Europ.J.Hort.Sci., **73** (5). S. 189–195, 2008, ISSN 1611-4426. © Verlag Eugen Ulmer KG, Stuttgart

Modelling Production Subsystems at High Abstraction Level – A Review. IV. Development – Photoperiodism – Reproduction and Yield (Focussed on Vegetable Crops)

H. Krug and K. Kahlen
(Institute for Biological Production Systems, Section Vegetable Systems Modelling, Leibniz Universität Hannover, Germany)

Summary

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

Key words. crop production – development – modelling – photoperiodism – reproduction – temperature – yield

Introduction

After discussing modelling crop growth in parts I and II and basics and meaning of the developmental process vernalisation in part III, this chapter will outline photoperiodism and photo-thermoperiodism on reproduction and yield.

Basics of photoperiod responses

Photoperiodism is the reaction of creatures on day length, more precisely on night length. As vernalisation, it is a process of adaptation to the seasonal cycle, especially winter cold and summer drought, and it controls development in many species. In contrast to vernalisation, whose effects are more or less restricted to the conversion from the vegetative to the generative phase and its consequences on dry matter distribution, the photoperiod controls numerous developmental processes: Besides the switch to the generative phase, the initiation and development/growth of other reproduction organs as well as activity/rest periods and therewith fundamental effects on sprout and root growth, including leaf area and with the ontogenetic cycle leaf area duration (LAD). Salisbury (1982) states: Photoperiod influences virtually every aspect of a plants life circle.

The physiology of photoperiodism is reviewed by several authors (e.g. Withrow 1975; Vince-Prue 1975; Zeevaart 1976; Salisbury 1982, compendium of Atherton 1987). Its kinetics and mathematical derivations are especially exposed by Withrow 1959; Thornley 1987; Roberts and Summerfield 1987; Roberts et al. 1997; Thornley and Johnson 2000 and from a molecular genetic and mathematical point of view by Yan and Wallace (1996). Its impacts on vegetable production are outlined by Krug (1967, 2002).

In spite of this multiplicity of actions, the main criterion, especially in botanical investigations, is the conversion of the apex from the vegetative to the generative stage. However, with some species, such as cereals, the initiation of the flower primordia rather than of the inflorescence show a stronger photoperiodic reaction and dominates further development and growth (Krug 1967). Moreover, consequences of flower initiation, such as bolting and leaf growth, may be of dominating interest for crop production purposes.

In other species, especially cultivated ones, vegetative reproduction dominates development and growth. An example is the potato, where – at least when grown from tubers – the initiation of inflorescence primordia is day neutral, flowering is favoured by LD, tuber initiation and tuber growth by SD. In present day cultivars, dry matter partitioning and the developmental cycle are definitely determined by tuber growth. The author recommended classifying photoperiodic reaction types according to the photoperiodic control of the main physiological sink, e.g. the potato is a SDP (Krug 1967).

Photoperiodically effective are "day lengths", compost of the astronomic day length plus parts of the dawn. In experiments with day lengthening by incandescent light, SDP already reacted to minimal 4–100 lx, LDP even to lower irradiances. This corresponds to the fact that the short half of the dawn is photoperiodically effective (Krug 1960). Later experiments, calculating the red/fared relationship, resulted in a shorter prolonging of the astronomic day length by dawn (detailed discussion in Salisbury 1982; according to Rees (1987) 18–90 W m^{-2} (400–800 nm)). The sensitivity to changes in day length is – at least for some tropical SDPs – high, they react to changes down to about 10 min per day.

Traditionally the reaction of plants is characterised by the following criteria: Critical day length, position of the optimum, photoperiodic sensitivity, and – at least con-

cerning SDPs – the duration of the induction period required (Fig. 7). The **critical day length** is the borderline from inductive to non-inductive conditions. The **optimum**, the day length with the strongest induction power or the shortest induction period, may vary, but it is less important. The term **photoperiodic sensitivity** describes the intensity of the reaction from pass-fail reactions (qualitative reaction, strong photoperiodic sensitivity) to alleviated reactions, where mostly no clear critical photoperiod exists; in exchange KRUG (1967) recommended the turning point of the reaction curve – (quantitative reaction, low photoperiodic sensitivity).

With a qualitative reaction the critical day length clearly separates the inductive and the non-inductive range of day lengths. Photoperiodic sensitivity may change with ontogenetic development: Some species/cultivars are insensitive during early developmental phases, termed '**juvenile phase**' (also named pre-inductive phase), which may last a few days after leaf expansion (the receptive organ) to weeks or – for woods – even many years. In general, some authors state an increasing photoperiodic sensitivity (less cycles needed for induction) with aging. ROBERTS and SUMMERFIELD (1987), however, deduce "... there is no change in photoperiod sensitivity per se during the inductive phase, and that its duration is a simple consequence of the number and duration of the photoperiodic cycles which are required to complete the induction stimulus".

