daily mean temperatures of 5–18 °C an exponential function was used, supplemented for days < 5 °C by a polynomial 4th grade:

$$t_{(5-18°C)} = 38.3 + 0.000392 \times e^{0.718T} \quad (39)$$

$$t_{(3-<5°C)} = 262.85 - 108.37\,T + 18.632\,T^2 - 1.3679\,T^3 + 0.0365\,T^4 \quad (40)$$

b) Crown sprouting: The general trend of sprouting ability, disregarding the special effects of the temperature gradient, is parameterised by a modified 'absolute value function':

$$n = 0.568 + 4.513 \times |T - 15°C|^{0.351} \quad (41)$$

In order to check the general validity of these growth chamber-relationships, fern "ripening" in open fields was simulated by summing up the reciprocal fractional values of days given by the response surface for the respective daily temperature means in the fields until the value of one was reached. Field temperature data were available for 4 years in Hannover, for 6 sites in Japan (friendly let by S. Matsubara, for Israel by E. Pressman, for Taiwan by Luh). Simulated and scored data of the winter cold climates of Germany ($R^2 = 0.79$) and Japan correlated very well, also the absence of endodormancy in tropical areas was calculational confirmed. In the warm subtropics of Taiwan and especially in the subtropical climate of Israel with fall temperatures >15 °C, time of "ripening" was overestimated. Potential causes of these deviations are discussed by KRUG (1999b).

Vegetable species adapted to summer dry climates:

Onion (*Allium cepa* L.), outlive with bulbs:

Bulbing of onion plants is enabled and/or forced by high temperature with LD. The rate of bulbing (RB) is parameterised by BREWSTER (1994, p. 75):

cultivar 'Keepwell':

$$RB = -0.079 + 0.0043 \times P + 0.0027 \times T \quad (42)$$

cultivar 'Hyton':

$$RB = -0.066 + 0.0032 \times P + 0.0018 \times T \quad (43)$$

The same conditions and dryness cause "ripening", that means dying off of leaves and induction of endodormancy of the bulbs (summarised by KRUG 1966; KOMOCHI 1990; BREWSTER 1994, 1997). Thereafter depth of endodormancy abates gradually. The duration of endodormancy varies considerably with the cultivars: When 50 % visible sprouting on moist substrate is used as a criterion between 10 and 156 d (KRUG 1983; BREWSTER 1994), in dry storage from 149–310 d (BREWSTER 1994). Therefore root growth accelerates sprouting, presumably by production of phytohormones. In dry storage endodormancy lasts shortest at temperatures of 9–13 °C, longer at 0 °C and 30 °C; at ≥40 °C the duration of endodormancy decreases (ABDALLA and MANN 1963). Endodormancy can be weakened by defoliation before approaching maturity (inhibitors) and in moist conditions. It can be broken by watering (leaching of abscisic acid?), by high temperature (37 °C, higher temperatures cause damages) in moist peat and/or by wounding (shaking, neck cut).

A broad quantitative description of growth and development of onions and the effect of bulb temperature on endodormancy is published by ABDALLA and MANN (1963), RABINOWITCH and BREWSTER (1990), and BREWSTER (1994). These data can be used for more detailed modelling of growth and development of onions.

Garlic (*Allium sativum* L.), outlive with axillary buds of the interior leaves (cloves):

Despite of differences in morphology, garlic response to the environment is similar to that of onions, but cultivars vary highly in bolting and – mostly poor – seed production. Clove formation is induced by LD (≥ 2 weeks, KAMENETSKY et al. 1990). The growth of the cloves depends on degree and duration of temperature in the dor-

mant state of the mother clove in storage or after planting and – thereafter – is accelerated by warm temperature and LD. Warm temperature and LD also cause maturation; all organs except the cloves die, the cloves have entered endodormancy. Summaries are presented by TAKAGI (1990) and BREWSTER (1994). The rather complicated interaction is exemplified in graphs of BREWSTER (1994, his Fig. 4.11 and for florogenesis by KAMENETSKY et al. 2004) and may be a base for modelling.

Conclusions

Dormancy is a well-known aspect in commercial practise and is dealt with empirically, but in contrast to fruit science, forestry and also to floriculture, in vegetable science it attained little attention. Accordingly the physiological knowledge is insufficient and modelling is still in an early stage. Therefore more investigations are desirable to support management in vegetable production, especially in timing growth and development, in storing and in forcing.

Abbreviations

CU = cold unit (one hour at the chilling temperature, non-optimal temperatures were assigned fractional values), cv = cultivar, LD = long day, n = number of .., P = photoperiod (h), RB = rate of bulbing, S = temperature sum, SD = short day, t = time in days, T = temperature (°C).

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(Due to the restricted pages only the most important literature can be cited)

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