Modelling post-emergent hemp phenology (*Cannabis sativa* L.): Theory and evaluation

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Abstract

Temperature and photoperiod can be used to simulate post-emergent hemp (*Cannabis sativa* L.) phenology. With reference to hemp in Italy, our main objective was to model field crops grown under a range of temperature and day length regimes. Dates of emergence and 50% of flowering were collected at Cadriano (Bologna) from serially sown field experiments (1996–1999, 2003–2005) on five cultivars: Carmagnola (late maturity), Felina 34 (medium maturity), Fibranova (late maturity), Futura (medium-late maturity), and Tiborszallasi (medium-late maturity). The database of phenological records was segregated into calibration and validation subsets. A phenology model was developed which utilises the beta function for response to hourly air temperature, and a switch-off function for response to day length. The life cycle of hemp from emergence to 50% of flowering was defined in terms of physiological development days (chronological days at the optimum photoperiod and temperature) and considered in three phases: juvenile phase (BVP), photo-sensitive phase (PIP), flower development phase (FDP). Critical temperatures (T_b, base; T_o, optimum, T_c, ceiling), which did not vary widely across phases and cultivars, were estimated as common values: $T_b = 1.9\,°C$ for BVP and $11.3\,°C$ for the other phases, $T_o = 26.4\,°C$ and $T_c = 40.0\,°C$ for all phases. Other parameters, i.e. day length of half-maximum development rate at PIP, and physiological development days for FDP, were also estimated as common values for all cultivars. Different genotypes were mainly characterised for the sensitivity to photoperiod (shape parameter n) and BVP length. With $n \sim 50$, Felina 34 and Futura are regarded as low sensitive cultivars. Tiborszallasi was estimated as the highest sensitive cultivar (n close to 70), whereas Carmagnola and Fibranova showed an intermediate sensitivity ($n \sim 62$). Felina 34 also differentiated for its relatively short BVP length at optimum conditions, i.e. ~ 13 days; duration of about 20 days was the estimate for the other cultivars.

Model performance against calibration dataset was good (percent relative root mean square in the range ~ 6–20%), and comparison against independent data also confirmed the general applicability of this model. Owing to the importance of flowering date in hemp management techniques, these results can be used in decision support for hemp production though further evaluation of the model under a variety of latitudes is required.
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1. Introduction

Hemp (*Cannabis sativa* L.) is traditionally grown for its long bast fibre but can also be grown for its short fibre content (Karus, 2002) and biomass energy (Biewinga and van der Bijl, 1996). For each of uses, flowering time is a determinant factor of the fibre or biomass yield, in terms of both quantity (Van der Werf et al., 1994, 1996; Struik et al., 2000) and quality (Keller et al., 2001; Mediavilla et al., 2001; Amaducci et al., 2005a). Early flowering has been recognised as one of the major factors limiting yield because it generally stops stalk growth (Meijer et al., 1995). This was observed, for instance, when hemp cultivars adapted to Northern European conditions were cultivated in Southern European sites (Crescini, 1951), or when cultivars from the Northern hemisphere were grown in South Africa (Dippenaar et al., 1996) and Australia (Ditchfield et al., 1997). Crop failures because of very early flowering, described as "pre-flowering" are also documented for sites like Southern Italy where hemp was once traditionally grown (Barbieri, 1952).

Although Garner and Allard (1920) with their studies on soybean are given the credit for discovering the influence of photoperiod on plant development, Tournois (1912) was the first to report on experiments that demonstrated the photoperiodic induction of flowering in hemp and Japanese hop (*Humulus*

japonicus L.), two species belonging to the family *Cannabaceae*. Further studies confirmed the short-day nature of hemp and investigated the effect of day length on sex expression (McPhee, 1924; Schaffner, 1926, 1928, 1931; Crescini, 1930a,b; Heslop-Harrison and Heslop-Harrison, 1969) and leaf shape changes (Helsop-Harrison and Helsop-Harrison, 1958). Extensive literature highlighting the joint role of photoperiod and temperature in modulating development in both short-day and long-day plants has since followed, and many models simulating plant phenology have been based on these two factors (Summerfield and Roberts, 1987; Yan and Wallace, 1998).

Based on the general scheme from Major (1980) and the criteria of Carberry et al. (1992) for kenaf (*Hybiscus cannabinus* L.), a short-day plant similar to hemp, Lisson et al. (2000a,b) modelled the response of hemp to photoperiod and temperature. In addition, the same approach (but this time including the modelling of leaf appearance, expansion and senescence, Lisson et al., 2000c) was introduced into the daily time-step simulation framework of the Agricultural Production Systems sIMulator (APSIM) model (McCown et al., 1996), referred to as APSIM-Hemp (Lisson et al., 2000d). Air temperature was the primary factor governing the duration from sowing to emergence, where the rate of development increases linearly with temperature between a base temperature and a cut-off temperature (Lisson et al., 2000a). The key parameters describing the photoperiodic response were required to simulate post-emergence phenology (Lisson et al., 2000b). The vegetative phase of development from emergence to floral initiation was divided into a temperature-dependent basic vegetative phase (BVP) and a day length-dependent photoperiod induced phase (PIP). BVP is equivalent to the early phase of development and is also known as the "juvenile" phase (Thomas and Vince-Prue, 1984) or "pre-inductive" phase (Roberts et al., 1986). The duration of PIP was assumed to be instantaneous for optimal day length conditions, that is day length lower or equal to the limit referred to as the "maximum optimal photoperiod" (Major, 1980) or "critical photoperiod" (Hadley et al., 1984). A day length longer than the maximum optimum value (until a critical photoperiod above which the plant no longer flowers) increases the duration of PIP. The duration from floral initiation to appearance of the first flower was referred to by the authors as the flower development phase (FDP).

The research carried out by Lisson et al. (2000a,b) to develop the aforementioned phenology model was based on one growth chamber experiment and limited to two cultivars (Kompolti and Futura, 77) and was validated against field data from a limited range of environments (Lisson et al., 2000d). Prior to the cited works of Lisson et al. (2000a,b,c,d), and in order to improve the understanding on the environmental factors governing flowering time in hemp (and, more in general, its phenology) field investigations where different cultivars were grown under a variety of conditions were established (Amaducci, 1998; Amaducci et al., 2002a,b). Detailed and systematic information on the effects of air temperature on the phenological development of hemp is needed to be able to understand its widespread distribution-growth capacity at different latitudes. The same information is essential for the development of a mechanistic model. To provide biological information for modelling purposes, the objectives of this research were to characterise the phenological development of post-emergent hemp in response to variations in temperature and photoperiod by determining the duration of the juvenile phase and the effects of temperature and photoperiod on reproductive development. The amount of field data collected under various air temperature–photoperiod combinations offered a unique opportunity to identify key parameters and relationships to build a model of hemp phenology, taking multiple environmental interactions into account.

We present a novel phenological model for post-emergent hemp which includes response functions for the effect of temperature and photoperiod on development rate. Specific objectives of this research were: (1) to determine cardinal temperatures and photoperiod for hemp development, (2) to determine which parameters characterise different responses in different cultivars, and (3) to evaluate model estimates against observations of flowering time.