In contrast to the traditional view SALISBURY (1982) states: "... the response to photoperiod is either to in-

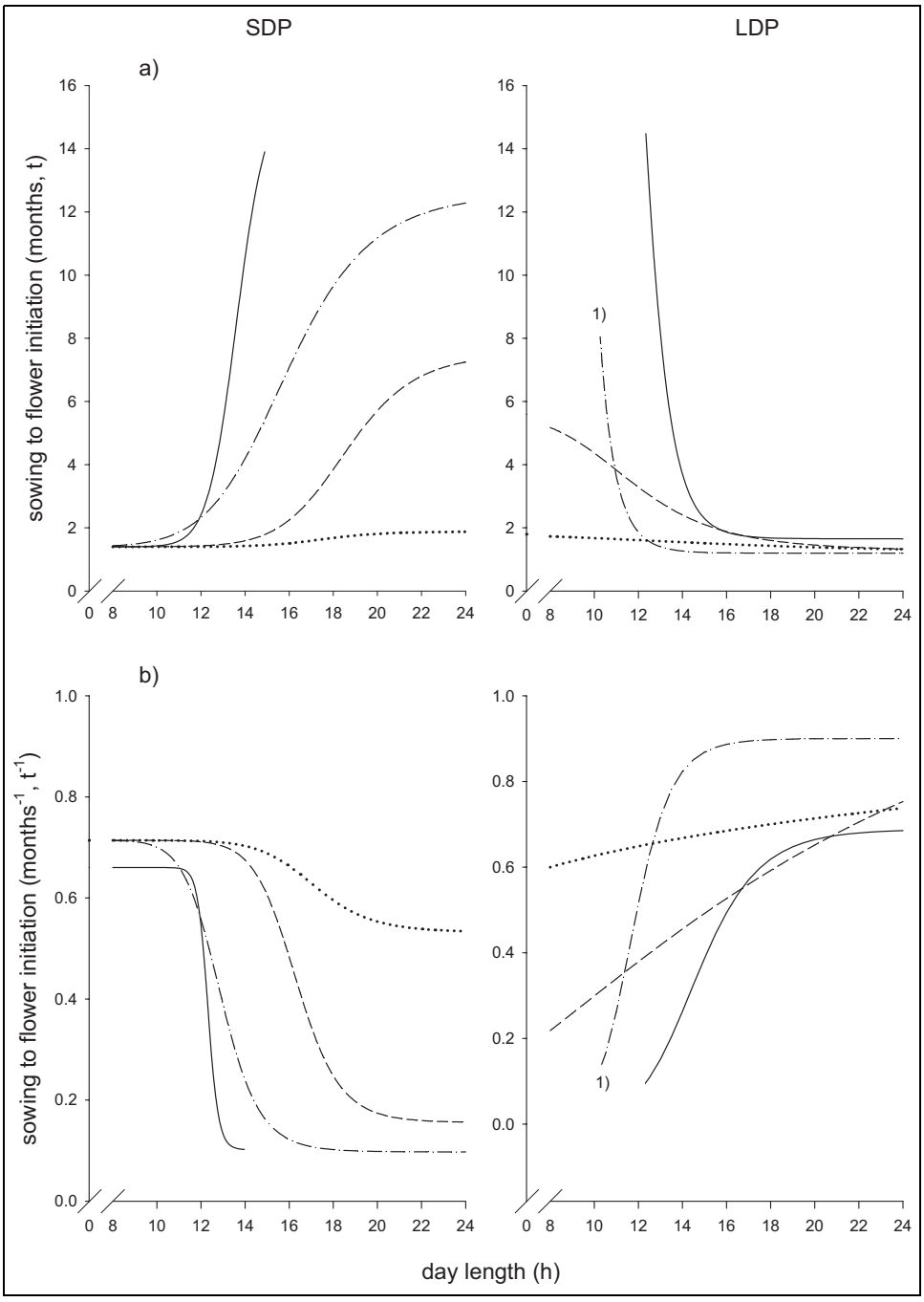


Fig. 7. Schematic presentation of day length reactions of SDPs (rice cultivars) and LDPs (summer cereal cultivars, acc. to BEST 1960 and [1)]*Hyoscyamus niger* L. acc. to LANG and MELCHERS 1943). The hand drawn curves for duration from sowing to flower initiation (t), composed in KRUG 2002, are parameterised a) by a logistic equation, in SD with minimum values of 1,4; b) by logistic equations, in SD with a maximum of 0.714.

creasing day length (type LD) or to decreasing day length (type SD), ...". The important point is that the response is not to some arbitrary long or short days (e.g. 8 or 16 h), but to increasing or decreasing day length ...". This would mean that after solstice in summer SD conditions prevail and in winter LD conditions prevail. This does not agree with conventional experiences, but an influence of an increasing or decreasing day lengths cannot be excluded.

