A modelling approach for evaluating phenology and adaptation of two congeneric weeds (*Bidens frondosa* and *Bidens tripartita*)

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ABSTRACT

The exotic species *Bidens frondosa* is rapidly spreading in northern Italian arable fields, while *Bidens tripartita*, a native congeneric, shows less invasive capacity. To characterise and model the phenology of the two species, a two-year study was conducted involving sowings at 15-day intervals between March and August. The length of the sowing-emergence phase was well described by a simple thermal model, with a base temperature of 4.5 °C, for both species. A multiplicative photothermal model was found to be the best for the emergence-flowering phase. *B. frondosa* resulted as being less macrothermal and more sensitive to photoperiod. The flowering-maturity phase lasted for 30–32 days, on average, and was well described by a model based on soil water availability: this phase shortens when there is a lack of water, particularly in *B. tripartita*. The more relevant differences between the two species seem to be related to the vegetative phase length, which varied from 150 to 46 days and from 123 to 42 days in *B. frondosa* and *B. tripartita*, respectively. Thanks to the high elasticity of its vegetative phase, *B. frondosa* can grow taller than *B. tripartita* and acquire higher competitivity and seed production potential, both relevant factors in determining the success of a species.

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1. Introduction

Weed flora evolution forces farmers to modify their control programmes frequently (every 4–5 years on average) in order to maintain a high control efficacy. For example, in the Po Valley (Northern Italy), the transformation rate of the weed communities in maize, measured using the Guillerm et al. (1989) indexes, reached an annual 4% in the period 1960–1990 (Sbriscia Fioretti et al., 1998). These changes are due both to the disappearance of existing species from the fields and the appearance of new ones. The species in the latter category can be divided into two groups: (a) species already present in the agroecosystem but of little relevance for the cultivated fields and (b) newly introduced species.

Cousens and Mortimer (1995) defined the species in the first group as "pre-adapted weeds" and they have the following traits: (a) they are in a natural plant community within dispersal distance of the crop (or other habitat) and (b) become predominant as a consequence of a change in crop and weed management practices.

A plant can become a weed with no change of its characters, just a change of habitat (Williamson, 1996), as occurs when cropping

practices are changed. *Bromus sterilis* L. and *Lactuca serriola* L. in winter wheat and *Equisetum* sp.pl. and *Sycios angulatus* L. in maize are good examples of this phenomenon. Nevertheless, the introduction of exotic (or alien) weeds represents, from the quantitative point of view, the major cause of evolution of weed communities and one of the most worrying phenomena, both agriculturally and ecologically. Invasions by species that alter ecosystem processes can have cascading effects, leading to the decline or extinction of many native species (Abbott and Milne, 1995; White and Schwarz, 1998). The botanical shift of summer crop weed communities in the Po Valley has mainly been due to species belonging to this category, with *Abutilon theophrasti* Medicus, *Xanthium strumarium* L., *Datura stramonium* L., *Ambrosia artemisiifolia* L. and *Bidens frondosa* L. being among the most important. Amongst these, *B. frondosa* currently has the highest expansion rate (Otto et al., 1994). This species, originating from North America, was introduced into Italy as an ornamental plant in the second half of the 1700s (Saccardo, 1909). It was first reported as a naturalised weed in Tuscany in 1849 and some years later in Sicily (Caruel, 1860). In Veneto (north-eastern Italy) it was reported for the first time in the mid 1960s (Ziliotto, 1966) and has now spread over the entire Po Valley, particularly in summer crops (maize, soybean, sugarbeet, dry-sown rice, etc.) and uncultivated areas (canal banks, hedges, etc.) (Otto and Lazzaro, 2004). According to the definition of Groves (1999), it behaves as an agricultural and environmental weed. The species, pertaining

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to the *Asteraceae* family, is systematically close to *Bidens tripartita* L., its native congeneric, but has a much higher invasive capacity, as also demonstrated in Germany by Kock (1988), in Portugal by Ferreira and Moreira (1995) and in the Czech Republic by Bendova and Gruberova (1999a).

To study the reasons for their differences in invasive ability, a research programme was set up to try to understand the reasons for the ecological success of *B. frondosa* compared to *B. tripartita* in man-made habitats. A joint ecophysiological study of two systematically close species is considered useful for highlighting the causes of the success of an exotic plant in a given environment (Maillet and Lopez-Garcia, 2000; Hinz and Schwarzlander, 2004).

This paper presents experimental results and a modelling approach related to the phenology of the two congeneric species. Phenology is considered an important factor for the adaptation and spread in a new environment (Van Der Weide, 1992; Ghersa and Holt, 1995; Kubinova and Krahulec, 1998; Maillet and Lopez-Garcia, 2000; Ren and Zhang, 2009). An understanding of the effects of the environmental variables on weed phenology is also essential for developing cropping system simulation models (Hodges, 1991; Swanton et al., 2000).