2. Materials and methods

2.1. Model description

A model of post-emergence hemp phenology was developed, which makes use of daily length and hourly air temperature. The model implements concepts derived from Carberry et al. (1992) and Lisson et al. (2000a,b). Post-emergent plant development is divided into three phases: (1) juvenile phase (BVP), (2) photosensitive phase (PIP), (3) flowering development phase (FDP, from the end of PIP to 50% of opened flowers). The length of phases 1 and 3 is expressed as thermal time accumulation. A photoperiod × air temperature interaction model is used to simulate the length of phase 2. Non-linear relationships assuring gradual transition over time were used to describe plant development. The non-linear beta function (initial quasi-expolinear response reaching an optimum after which the response declines more or less steeply) described developmental response to air temperature in diverse crops, including cassava, maize, rice and sorghum (Yan and Hunt, 1999; Yin et al., 1995). This function was used to represent the thermal factor (fT) in the air temperature range of viable development, (x indicating phenological phases from the first, BVP, to the third, FDP):

$$\mathrm{fT}(x)\,[x = 1, 2, 3]$$

$$= \begin{vmatrix} 0 & T \leq T_b,\ T \geq T_c \\ \dfrac{T_c - T}{T_c - T_o}\left(\dfrac{T - T_b}{T_o - T_b}\right)^{(T_o - T_b)/(T_c - T_o)} & T_b < T < T_c \end{vmatrix} \tag{1}$$

where T (°C) is the mean hourly air temperature, T_b (°C) the base air temperature for development, T_c (°C) the ceiling air temperature at which development ceases and T_o (°C) is the optimal air temperature at which the maximum rate of development occurs.

The response to day length was quantified by a photoperiodic factor (fP), modelled by a sigmoid, switch-off function

(Thornley and Johnson, 1990):

$$fP = \frac{K^n}{K^n + P^n} \qquad (2)$$

where P (h) is the day length, K (h) and n are the parameters setting the switch-off point (day length giving $fP = 0.5$) and the sharpness (shape parameter) of the response, respectively. Higher values of n accelerate the developmental rate for conditions of low photoperiod, whereas lower values make the photoperiodic response faster with long days.

Developmental rates, $R_{dev}(x)$ (d^{-1}), in the range from 0 (no development) to 1 (maximum developmental rate), are calculated during the three phases ($x = 1, 2, 3$ to indicate BVP, PIP and FDP, respectively) as follows:

$$R_{dev}(x) = \begin{vmatrix} \dfrac{fT(1)}{D_1} & x = 1 \\[2mm] \dfrac{fT(2)fP}{D_2} & x = 2 \\[2mm] \dfrac{fT(3)}{D_3} & x = 3 \end{vmatrix} \qquad (3)$$

where D_x (physiological developmental days) indicates the number of days needed to complete the respective phenological phase under optimal climatic conditions (Gayler et al., 2002), which is the inverse of the maximum rate of development for each phase.

For the conditions introduced (same values of T_b assigned to PIP and FDP, Eq. (2)), it results $fT(2) = fT(3)$. In Eq. (3), the factors fT (Eq. (1)) and fP (Eq. (2)) vary in the range between 0 (no development) and 1 (maximum development). $R_{dev}(x)$ has an hourly time step. A stage terminates as the sum of hourly $R_{dev}(x)$ reaches 1 and, then, the next stage begins. The model was developed using the visual programming environment Simulink (Mathworks) and, for the integration computation, the Eulero scheme was adopted.

2.2. Database generation

Phenological datasets were collected in the years 1996–1999 and 2003–2005 from separate field trials (Table 1), conducted as part of both national (Ranalli, 2002) and international (Cromack et al., 1997; Amaducci, 2003) studies. All trials were carried out at Cadriano Experimental station of the University of Bologna, Italy (latitude: 44°33′ North; longitude: 11°21′ East; altitude: 32 m a.s.l.).

The model was developed and tested using meteorological and phenological data from five hemp cultivars of different origin, sexual type and maturity group (Table 2). Genotypes listed in Table 2 were grouped according to their relative flowering date as it was observed in field trials carried out in Cadriano (Amaducci, 1998; Amaducci et al., 1998, unpublished data).

Table 1
Field trials carried out at Cadriano (BO, Italy) and used for the modelling of hemp phenology

Years	Cultivars	Sowing dates	Treatments
1996	Felina 34	27/4	N–D
	Futura 77	27/4	N–D
	Carmagnola	9/4	N–D
1997	Carmagnola	29/4	Var
	Felina 34	29/4	Var
	Fibranova	29/4	Var
	Futura 77	29/4 (28/3–18/4–6/5–4/6–24/6–16/7)	Var–M–N–D
1998	Carmagnola	2/4 (2, 9, 23, 30/3–6, 14, 20/4–11/5–4/6–30/6–4/8)	Var–M
	Felina 34	2/4 (2, 9, 23, 30/3–6, 14, 20/4–11/5–4/6–30/6–4/8)	Var–M
	Fibranova	2/4 (2, 9, 23, 30/3–6, 14, 20/4–11/5–4/6–30/6–4/8)	Var–M
	Futura 77	2/4 (2, 9, 23, 30/3–6, 14, 20/4–11/5–4/6–30/6–4/8)	Var–M–D
1999	Carmagnola	26/3–7/4	Var–D
	Felina 34	26/3	Var
	Fibranova	26/3	Var
	Futura 77	26/3	Var–D
2003	Carmagnola	16/4 (29/4–12/5–28/5–1/7)	Var–M
	Felina 34	16/4 (29/4–12/5–28/5–1/7)	Var–M
	Fibranova	16/4	Var
	Futura 75	(16/4 29/4–12/5–28/5–1/7)	Var–M
	Tiborszallasi	(16/4 29/4–12/5–28/5–1/7)	Var–M
2004	Felina 34	(23/3–1/4–6/4–23/4–7/5–9/6–20/7)	Var–M
	Fibranova	6/4 (23/3–1/4–6/4–23/4–7/5–9/6–20/7)	Var–M
	Futura 75	(23/3–1/4–6/4–23/4–7/5–9/6–20/7)	Var–D–M
	Tiborszallasi	(23/3–1/4–6/4–23/4–7/5–9/6–20/7)	Var–D–M
2005	Futura 75	6/4–22/4–10/5	M–D
	Carmagnola	6/4–22/4–10/5	M
	Fibranova	6/4–22/4–10/5	M
	Tiborszallasi	6/4–22/4–10/5	M

Var, varietal trials; M, multiple-sowing trials; D, sowing density trials; N, nitrogen fertilisation trials.

Table 2
Origin, sexual type and maturity group of the hemp cultivars used in this study

Cultivar	Origin	Sexual type	Maturity group
Carmagnola	Italy	Dioecious	Late
Felina 34	France	Monoecious	Medium
Fibranova	Italy	Dioecious	Late
Futura	France	Monoecious	Medium-late
Tiborszallasi	Hungary	Dioecious	Medium-late

The relative flowering date of French cultivars was also confirmed by the Fédération Nationale des Producteurs de Chanvre (Béhérec, personal communication).

The crops were planted both before and after the summer solstice, thus encountering either increasing or decreasing day lengths. Sources of variation (i.e. plant density, nitrogen supply) were randomised in a split–split plot design. The minimum sub-sub plot size was 50 m^2. Details on the field trials are provided in Amaducci (1998) and Amaducci et al. (2002a,b, 2005a,b). De Meijer (1995) reviews the origin, breeding history, registration, availability and agronomic features of the cultivars used in this study.

Air temperature data were used as a proxy of plant temperature. Daily values of maximum and minimum air temperatures were supplied by a weather station positioned in the vicinity of the field trials. Hourly air temperature values were registered at the same station for the years 1997–1999. Hourly measured data were used to calibrate the model of Campbell (1985) for estimation of hourly air temperatures, in turn, used to estimate the missing hourly values. Based on solar geometry, the latitude of the site and the day of the year were used to calculate day length (Spitters et al., 1986).