SDs must not necessarily act on the total growth period, a full SD-effect can already be induced by a restricted **number of cycles**. The required number of days for an irreversible induction may vary between species and cultivars from 1 day (e.g. *Xanthium*) to more than 8 weeks. Potato cultivars in medium temperatures (mean approximately 16 °C) required for an irreversible SD-induction between 24 to 40 SD cycles, related to earliness (KRUG 1960). In general, the required induction period is longer with a low photoperiodic sensibility, lower ER (late cultivars), low temperature, lower irradiance during the light period and lower photoperiodic stimulus and it is reduced with older plants. An incomplete induction was followed by a return to "long day behaviour" with after-effects of the short day reaction. With the LDP onion, however, the leaves have to be exposed continuously to LD to start and to complete bulbing (BREWSTER 1997). Brewster assumes that the rate of bulbing depends on current photoperiods and temperatures alone, whose effects have to be added. In some species a post flowering photoperiodic sensitivity with a considerable impact on yielding is demonstrated (e.g. soybeans – KANTOLIC and SLAFER 2005).

These reactions, especially photoperiodic sensitivity, are varied by **temperature** and – to a smaller extent – by other factors, such as irradiance levels, nutrient levels or water potential of the plant. With oats the intensity of the temperature effect varied between the differentiation of inflorescence primordia and flower primordia. In many experiments an immense number of interactions of photoperiod and temperature are proved. Restricting to the phenological reactions, in general low temperature reduces photoperiodic sensitivity and expands the range of photoperiodic effectiveness. That means also that more inductive cycles are required. According to ZEEVAART (1976) photoperiodic restraints may also disappear at high temperature. Drastic examples for the influence of temperature on the photoperiodic behaviour of potato cultivars and their suitability for production in different climates are presented by KRUG (1967, see Fig. 10). Besides the effect of temperature on the photoperiodic behaviour, the fact that temperature interacts with growth rate, always has to be considered.

Four reaction types can be distinguished (for a more detailed classification see SALISBURY 1982):

- SDPs, the development (e.g. initiation of flower buds or reproductive organs such as tubers) is enabled or accelerated by day lengths shorter than the critical day length.
- LDPs, development is enabled or accelerated by day lengths longer than the critical day length.
- LSDPs and SLDPs (e.g. celeriac) are adapted to a special sequence of day lengths – an adaptation to a special course of day lengths.
- Day neutral plants do not react to day length.

Since the species in their ontogenetic cycles adapted to the respective day lengths, different organs of reproduction may react in different manner to the photoperiod. If the vegetation cycle provides enough time, plants develop seeds, the most effective way of reproduction and proliferation; if the remaining time is shorter, plants may reproduce by developing e.g. tubers and, in extreme, survive by one stem tuber only. According to the dominating development process (with most plants flower bud initiation, with others (e.g. potatoes) tuberisation), plant species may be assigned to different classes. For example potatoes (grown from tubers) have to be classified: Inflorescence bud initiation – day neutral; flowering a LDP; tuber initiation, tuber growth, "ripening" and rest period of the tuber buds a SDP. The reaction types of main vegetable species are presented in Table 12 (a general survey on plants is presented by SALISBURY (1982) and for field crops by ROBERTS and SUMMERFIELD (1987). However, cultivars may react differently and this is a decisive character of earliness and yielding (see Fig. 8 and 9).

As already mentioned for vernalisation, YAN and WALLACE (1996) introduced a new concept on the basis of a molecular genetic point of view. As with vernalisation a gene(s) controls a repression of the inherent capability of rapid development to flowering with non-optimal day lengths; the photoperiodic action is always interacting with temperature and a sufficiently low temperature prevents all photoperiod gene activity.

Table 12. Photoperiodic reactions of vegetable species (concerning: f = flower, v = vegetative organ, r = rest period, ( ) widely day neutral; very soft reactions are not recognised (KRUG 2002, table 3.1–1)

Short day		Short → long day		Long day				Day neutral	
okra	f	radish	v→f	onion	f, v, r	fennel	f	water melon	f
sweet potato	f, v	celeriac	f	leek	f	dill	f	eggplant	f
(cucumber)	f	(carrot)	f	garlic	v	radish (nigra)	f	pepper	f
(corn)	f	artichoke	f	chicory	f	red beet	f	cucurbit	f
(bean)	f			black falsify	f	spinach beet	f	tomato	f
potato	v			pea	f	spinach	f	purslane	f
rhubarb	r			broad bean	f	lettuce	f	cauliflower	f
chives	r			turnip	f	endive	f	cabbage	f
soybean	f			chinese cabbage	f	lamps lettuce	f	kohlrabi	f
				potato	f			asparagus	f, r
								broad bean	f

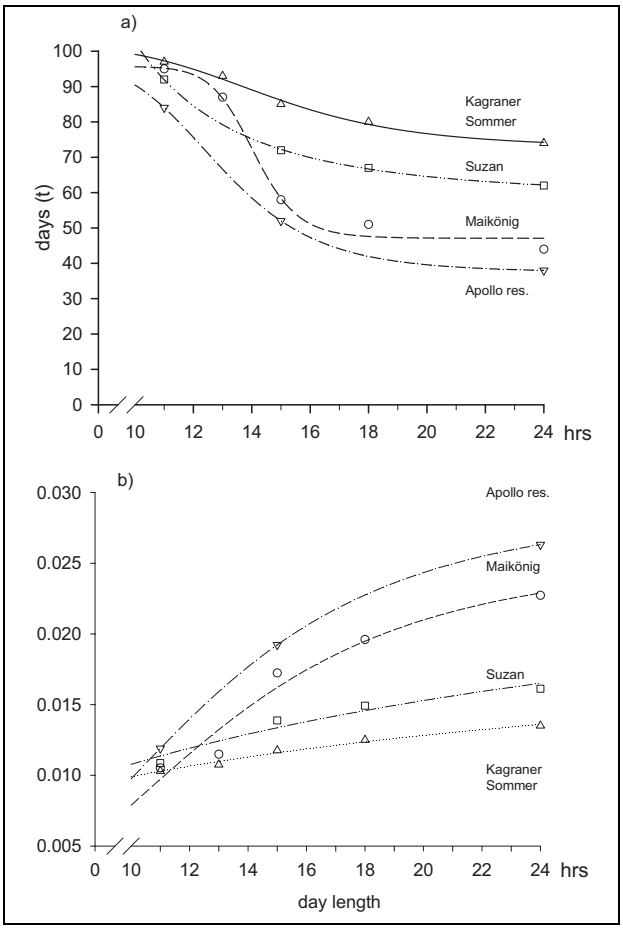


Fig. 8. Photoperiodic reactions of lettuce cultivars of different earliness, demonstrated by duration to 25 cm stem length, a) in days [t (WIEBE and KRUG 1985)], here interpolated by a logistic equation; b) ER (t^{-1}), interpolated by a logistic equation to check linearity.

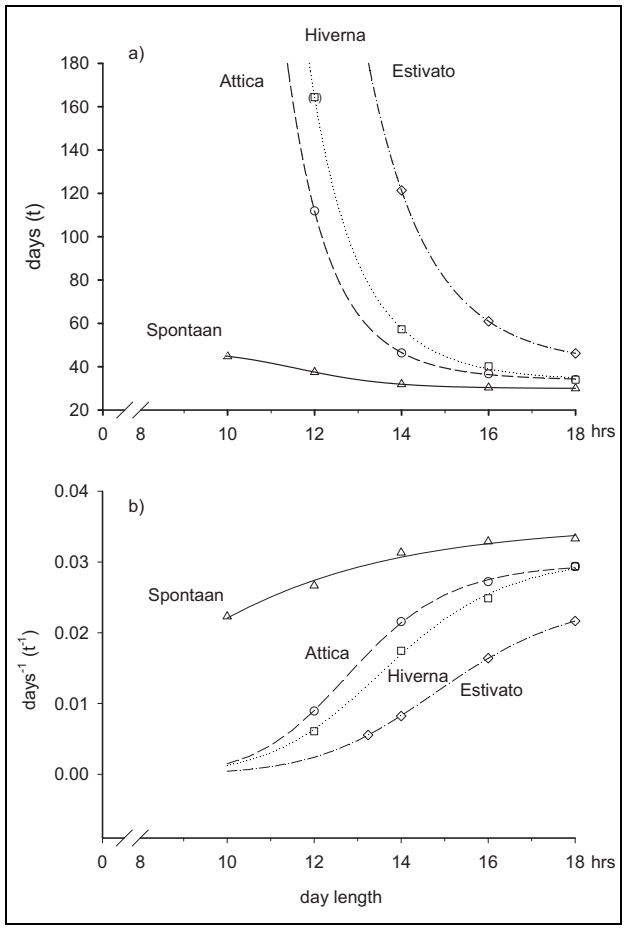


Fig. 9. Photoperiodic reactions of spinach cultivars of different earliness, demonstrated by duration to 5 cm stem length, a) in days [t (WIEBE 1987)], here interpolated by a logistic equation; b) ER (t^{-1}), interpolated by a logistic equation, to check linearity.

Modelling photo(-thermo)periodism, compared to vernalisation, some special aspects have to be considered:

- Besides flower formation photoperiod controls other developmental processes, such as tuberisation, resulting not only in varying ERs and in different growth patterns, caused by dry matter allocation.
- There are separate response surfaces for SDPs (logistic function) and LDPs (inverse logistic function) with strongly varying slopes. These represent very different photoperiodic sensitivity, which is primarily caused by temperature (Fig. 7).
- Duration of required SD-induction usually is not especially considered and the photoperiodic induction rate is difficult to determine.
- Photoperiodic induction by a number of SDs shows some parallelism with the accumulation of cold units in vernalisation; but it is not assumed to work with LDPs.
- Day length does not fluctuate, as temperature does, but follows a constant seasonal cycle, which is only marginally changed by cloudiness or spectral differences (red/far-red relationships).
- Temperature influences the photoperiodic behaviour more pronounced than photoperiod influences the vernalisation process.