The observed dates of planting, emergence and flowering were retrieved from the full database and used for modelling purposes. Count of flowering plants was carried out on 20–50 plants per plot on a weekly basis with observational resolution increasing (up to every 2 days) near and during flowering. For both monoecious and dioecious genotypes a plant was recorded as flowering when male flower and/or stigma became visible during the field inspections. Because an irregular dynamic between beginning and end of flowering was observed across different trials (up to 60 days from the appearance of the first to the last flower), the date when 50% of plants had visible flowers was selected as the temporal reference point for all flowering observations. Phenology calculations based on 50% of flowering are not new with regard to hemp (Van der Werf et al., 1994) or other crops (e.g. Carberry et al., 1992; Ntare et al., 1998). The observed variation of plant emergence date was much more limited (about 7 days from the emergence of the first to the last seedling), and thus a temporal reference point in each plot was approximated by the average emergence date.

2.3. Model evaluation

The database of phenological observations was split into two datasets (I, II). To determine model parameters, a calibration dataset (dataset I) was created from the trials conducted over the years 1996–2004. Dataset II (validation dataset) contained the remaining data (trials of the year 2005) that were used for validating the model. This choice implies robust calibration, performed over several years of data and leading to results that are expected to be rather insensitive to minor changes in the experimental conditions. Durations of juvenile and photo-inductive phases (vegetative period) were estimated by the calibration algorithm without comparing the estimates against the boundary (not determined experimentally) between one stage (basic vegetative phase) and the next (photo-inductive phase).

After preliminary runs, some simplifications were incorporated into the parameterisation strategy for optimisation of the model parameters. One simplification was to estimate a single value for common parameters: (1) in Eq. (1), common values of T_o and T_c were estimated for all the phases, (2) in the same Eq. (1), PIP and FDP were represented by the same base temperature. A second form of simplification was not to consider cultivar-specific parameterisation for thermal parameters. A common value of the parameter D_3 (Eq. (3)) identifying the physiological developmental days for the FDP was also estimated for all cultivars. Moreover, in Eq. (3), parameter D_2 was set equal to 1 day for all cultivars (regarded as the instantaneous PIP occurring the day after BVP completion under optimum conditions of air temperature and day length).

With the exception of D_2, the model parameters were derived via calibration against observed dates from dataset I, by using the Gauss–Newton algorithm that minimises the square error of estimation (routine *lsqnonlin* of MATLAB®, http://www.mathworks.com). The 95% C confidence bounds for fitted coefficients were computed with the MATLAB® function *nlparci*, which uses the formula:

$$C = b \pm t\sqrt{S} \qquad (4)$$

where b is the array of the coefficients produced by the fit, t the inverse of Student's t cumulative distribution function at 0.95 probability, and S is a vector of the diagonal elements from the covariance matrix of the coefficient estimates. Standard error associated to each optimised parameter was estimated as a square root of S using $t = 2$ as an approximation of the inverse Student's t-distribution.

The data included in the calibration set had a minimum of 13 observed dates across 2 or more years of trials: Carmagnola, 16 dates, 4 years; Felina 34, 23 dates, 6 years, Fibranova, 27 dates, 5 years; Futura, 35 dates, 6 years; Tiborszallasi, 13 dates, 2 years.

The agreement between the model outputs and field observations was evaluated by the inspection of time series (durations of phases between events). On the calibration dataset, further evaluation was performed via elementary statistics (mean, standard error, simple deviation) and the following performance indices: percent relative root mean square error, RRMSE (Eq. (5)); modelling efficiency, EF (Eq. (6)); coefficient of residual mass, CRM (Eq. (7)) (Loague and Green, 1991):

$$RRMSE = \sqrt{\frac{\sum_{i=1}^{N}(E_i - O_i)^2}{N}} \frac{100}{\bar{O}} \qquad (5)$$

$$EF = 1 - \frac{\sum_{i=1}^{N}(E_i - O_i)^2}{\sum_{i=1}^{N}(O_i - \bar{O})^2} \quad (6)$$

$$CRM = \frac{\sum_{i=1}^{N} O_i - \sum_{i=1}^{N} E_i}{\sum_{i=1}^{N} O_i} \quad (7)$$

where E is the estimated value, O the observed value, $\bar{O}$ the mean of the observed values, i the ith E/O pair, and n is the number of E/M pairs. RRMSE ranges from 0 (best) to positive infinity. EF can give either positive or negative values, 1 being the upper limit, while negative infinity is the theoretical lower boundary. Negative values of EF indicate that the model introduces more ambiguity than that introduced by simply using the mean value of the observations as an estimator. CRM can be either positive (under-estimation) or negative (over-estimation), 0 being the optimal value. Dedicated libraries provided with the tool IRENE_DLL (Fila et al., 2003) were used for computing these performance indices.

A sensitivity analysis was performed to assess the influence of each model parameter on the simulation of 50% of flowering. Simulation runs were performed changing parameter values in small amounts over a wide range (greater than $\theta \pm 3$ standard error, where θ is the estimated parameter value), and comparisons were made to actual data from each trial. Mean residual square error (MSE) was computed to quantify the effect of parameter variation on the output:

$$MSE = \frac{\sum_{i=1}^{N}(E_i - O_i)^2}{N} \quad (8)$$

3. Results

3.1. Air temperature and day length conditions

This study used air temperature records and photoperiod estimations from different years (1996–1999 and 2003–2005). Planting conditions varied widely, ranging from low air temperatures (early March) to high air temperatures (July–August). On average, the air temperature conditions at the site remained nearly unchanged across years. The growing-season distributions of daily mean air temperature are shown in Fig. 1. Peaks of mean air temperature above $30\,^{\circ}C$ were observed in 1998 and 2003. An early season frost is certainly a possibility at the site, but mean air temperatures below $0\,^{\circ}C$ were registered only in 2005 before sowing time (beginning of March). The crops encountered different day length patterns, with day length increasing from about 11 h in March to the peak of 15.2 h achieved at summer solstice.

3.2. Model parameterisation

Parameterisation towards air temperature and photoperiod is reported in Table 3. Some discrimination among cultivars is possible, based on the BVP duration under optimum conditions (parameter D_1). The greatest value of D_1 was found for cultivar Fibranova ($\sim$24 days) and the lowest value was
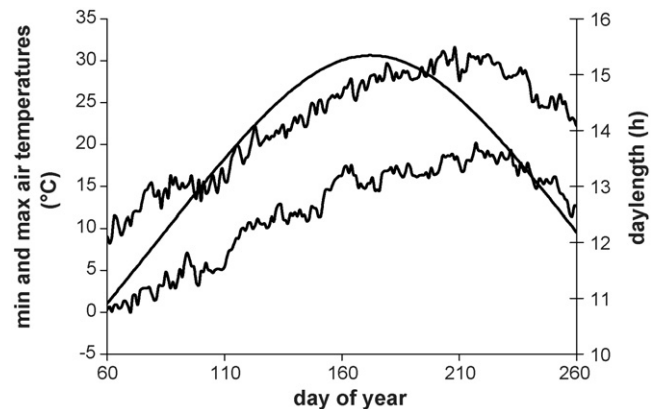

Fig. 1. Daily mean air temperature registered and day length calculated at Cadriano (Italy) during the hemp growing seasons. Air temperature patterns are reported for the different years studied (1996–1999 and 2003–2005).

found for cultivar Felina 34 ($\sim$13 days). Differences among cultivars are also quantified by the shape parameter (n) of the photo-inductive phase. Cultivar Tiborszallasi was estimated to be the most sensitive to sub-optimal day lengths ($n = 66.7$), whilst Carmagnola and Fibranova were characterised by an intermediate sensitivity ($n \sim 62$), and Felina 34 and Futura were the least sensitive ($n \sim 50$). Fig. 2 displays the photoperiodic response of the five cultivars for a range of day lengths.