Therefore, though many hand-drawn response surfaces and reaction curves, respectively, are elaborated to show the reaction type or ER, the database for modelling crop reactions to day length is smaller than for vernalisation and modelling photoperiodic reactions is rather complex.

When photoperiodism and flower formation (including bolting) is concerned (Fig. 8 and 9), modelling agrees with vernalisation: To sum up the ERs, derived from the response surfaces. Whether the development of vegetative reproductive organs may be modelled with this approach has to be tested. More difficulties will evolve from changing developmental patterns, such as competition between flowering and tuberisation with potatoes (see Fig. 10).

Published approaches to model and parameterise response surfaces of photoperiodic processes are rare and not comprehensive:

WITHROW (1959) gave a review on the kinetics and quantified some light responses:

- response to incident energy for photoperiodic stimuli, threshold value with linear increase to a plateau (Fig. 7 in WITHROW 1959)
- time-phase-requirement, time of a night breaking flash during the night of a SDP (Fig. 13 in WITHROW 1959).

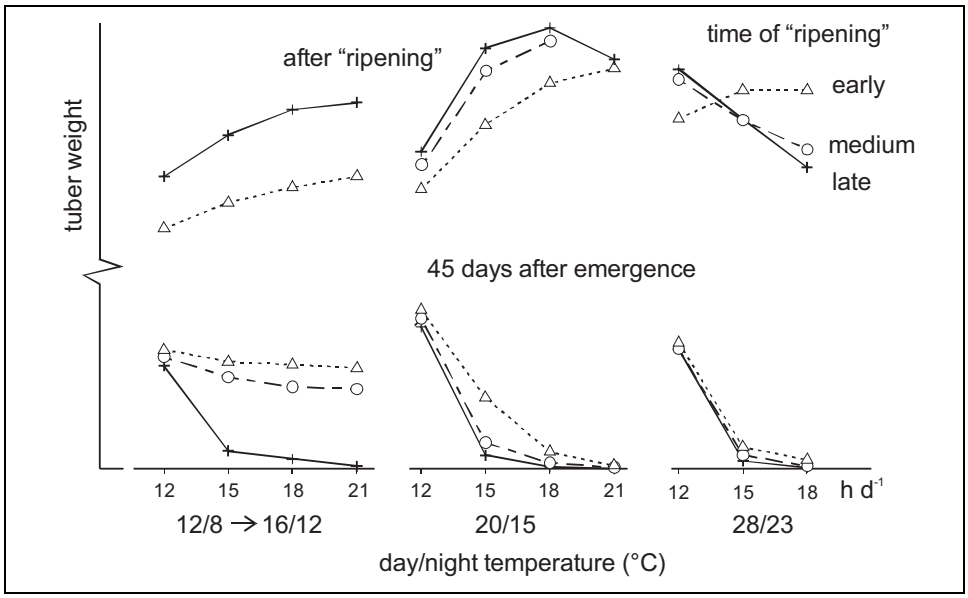


Fig. 10. Tuber weight 45 d after emergence and after "ripening" of early, medium and late potato cultivars, related to photoperiod and temperature [interpolated from several experiments (KRUG 1967)].

In an extensive discourse on modelling flower initiation THORNLEY (1987) discussed three model types and concluded that teleonomic models are rare exceptions; mechanistic approaches suffer from the lack of basic knowledge; empirical models, however, "work very satisfactorily" and have a "distinctly 'mature' appearance".

THORNLEY (1987) integrated photoperiodic reactions into equations for temperature effects. Assuming these factors act linear and are non-interacting, he offered an additive term for flower initiation ($h = d^{-1}$):

$$h = \sum_{j=1}^{n} (a(T_j - T_0)_+ + b(P_j - P_0)_+ + c(J_j - J_0)_+) \quad (31)$$

When the factors interact a multiplicative term is proposed, written in the general form as:

$$h = \sum_{j=1}^{n} f_T(T_j) f_P(P_j) f_J(J_j) \quad (32)$$

where f_T, f_P, and f_J represent functions of temperature T, day length P and radiation receipt J.

According to ANGUS et al. (1981, cited by THORNLEY 1987) a negative exponential function described satisfactorily wheat development as a function of temperature and correspondingly of photoperiod:

$$f_T(T) = 1 - e^{-b(T - T_0)+} \quad (33)$$

ROBERTS and SUMMERFIELD (1987) and ROBERTS et al. (1997) presented a comprehensive analysis and modelling of temperature and photoperiod responses providing a linear relation between the ER and thermal time as well as with photoperiod in the respective ranges. They parameterised for e.g. soybean cultivars, common bean and pea:

- the critical photoperiod and the ceiling photoperiod (SDP at and above which the greatest delay in flowering occurs, LDP maximum delay of flowering);
- the minimum temperature necessary for the expression of photoperiod-sensitivity;
- a triple rate model of development, applicable to a wide range of species;
- the delay of flowering as a function of temperature and photoperiod in non- inductive conditions (short day plants in long days and, *vice versa*, long day plants in short days) by a linear relationship:

$$h = a + b \times T + c \times P \quad (34)$$

- ROBERTS and SUMMERFIELD (1987) and ROBERTS et al. (1997) derived photoperiodic-thermic suitable sites and cultivars, respectively, and they predicted development stages of crops;
- they present the application of photo-thermal coefficients in genetic analysis.