Table 3
Estimated phenological parameters and standard errors (ND: not determined)

Cultivar	Basic vegetative phase			
	T_b	T_o	T_c	D_1
Carmagnola				23.3 ± 0.7
Felina 34				13.2 ± 0.4
Fibranova	1.9 ± 0.4	26.4 ± 0.1	40.0 ± 0.2	23.6 ± 0.6
Futura				19.7 ± 0.3
Tiborszallasi				18.5 ± 1.0

Cultivar	Photo-inductive phase (thermal parameters as for the flowering development phase)		
	K	n	D_2[a]
Carmagnola		62.0 ± 0.6	1
Felina 34		47.0 ± 0.7	1
Fibranova	$14.1 \pm \sim 0.0$	61.9 ± 0.8	1
Futura		52.1 ± 0.4	1
Tiborszallasi		$66.7 \pm ND$	1

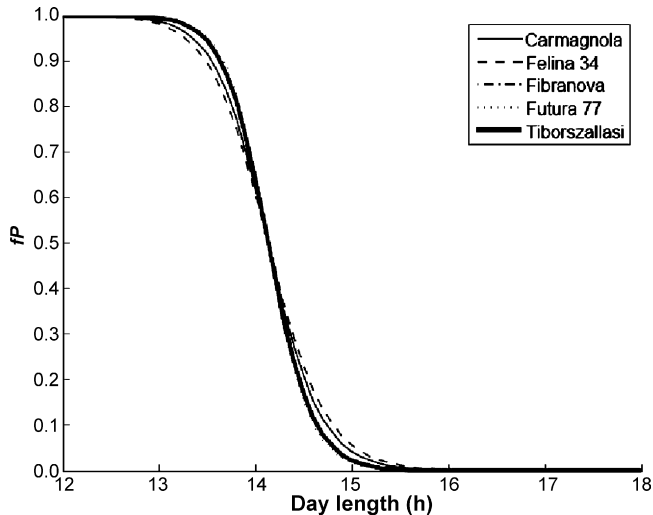| Cultivar	Flowering development phase			
	T_b	T_o	T_c	D_3
Carmagnola				
Felina 34				
Fibranova	11.3 ± 0.3	26.4 ± 0.1	40.0 ± 0.2	4.7 ± 0.5
Futura				
Tiborszallasi				

See text for explanation.
[a] Parameter set constant to 1.

Fig. 2. Photoperiodic factor (fP) estimated for five cultivars as a function of day length.

3.3. Observed dates and modelled phases

Flowering observations from multi-year, serially sown field experiments provided dates of first flower, 50% of flowering and last flower. For each cultivar, the flowering pattern is summarised in Fig. 3 (1996–2004, calibration dataset) and Fig. 4 (2005, validation dataset), together with the phase lengths estimated by the model. In all cases, a wide range in days and spread of flowering dates are apparent. The observed durations from emergence to 50% of flowering varied as much as three- to seven-fold. Durations for Felina 34 ranged from 11 to 83 days. The range in days between emergence and 50% flowering was wider for the other cultivars, for example from 18 to 131 days for Carmagnola. For this cultivar, crops sown in March–June flowered at nearly the same time in late July–early August, but flowering was delayed until September when the crop was sown in July (the latest sowing date of 1998, Fig. 3). A similar response was observed with Tiborszallasi and Fibranova. Felina 34 and Futura were the most heterogeneous in the flowering time. Flowering dates of Felina 34 indicate that this cultivar flowered earlier when planting was earlier, and vice versa. In Futura flowering times were not obviously related to planting date.

The agreement between estimated and actual days from emergence to 50% of flowering is given in Table 4 (calibration data set). Modelling efficiency was generally high (EF > 0.6), together with a good balance between over- and under-estimates

Table 5
Mean estimated thermal time (°C d) and days for completion of each phase in different cultivars (minimum and maximum thermal requirements are in brackets)

Cultivar	BVP	PIP	FDP
Estimated degree-days (°C d)			
Carmagnola	605 (596–615)	1058 (23–1369)	116 (102–124)
Felina 34	341 (329–350)	321 (16–897)	114 (101–124)
Fibranova	612 (600–622)	999 (18–1398)	113 (103–123)
Futura	510 (498–518)	751 (25–1154)	113 (103–125)
Tiborszallasi	480 (470–489)	1051 (34–1528)	114 (102–124)
Estimated days			
Carmagnola	37 (27–53)	51 (2–59)	6 (5–9)
Felina 34	24 (15–36)	18 (2–45)	7 (5–13)
Fibranova	36 (27–53)	48 (1–68)	6 (5–8)
Futura	32 (22–48)	39 (2–56)	6 (5–10)
Tiborszallasi	27 (21–38)	51 (2–73)	6 (5–6)

(CRM ∼ 0). The relatively high variability observed with Felina 34 (RRMSE > 20%) corresponds to some discrepant flowering dates estimated in 1998 and 2004 (Fig. 3). Fig. 4 shows a reasonable match between estimated and observed dates from the validation dataset, but over-estimations were observed with Futura (33 days with the earliest sowing date) and Tiborszallasi (24 days with the latest sowing date).

The thermal requirements computed with the beta function (Eq. (1)) indicate a limited variability in those phases for which duration is only affected by air temperature (Table 5). In number of days, the estimated average duration of BVP was the lowest with Felina 34 (24 days) and the longest with Carmagnola (37 days). Cultivars did not differ in duration of FDP (6–7 days estimated on average for each cultivar). For the PIP interval, a notably short duration (18 days on average) was found for cultivar Felina 34; on average, it was ∼40 days for Futura, and ∼50 days for the others.

For the calibrated cultivars, Fig. 5 shows the profile plot of a simulation study (5-day time step) performed with the model in selected trials (we excluded results of trials with less than four sowing dates). Comparison of the simulated and actual number of days elapsed from emergence to flowering indicates how temperature–photoperiod interaction easily turns into non-linear response. The general ability of the model to reproduce the fluctuation of the durations for different years is shown, but some discrepancies are apparent. Felina 34 for example has the shortest emergence-flowering time (from 10 to 80 days) and this seems to be a restraint for the model, with both over- and under-

Table 4
Basic statistics (number of data, mean, standard error) and indices of agreement for estimated and actual days from emergence to 50% of flowering (RRMSE, percent relative root mean square error; EF, modelling efficiency; CRM, coefficient of residual mass), computed using the calibration data set

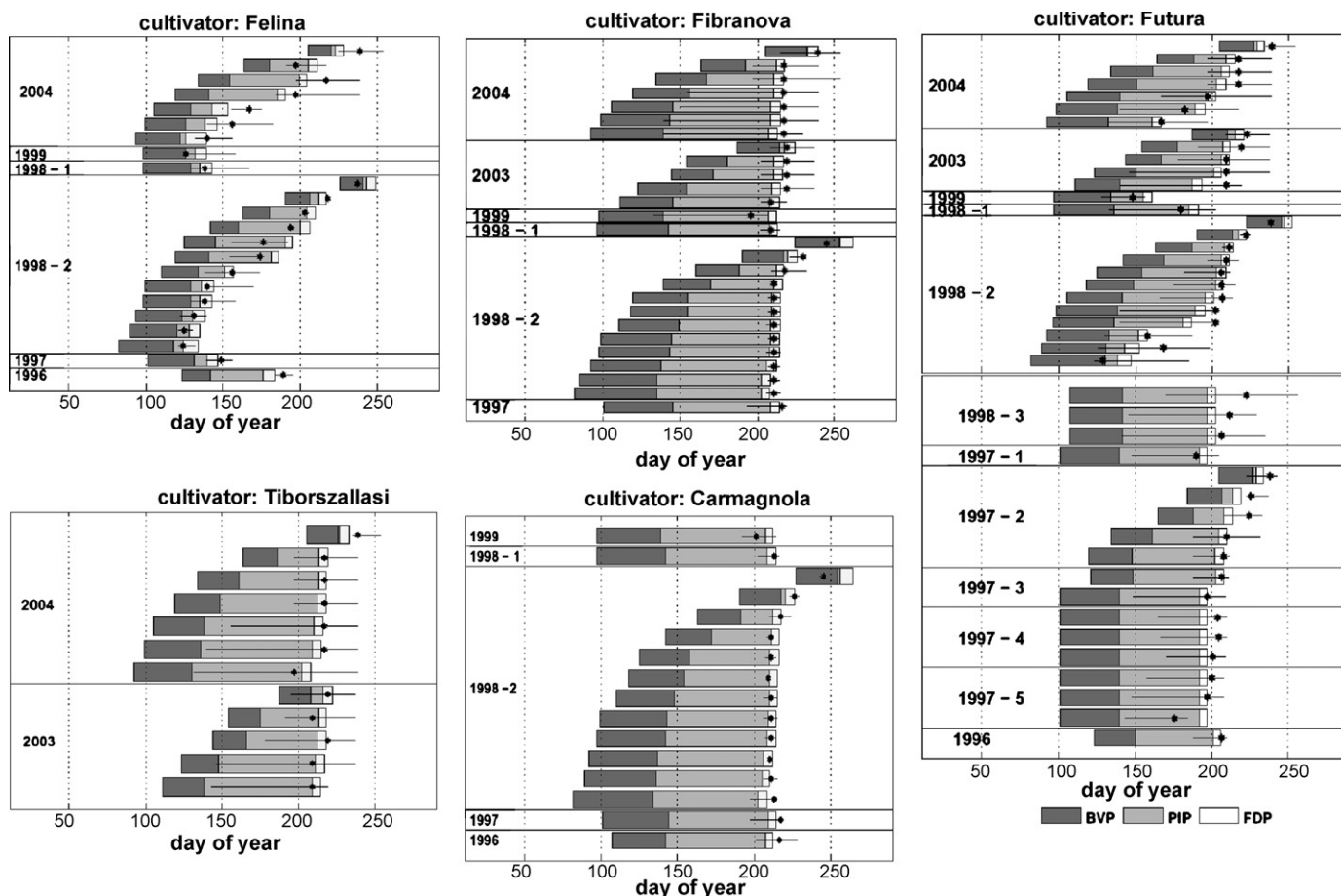| Cultivar	Number of data	Actual		Estimated		RRMSE (%)	EF	CRM
		Mean	Standard error	Mean	Standard error			
Felina34	23	46	3.4	49	2.8	21.3	0.622	−0.063
Fibranova	27	89	6.1	90	5.9	6.2	0.969	−0.018
Futura	47	77	3.6	16	3.3	11.3	0.871	0.017
Carmagnola	17	91	7.5	94	7.0	7.6	0.948	−0.039
Tiborszallasi	12	19	8.5	82	8.8	6.8	0.964	−0.032

Fig. 3. Phase durations (bars) estimated from the calibration dataset and observed dates of 50% of flowering (black dots). Dark grey bars: basic vegetative phase; light grey bars: photo-inductive phase; white bars: flowering development phase. Black lines indicate the flowering time from the appearance of the first flower to the last.

estimations. The duration of the emergence-flowering period showed a trend for Felina 34 and Futura that differed from that of the other cultivars. Cycle length of Felina 34 and Futura tends to get longer as the emergence date is postponed until the point (about mid-May with Felina 34, and end of April with Futura) where it shortens with further postponement. For the other cultivars, cycle length decreases uniformly with emergence date until it levels off.

3.4. Sensitivity analysis

The profile plots of Fig. 6 (for parameters common to all cultivars) and Fig. 7 (for cultivar-specific parameters) show the responses in MSE (mean residual square error) for model fitting to the data of 50% flowering, as each parameter was varied individually. In a number of cases, it is evident that small changes in the model parameters have a noteworthy impact on flowering date.

In Fig. 6, MSE values of switch-off photoperiod (parameter K) varied between ∼60 and ∼500 over a quite narrow range of parameter values (13.9–14.3 h). Big variations on MSE (∼60–300) were also observed for optimum and critical temperatures (T_o, T_c). The degree of responsiveness of both base temperatures (T_b) and physiological development days for the

flowering phase (D_3) was instead low. In Fig. 7, different cultivars responded differently to variation of specific parameters. The sensitivity to changes of both the photoperiod shape parameter (n) and the BVP physiological development days (D_1) was more pronounced with Futura (MSE ∼ 75–250 and ∼80–170, respectively), while it was lower for the other cultivars. Cultivar Fibranova was the least influenced by parameter changes.

4. Discussion

4.1. Modelling approach

The phenology model of post-emergent hemp developed herein is based on the concept of physiological day requirement (i.e. minimum duration in days at optimum photoperiod and/or temperature), which is considered more transparent and easier to understand than a thermal time target (e.g. Soltani et al., 2006). In principle, the model accounts for specific thermal parameters (base, optimum and ceiling temperatures) in each of three phenological phases (BVP, basic vegetative phase; PIP, photo-inductive phase; FDP, flowering development phase). Such a portrayal looks realistic in representing what is known of post-emergent hemp development, and makes sense in terms of parameterisation and estimation accuracy. Modelling
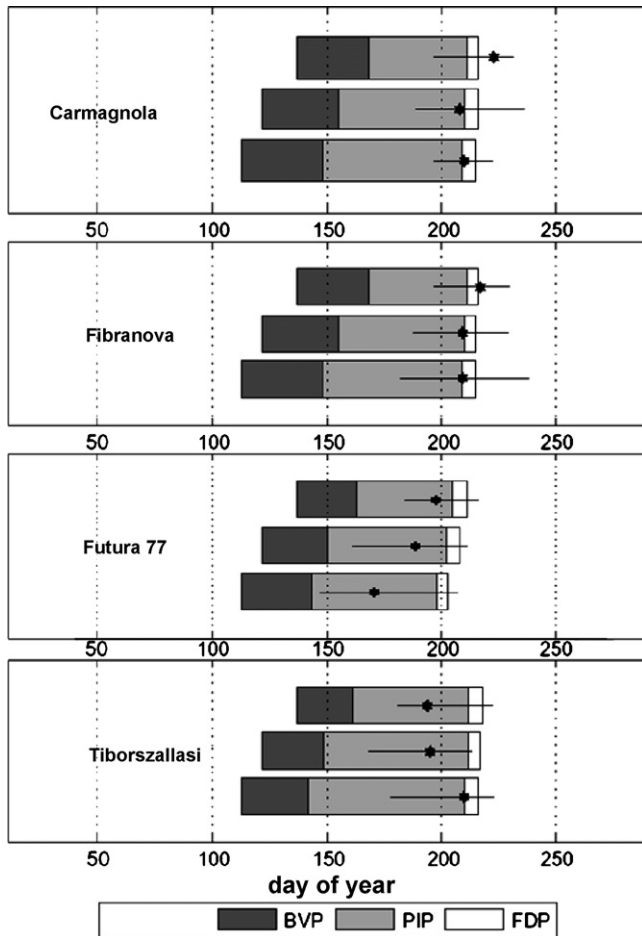
Fig. 4. Phase durations (bars) estimated on the validation dataset and observed dates of 50% of flowering (black dots). Dark grey bars: basic vegetative phase; light grey bars: photo-inductive phase; white bars: flowering development phase. Black lines indicate the flowering time from the appearance of the first flower to the last.