Equation (34) also holds for the bulbing response of onions to temperature and photoperiod (BREWSTER 1997). Figures on the responses ($h = d^{-1}$) of soybean, common bean and pea to photoperiod and temperature are presented by ROBERTS and SUMMERFIELD (1987). Their derivations for such as the SDP soybean and the LDP chickpea, however, exceeded the ranges tested for linearity by far.

YAN and WALLACE (1996) modelled the photoperiod gene control of nodes to flowering (NTF) of pea and sorghum by:

$$NTF = N_b + S_p \times (P - P_{opt})^2 \times (T - T_{bp})^2 \quad (35)$$

This means that "NFT is a measure of the expressed level of photoperiod gene activity" and "delay of flowering by the photoperiod gene(s) occurs only when the plants are under non-optimum photoperiod" and when the temperature is higher than T_{bt}, which allows activity of the photoperiod gene(s).

For the response of days to flowering (DTF) to temperature and photoperiod Yan and Wallace derived an integrated model (for SLDP or LSDP see his equ. 9):

$$DTF = D_b + S_p \times (P - P_{opt})^2 \times (T - T_{bp})^2 + S_t \times (T - T_{opt})^2 \quad (36)$$

or for vernalisation requiring and photoperiodic sensitive plants:

$$DTF = D_b + S_v \times (v - V'_{req})^2 + S_t \times (T - T_{opt})^2 + S_p \times (P - P_{opt})^2 \times (T - T_{bp})^2 \quad (37)$$

Due to its general importance, **linearity** was checked by generalised response surfaces (KRUG 2002) and other experiments. The generalised hand drawn response curves in Fig. 7 are parameterised by logistic and inversed logistic equations, respectively. The calculated curves reflect the free-hand ones rather precisely. The reciprocal curves (t^{-1}) show linearity, however, only in restricted ranges. Approximate linearity is given for SDPs with high and low photoperiodic sensitivity, for medium sensitivity only from 11–15 h and 14–18 h day length, respectively. For LDPs approximate linearity is given for plants with low photoperiodic sensitivity and with higher sensitivity only in the ranges of 10–13 h and 13–18 h.

Linearity was also checked for respective response curves of the LDPs lettuce (WIEBE and KRUG 1985) and spinach (WIEBE 1987). Concerning lettuce (Fig. 8) the measured values for t are nicely interpolated by the logistic equation (2) and t^{-1} shows approximate linearity for cultivars with higher sensitivity only at >15 h day length. The spinach cultivars react accordingly (Fig. 9).

With regard to modelling, this means that in lower latitudes approximate linearity is acceptable (medium sensitive SDP only above14 h). In high latitudes with long days the same is true for low sensitive plants, but for higher photoperiodic sensitivity with restrictions only. For precise modelling, therefore, linearity should be checked and with non-linear relationships the effect of the photoperiod weighted corresponding to the t^{-1} value calculated by a logistic equation.

Basics of **yielding** and modelling yielding are complicated by the plurality of reactions that control dry matter distribution. This is especially true when non-fruits (e.g. tubers) are harvested. There are, however, some investigations giving an insight to photoperiodic behaviour of species/cultivars and to its impacts on yield formation, presenting a first approach for modelling. Regarding species with fruits, data for a preliminary mechanistic approach are presented for peas (KRUG 1997, p.107). For harvesting leaves/heads some basic data are published for the LDPs spinach (WIEBE 1987) and lettuce (KALLOO and KRUG 1980; WIEBE and KRUG 1985). Concerning the critical day length with lettuce as well as with spinach the differences between cultivars were small [spinach cv. 'Hiverna' <12 h, 'Estivato' ≈13 h (WIEBE 1987)] or not significantly identifiable [4 lettuce cultivars (KALLOO and KRUG 1980)]. In either species cultivar-behaviour is mainly influenced by photoperiodic sensitivity, but in a different manner. With spinach the response to day length of early cultivars is weak the one of late ones is stronger. With lettuce the reverse is true. Spinach cultivars differ in LD mainly by their genetic (not photoperiodic influenced) ER, in SD early cultivars bolt earlier, they have a greater ER and a higher GR (leaf weight). PARLEVLIET (1967) and HUYSKES (1971) claimed a causal relationship between the dimensions of ER and GR, but WIEBE (1987) deduces that this correlation should be the consequence of different conditions during selection.

With lettuce the differences of days to 25 cm sprout length between cultivars are small in SD and spread in LD. In SD the cultivars differ mainly in their genetic ER. In LD the late cultivars yield higher due to later bolting (details see original literature and KRUG 2002, pp. 382–384). These reactions are important features of the culivar-characters and show their complexity, but still other factors are involved.