of post-emergent hemp phenology is elaborated, and requires 13 parameters to represent it. Simplified modelling solutions, although roughly reproducing the overall crop cycle duration do not result in a good parameter setting for optimisation, easily disclosing nonsense values (data not shown). Therefore, although composite, the model proposed is simple enough that the necessary mathematics can be handled, while capturing the basic mechanisms of hemp development. In this study, simplifications were introduced in the model parameterisation (not in the model structure) for reducing the number of parameters required to run the model (while preserving the basic processes) and at the same time limiting cultivar differences to the most sensitive parameters. In particular, 8 out of 13 parameters have to be estimated to run the model and only a sub-set of them represent cultivar differences. According to previous research on hemp phenology (Lisson et al., 2000d), cultivar-specific parameterisation was not considered for temperatures. Thermal parameters common to more phenological phases (same values of T_o and T_c for all phases, and same T_b value for PIP and FDP) did not alter the estimation accuracy because little difference in these parameters was observed as a result of preliminary runs where phase-

specific parameters were estimated. We also made the choice of a common value for the parameter D_3 (Eq. (3)) that identifies the physiological developmental days for the FDP, because cultivar variability resulted negligible after the preliminary runs. The parameter representing physiological developmental days was set equal to 1 day to interpret the instantaneous PIP (parameter D_2 of Eq. (3)). This may appear as an arbitrary choice but, as a matter of fact, during the first optimisations we had noticed a general tendency for parameter D_2 to converge to values close to 1. More detailed estimates of this parameter did not noticeably improve the fit. Moreover, $D_2 = 1$ (which means that a single inductive cycle with optimum photoperiod and air temperature promotes flower induction) is consistent with experimental observations for hemp and other short-day crops. Lisson et al. (2000b) had set it equal to 0 in their controlled-environment study. Besides appearing quite restrictive for open-air crops, $D_2 = 0$ makes the mathematical solution of Eq. (3) (stage 3) impossible whilst $D_2 = 1$ is a mathematically suitable, and practically advisable solution. The choice made to not fit complete sets of cardinal temperatures and durations for all cultivars reduces the correlation between parameters, and makes it possible to fit the model to limited size datasets. Moreover, it enables a number of crop-specific (not cultivar-specific) parameters to be estimated, while identifying a restricted number of parameters (such as photoperiodic parameters and durations of the juvenile phase) that are relevant for cultivar characterisation.

4.2. Model assessment

Estimated base temperature for juvenile phase ($T_b = 1.9\,^\circ$C), and optimum and ceiling temperatures ($T_o = 26.4\,^\circ$C; $T_c = 40.0\,^\circ$C) are close to the values of 1, 29 and 41 $^\circ$C given by Lisson et al. (2000d). The same authors did not differentiate among thermal requests for different phases, so we do not have a comparison to offer for T_b value (11.3 $^\circ$C) derived for PIP and FDP. The specifics of the iterative optimisation procedure (i.e. Gauss–Newton algorithm) used for model parameterisation are no guarantee that the solution obtained is unique and optimal (Sinclair et al., 1991; Grimm et al., 1993; Yin et al., 1997b) because there might be a series of solutions with similar square error but different parameter estimates. In addition, the correlation between temperature and photoperiod may cause some compensation between parameters under field conditions like this one (Olsen et al., 1993). However, in this study the degree of uncertainty in parameter estimates is reduced because datasets covering a wide range of environmental conditions were included in the optimisation procedure (Soltani et al., 2006). Sensitivity analysis plots (Figs. 6 and 7) showing that, in each case, there was an interval over which the MSE was minimised are an indication of no redundancy in the number of parameters employed in the model.

Thermal time requirements computed for BVP and FDP tended to be quite stable in each cultivar (Table 5). In particular, the thermal time requirements for juvenile phase in the range 329 $^\circ$C d (lowest value with Felina 34) to 622 $^\circ$C d (highest value with Fibranova) are quite similar to the values 383 and 390 $^\circ$C d calculated by Lisson et al. (2000b) with base air
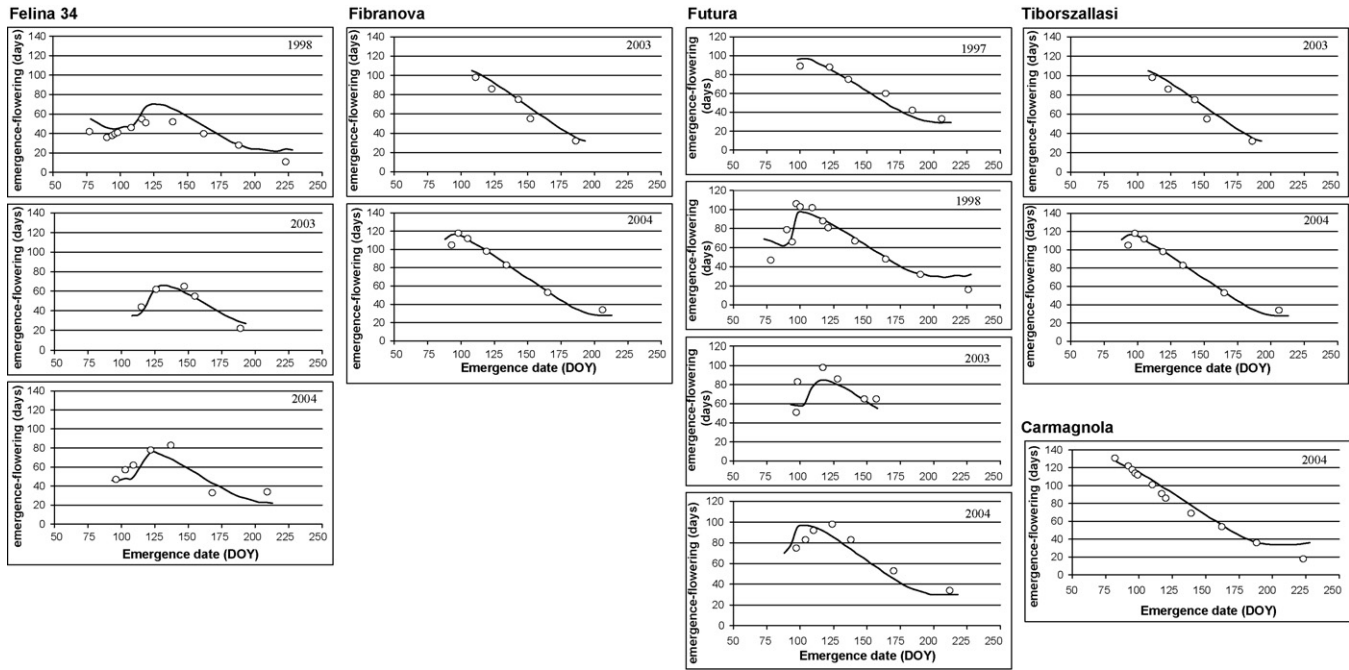
Fig. 5. Comparison of simulated (line) and actual (dots) durations from emergence to 50% of flowering for calibrated cultivars at selected trials. DOY: day of year.

temperature set to $1\,^\circ\text{C}$. This supports the use of a non-linear function (such as the beta function) to convert the information expressed in degree-days to developmental rates (Kim and Reddy, 2004). The large variability in the estimated degree-days associated with PIP reinforces the assumption of the important modulating role of photoperiod in determining the duration of this phase. Again, difference among cultivars in duration from emergence to 50% of flowering was mainly related to differences in duration of the PIP segment. An optimum value for day length is not estimated here because photoperiodic factor is allowed to smoothly approach 1 with low day lengths (Eq. (2)). However, the estimated switch-point photoperiod $\sim$14 h

(with standard error approaching 0) is in accordance with the optimum values reported by Borthwick and Scully (1954) for cultivars Chilean and Kentucky, and by Lisson et al. (2000b) for Kompolti and Futura 77. The results of this work show that substantial genotypic variation of flowering response is the sensitivity to sub-optimal photoperiods, as expressed by the shape parameter (Table 4). Similar findings were reported on rice (Yin and Kropff, 1996; Yin et al., 1997a,c).

The diverse patterns of emergence-flowering duration (Fig. 5) can be ascribed to the combination of a different reaction to photoperiod and temperature. Response to the former is interpreted by the shape parameter (n of Eq. (2)) which is lower for
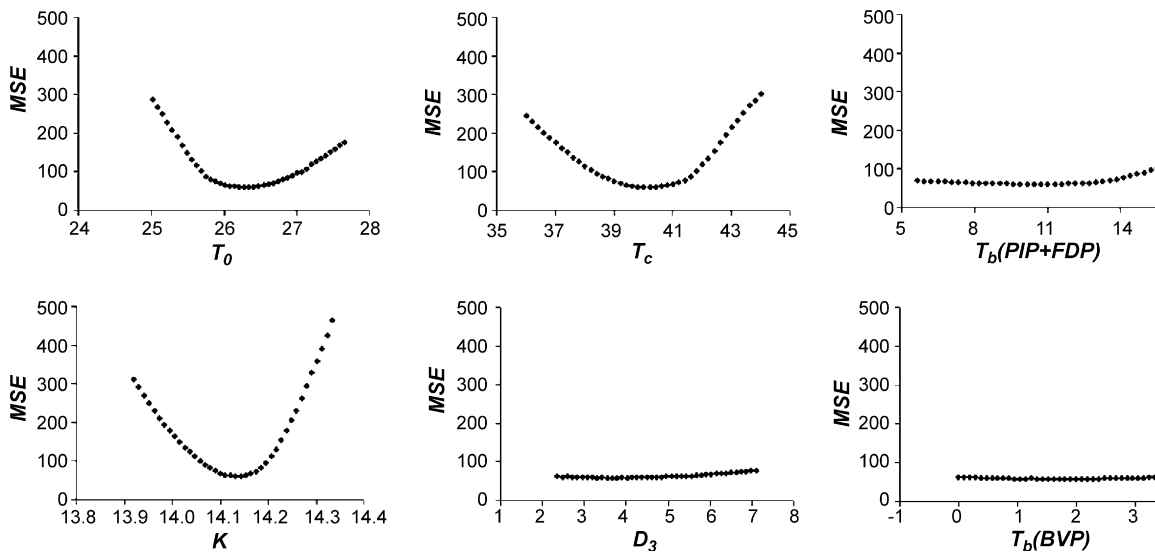

Fig. 6. Profile plots of MSE (mean residual sum of squares) for the six parameters of the model fitted to data for all cultivars; T_o is the optimum temperature, T_c is the ceiling temperature, T_b is the base temperature for basic vegetative phase (BVP) and the other phases (PIP + FDP), K is the switch-off photoperiodic parameter, D_3 is the number of physiological development days for flowering development phase.
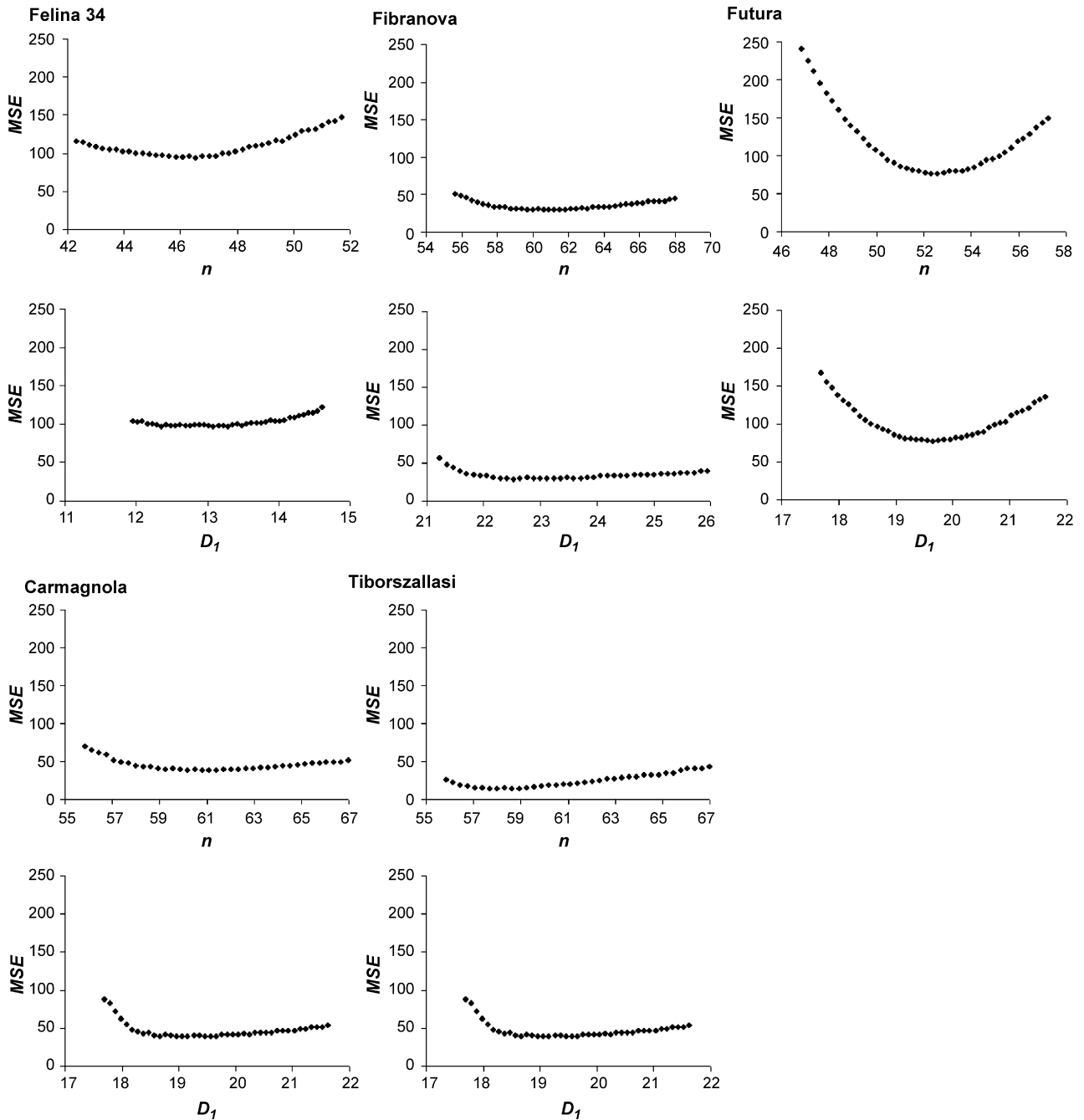
Fig. 7. Profile plots of MSE (mean residual sum of squares) for the two parameters of the model fitted to data for specific cultivars; n is the photoperiod sensitivity parameter, D_1 is the number of physiological development days for basic vegetative phase.