For harvesting bulbs, basic relationships are summarised by BREWSTER (1997), for harvesting tubers by KRUG (1965, 1967). Potato cultivars also differ in their photoperiodic response mainly due to their photoperiodic sensitivity, which is considerably modified by temperature. When early tuber growth acts as criterion for the photoperiodic-thermic response and final tuber weight shows the consequences for the interaction of the photoperiodic-thermic response times assimilation potential, the yielding characters of the potato cultivars are as presented in Fig. 10.

Early tuber growth is accelerated in SD, with about equal growth rates of all cultivars tested at high temperature. At low temperature, however, with early, less with medium cultivars and not with late ones the inhibition of tuber growth is alleviated and top (stem and leaf) growth is enhanced by LD. Concerning tuber growth this means less photoperiodic sensitivity. This response enables early yields in cool LD conditions in moderate climates. Decreased top growth combined with a shorter growth period (lower LAD) causes lower final yields, unless tuber growth is too strongly blocked at very high temperature. It follows that highest yields are formed in cool climates in LD, in hot climates in SD. For a strong LD-inhibition for early cultivars the temperature must be higher than for late cultivars. The medium cultivars react in between early and late cultivars. At medium temperature the turnover with increasing LD inhibition of tuber growth is nicely demonstrated. This means that the photo-thermic controlled balance between top and tuber growth is a decisive factor for yielding and for breeding or for the choice of cultivars has to be adapted to the respective climatic conditions.

Applications in commercial practice

In commercial practice, photoperiodism received not as much attention as vernalisation does. Reasons are the very expensive and cumbersome control of day length, especially in large areas and since it is easier and cheaper to adapt the crops to the respective conditions by the choice of cultivars, of seasons or of sites [e.g. onions (KRUG 1966), potatoes (CAESAR and KRUG 1965)]. This is done primarily empirically.

Potential applications for active day length control in vegetable production are day lengthening during the forcing of chives in greenhouses in hibernal SDs with suboptimal temperatures (FÖLSTER and KRUG 1977); with confinement (product quality) the lengthening of the harvest period in field grown chives in autumn to avoid rest induction; to avoid LD by artificial lightening of LDPs with vegetative yields (e.g. transplants of lettuce).

Conclusions

In photoperiodic-thermic reactions there is an immense diversity in general and between cultivar responses, aggravating modelling. When linearity between develop-

ment or ER and photoperiod is verified, modelling is alleviated by the Factor Sum Approach. But linearity has to be proved. For non-linear relationships exponential functions and especially logistic functions are adequate. They allow weighting photoperiodic or photoperiodic-thermic effects for the Factor-Sum-Approach by multiplication with the fractional values.

The examples presented show the importance of a more detailed physiological analysis to understand and model the many-sided development processes. This applies especially to the influence of temperature and other modifying factors, to the afforded induction period of SDPs (LDPs?, Photoperiodic Rate), when SD crosses over to LD and *vice versa.* Due to the multiplicity of reactions and drastic impacts on the growth pattern a main problem will be to integrate the complex effects into growth models.

Abbreviations

$_+$ subscript on the expression in brackets indicates that terms only contribute if they are positive; a, b, c = coefficients and weighting factors; acc. = according; cv = cultivar; D_b = shortest duration to flowering; DTF = days to flowering; ER = development rate; f = function; GR = growth rate; J = daily radiation receipt; LAD = leaf area duration (integral of leaf area over the disposal time for photosynthesis); LD = long day; LDP = long day plant; LSDP = long-short-day plant; N_b = smallest number of nodes at low temperature; NTF = nodes to flowering; P = day length (photoperiod, in h); P_0 = threshold value of P; P_{opt} = optimal photoperiod; SD = short day; SDP = short day plant; SLDP = short-long-day plant; S_p= sensitivity of plants to the deviation of P from P_{opt}; S_t = sensitivity to deviation of T from T_{opt}; S_v = sensitivity to vernalisation; t = time in days; T = mean temperature of the phase; T_0 = basic temperature; T_{bp} = basic temperature for photoperiod; T_{opt} = optimal temperature; v = days with low temperature treatment to promote rapid plant development; V_{req} = duration (d) of low temperature that is required to cause expression of N_b'.

Acknowledgement

The authors feel very much obliged to Anni Romey for her technical assistance and to Prof. Dr. G. Bünemann for his revision of the authors' English.

References

Angus, J. F., D. H. Mackenzie, R. A. Morton and C.A. Schafer 1981: Phasic development in field crops. II. Thermal and photoperiodic responses of spring wheat. Field Crops Research **4**, 269–283.

Atherton, J. G. 1987: Manipulation of flowering. Butterworth, London.

Best, R. 1960: Photoperiodism in plants as studied by means of response curves. Koninkl. Nederl. Akademie van Wetenschaappen, Amsterdam, Proc. Ser. C, **63**, No. 5, 676–691.

Brewster, J. L. 1997: Onions and garlic. In: Wien, Chr. (ed.): The physiology of vegetable crops. CAB International, Wallingford, UK, 581–619.