the monoecious cultivars (Table 3). Response to the temperature in the juvenile phase is also different for the monoecious cultivars, due to lower values for D_1 (Table 3). For Felina 34 and Futura, postponing sowing date in the first period of the year causes a longer emergence-flowering phase (Fig. 5). They complete BVP sooner than the other cultivars, whereas suboptimal day lengths generate a delay in the duration of PIP because of low values of parameter n. At later sowing times (and, therefore, later emergence dates), the rate of development towards flowering is hastened by warmer air temperatures and by photoperiods becoming more inductive as the PIP phase is pro-

gressively shifted after the summer solstice. The other cultivars showed an almost linear shortening of the emergence-flowering period from the earliest to the latest sowing time, without the initial delay observed for Felina 34 and Futura. These results can explain the different behaviour of contrasting cultivars. Earliness of Felina 34 (and its tendency to pre-flowering), for instance, is resolved in the model with a combination of effects. A rather short BVP ensures quite high rates of development even with relatively cool spring thermal regimes. This allows quick completion of BVP and initiation of PIP in a period characterised by increasing, yet still quite short, day lengths. The behaviour of

a late-flowering cultivar, such as Carmagnola is dominated by longer BVP and greater sensitivity to photoperiod. Carmagnola stays longer in the juvenile phase and enter PIP when day length is longer and the photoperiod response rather poor. In regimes characterised by short days and high air temperatures, Carmagnola flowers within a few days because of its fast completion of PIP.

The parameterisation obtained discriminates among cultivars. The differences shown in the cultivar parameters (Table 3) tend to reflect the differences in both the sexual and maturity features presented in Table 2. Moreover, duration of crop cycle (Table 5, sum of days for phases from emergence to 50% of flowering) confirms Felina 34 as the earliest-flowering cultivar in this study (49 days in average). On the contrary, Carmagnola (94 days in average) and Fibranova (90 days in average) are the latest-flowering cultivars. The approach described above therefore provides a relatively simple, yet versatile phenological model of post-emergent hemp, which has a sufficient number of parameters related to basic knowledge of crop biology. The inclusion of current understanding of air temperature–photoperiod interaction in the model gave generally satisfactory performances, also in comparison to previous models (data not shown). In particular, some limitations of the Lisson approach (Lisson et al., 2000b,d) were removed either by introducing non-linear thermal and photoperiodic responses, or cultivar-specific parameterisation.

Results from sensitivity analysis indicate that, among the model parameters, switch-point photoperiod (parameter K) is the most important single factor controlling flowering date (Fig. 6), while the shape parameter of photoperiod (parameter n) is also important for the cultivars that are less sensitive to sub-optimal day lengths (cultivar Futura and, to a lesser extent, cultivar Felina 34, Fig. 7). The fP factor in Fig. 2 does not seem to show important cultivar differences, but small changes in this factor (as a result of changes in the photoperiod parameters) can have a high impact on the model response. High sensitivity to photoperiodic parameters is therefore a point of remark here. Optimum and ceiling temperatures (parameters T_o and T_c) are also important. With the support of Lisson et al. (2000d), the estimates of T_o and T_c can be accepted as reasonable values for hemp. Some uncertainty affects base temperature in the phases following BVP, owing to the lack of specific knowledge about this parameter, but our model had limited sensitivity to this parameter in the range of values explored (~6–17 °C, Fig. 6). Estimated base temperature for BVP is also a parameter to which the model is not sensitive to (Fig. 6).

The authors are aware that the simulation of the lengths of BVP and PIP without the support of specific experimental data is prone to criticism. The idea to adopt the current model structure was taken in early phases of model development. A considerable improvement of simulation results was gained moving from a model with a single phase from emergence to flower onset (i.e. merging BVP and PIP into one phase) to a model taking BVP and PIP as distinct phases. Such estimation was introduced to provide a mathematical interpretation of the available knowledge on physiology of hemp flowering. This brought a certain degree of speculative content into the model (which is actually present in any mathematical model of biological systems) but, at the same time, offered the opportunity to genuinely reproduce the behaviour of the system. The reasons to use *a priori* the three-phase model were: current knowledge on physiology of hemp flowering, and availability of assorted datasets for testing the proposed hypothesis. *A posteriori*, reasons to maintain the model in its current structure are: the general goodness of results and fits, and the "reasonable" values obtained for both BVP and PIP durations, which interpret quite well known differences among cultivars and that are in accordance with the physiology of the system.

Flowering times were fairly well described by the model. Some discrepancies indicate that there are still aspects of uncertainty in the understanding of hemp phenology, but it should be added that deviations between model estimates and observations are somewhat unavoidable, and need to be accounted for when judging model performance and when applying the same model.

The extent of agreement between calculated and observed duration of phenological phases, and the accuracy of the model also depends on the method of inspection of flowering and on the cultivation practices used. In the first year of the experiment, flowering was determined at each count on different plants. Since this procedure increased data variability and was not practical, flowering counts in subsequent years were carried out on a given number of labeled plants. This methodology gave smoother flowering curves and better understanding of flowering dynamics, but it was less representative of the flowering of the whole population of plants. Cultivation practices proved to influence flowering time, and in particular plants cultivated at low plant populations (number of plants per unit surface) flowered sooner. This behaviour can be observed in Fig. 3 where the flowering data from Futura in 1998-1 and 1997-1 were collected in a plant population experiment (Amaducci, 1998). Flowering data from experiments carried out on Futura (1997-2) at different nitrogen levels did not differ (Fig. 3), which is in agreement with previous research (Borthwick and Scully, 1954; Heslop-Harrison and Heslop-Harrison, 1969). Conditions other than those taken into account in the current model could also influence the time to induction or to flower formation. Examples are the effect of plant age at the onset of flower induction as reported by Heslop-Harrison and Heslop-Harrison (1969) on hemp, or the effect of day and night temperatures as reported by Yin and Kropff (1996) on rice genotypes.

With reference to Futura, it should be mentioned that the registered name of this cultivar changed from Futura 77 to Futura 75 in 2001 after a reselection carried out by the breeder (Fédération Nationale des Producteurs de Chanvre, personal communication), which may have changed flowering behaviour. This would also have introduced an unknown extent of variation into the data collection process.

Finally, the importance of controlled-environment studies in understanding the flowering response of a crop to thermo-photoperiodic changes (Roberts et al., 1986) is not under-estimated by the authors, but it should be added that these experiments are costly. Continuous improvements in understanding the model processing should instead be made by testing the model with data collected over a wide range of latitudes.

5. Conclusion

This paper reports on a modelling study that included a beta function for response to temperature and a switch-off function for response to photoperiod to describe phenology in post-emergent hemp over a broad range of thermal and photoperiod conditions in Italy. Model parameters were estimated and discussed to show a pattern of dissimilarity among hemp cultivars. Differences among cultivars in cardinal temperatures and the critical photoperiod for response functions were small, so common values for thermal parameters could be used for modelling all the cultivars. Differences in development rate were characterised by differences in the inherent maximum rate of development for the basic vegetative phase ($R_{dev}(1) = 1/D_1$) and the photoperiod sensitivity coefficient (n). The phenology model developed for post-emergent hemp gave reasonable estimates of phenological development across years. The present study produced the necessary conceptual and quantitative knowledge for flowering of hemp. This model can be used in simulation models of hemp over a diverse range of temperature and photoperiod conditions but the basic equations must be substantiated against extended data sets across a range of latitudes and climates. This extended work is being done by the authors at Italian and European sites as part of the EU project HempSys (http://www.hempsys.net). The phenology model of post-emergent hemp will then be tested in the framework of decision support for hemp production.

Acknowledgements

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