Caesar, K. and H. Krug 1965: Zum Einfluß der Tageslichtdauer auf die Ertragsbildung der Kartoffelpflanze (*Solanum tuberosum* L.) in niedrigen Breiten. Eur. Potato J. **8**, 28–32.

Fölster, E. and H. Krug 1977: Influence of the environment on growth and development of chives (*Allium schoenoprasum* L.). II. Breaking the rest period and forcing. Sci. Hort. **7**, 213–224.

Huyskes, J. A. 1971: The importance of photoperiodic response for the breeding of glasshouse spinach. Euphytica **20**, 371–379.

Kalloo, H. and H. Krug 1980: Sortendifferenzierung bei Kopfsalat (*Lactuca sativa* var. *capitata*) – Vorläufige Mitteilung. Gartenbauwissenschaft **45**, 116–120.

Kantolic, A. G. and G. A. Slafer 2005: Reproductive development and yield components in indeterminate soybean as affected by post-flowering photoperiod. Field Crops Research **93**, 212–222.

Krug, H. 1960: Zum photoperiodischen Verhalten einiger Kartoffelsorten. Eur. Potato J. **3**, 47–79 and 107–136.

Krug, H. 1965: Zur Bedeutung der photoperiodisch-thermischen Reaktion der Kartoffelsorten für Züchtung und Anbau. Eur. potato J. **8**, 14–27.

Krug, H. 1966: Physiologische Grundlagen des Anbaus der Zwiebel (*Allium cepa* L.). Gartenbauwissenschaft **31**, 27–49.

Krug, H. 1967: Der Photoperiodismus im Dienste der Ertragsforschung. Angew. Botanik **41**, 255–270.

Krug, H. 1997: Environmental influences on development, growth and yield. In: Wien, Chr. (ed.): The physiology of vegetable crops. Wallingford, UK, 101–180.

Krug, H. 2002: Die Pflanze. In: Krug, H., H. P. Liebig and H. Stützel: Gemüseproduktion. Verlag Eugen Ulmer, Stuttgart, 74–106.

Lang, A. and G. Melchers 1943: Die photoperiodische Reaktion von *Hyoscyamus niger*. Planta **33**, 653–702.

Parlevliet, J. E. 1967: The influence of external factors on the growth and development of spinach cultivars (*Spinacea oleratia* L.). Meded. Landbouwhogeschool, Wageningen, **67**, 2.

Rees, A. R. 1987: Environmental and genetic regulation of photoperiodism – a review. In: Atherton, J. G. (ed.) 1987: Manipulation of flowering. Butterworth, London, 187–203.

Roberts, E. H. and R. J. Summerfield 1987: Measurement and prediction of flowering in annual crops. In: Atherton, J. G. (ed.): Manipulation of flowering. Butterworth, London, 17–49.

Roberts, E. H., R. J. Summerfield, R. H. Ellis, P. Q. Craufuard and T. R. Wheeler 1997: The induction of flowering. In: Wien, Chr. (ed.): The physiology of vegetable crops. CAB International, Wallingford, UK, 101–180.

Salisbury, F. B. 1982: Photoperiodism. Hort. Rev. **4**, 67–105.

Thornley, J. H. M. 1987: Modelling flower initiation. In: Atherton, J. G. (ed.) 1987: Manipulation of flowering. Butterworth, London, 67–79.

Thornley, J. H. M. and I. R. Johnson 2000: Plant and crop modelling. The Blackburn Press, Caldwell, New Jersey.

Vince-Prue, D. 1975: Photoperiodism in plants. McGraw Hill Book Comp. U. K..

Wiebe, H. J. and H. Krug 1985: Einfluß der Tageslänge auf Entwicklung und Wachstum von Kopfsalat (*Lactuca sativa* var. *capitata*). Gartenbauwissenschaft **50**, 202–206.

Wiebe, H. J. 1987: Einfluß der Tageslänge auf Entwicklung, Wachstum und Nitratgehalt von Spinatsorten. Gartenbauwissenschaft **52**,103–108.

Withrow, R. B. 1959: A kinetic analysis of photoperiodism. Reprinted from "Related phenomena in plants and animals". Amer. Assoc. for the Advancement of Science, Washington D.C.

Withrow, D. V. 1975: Photoperiodism in plants. Mc Graw Hill Publ., London.

Yan, W. and D. H. Wallace 1996: A model of photoperiod x temperature interaction effects on plant development. Critical Reviews in Plant Sciences **15**, 63–96.

Zeevaart, J. A. D. 1976: Physiology of flower formation. Ann. Rev. Plant Physiol., **27**, 321–348.

Received February 01, 2008 / Accepted June 19, 2008

Addresses of authors: Helmut Krug and Katrin Kahlen, Institute for Biological Production Systems, Section Vegetable Systems Modelling, Leibniz University Hannover, Herrenhäuserstr. 2, 30419 Hannover, Germany, e-mail: krug@gem.uni-Hannover.de.