2. Materials and methods

The trials were done over 1996–97 at the Experimental Farm of Padua University (Legnaro, Italy, 45° 12′ N, 11° 58′ E) in plots of $1\,m^2$ ($1.0\,m \times 1.0\,m$) with silty-loam soil (sand 39, silt 44, clay 17% of dry weight).

Between 20 April and 2 August 1996, eight sowings were done, while in 1997 there were eleven sowings from 27 March to 20 August. In both years, the intervals between sowings were about 15 days. Seeds of both species were sown in each plot at a depth of 3 cm, in two rows 50 cm apart. After emergence, they were thinned to 10 seedlings per row. No irrigation was applied.

The seeds used for the sowings of both species had been gathered, from 30 to 40 plants in the year preceding each trial, from wild populations existing in the experimental farm. Before sowing, the seeds had been stratified in the dark for one month, at 4 °C on moistened filter paper in Petri dishes, in order to eliminate dormancy.

2.1. Phenological measurements

The phenological events recorded were date of plant emergence from soil, date of flowering start and date of seed maturity. As emergences were always regular, the date of emergence was determined on a row basis. The duration of the other phases was assessed by daily checking of five plants selected after thinning. The first 7–10 heads appearing on each plant were labelled to give 35–50 heads per sowing time and species. The flowering date was attributed when 70% of the flowers on the heads were open; the date of seed maturity was attributed when the achenes became a dark brown colour. In addition, individual plant height was measured weekly, to obtain an estimation of plant growth.

2.2. Phenological models

Different models were tested for their ability to describe the length of phenological phases. Among these, the NOAA thermal model (National Oceanic and Atmospheric Administration, USA), a photo-thermal model and a water stress model were selected for the phases sowing-emergence, emergence-flowering and flowering-seed maturity, respectively, based on their goodness of fit to the experimental data and simplicity. The phenological models were implemented by the SEMoLa 6.4.3 simulation framework (Danuso, 1993, 2007).
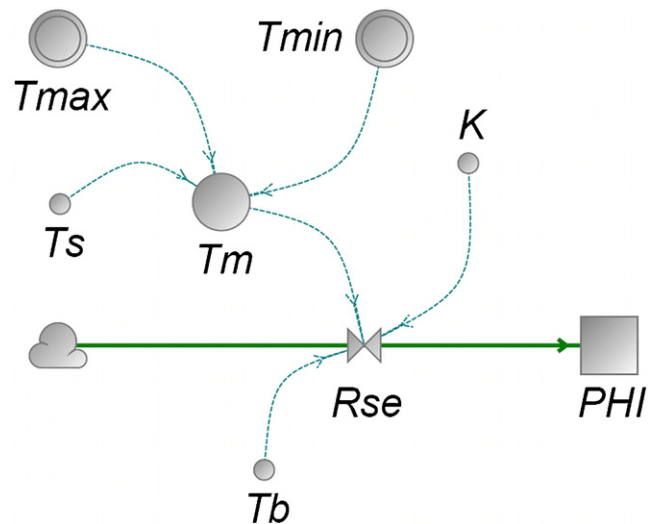

Fig. 1. Relational diagram for NOAA model created by SEMoLa. In this figure and in Figs. 2 and 3 dotted lines represent information links, solid lines fluxes of materials. Boxes are state variables, valves are rates, circles are auxiliary variables, double circles are exogenous variables and points are parameters. See Table 1 for explanation of symbols.

The models calculate a phenological index (*PHI*), from the beginning to the end of the considered phase, by summing the development rate *R* over the days of the phase:

$$PHI = \sum_{start}^{end} R$$

When *PHI* equals 100, the end of the phenological phase is considered as reached.

R is the percent of the phase completed in a day. Its average value can be estimated from data as $R = 100/N$, where *N* is the phase length in days.

2.3. NOAA model

The NOAA model has been applied to the sowing-emergence phase. This simple model states a linear relationship between the daily development rate for the phase (R_{se}) and air mean temperature (Fig. 1 and Table 1). The useful degrees, accumulated daily, are obtained as the difference between the daily mean temperature (*Tm*) and a low temperature threshold (*Tb*), defined as *base temperature*. If *Tm* is equal to or lower than *Tb*, the useful accumulated temperature degrees are set to zero. An upper threshold is also considered (*Ts* = 30 °C): if *Tm* is higher than *Ts*, the *Ts* value is retained, in place of *Tm*. The daily sowing-emergence development rate (R_{se}, percentage of phase per day) is calculated as:

$$R_{se} = K \cdot (Tm - Tb) \cdot (Tm > Tb)$$

where $Tm = (T_{max} + T_{min})/2$, if $Tm \le Ts$ and $Tm = Ts$, if $Tm > Ts$; $(Tm > Tb)$ is a logical expression equal to 1 if true, 0 if false; T_{max} is the daily maximum air temperature (°C); T_{min} is the daily minimum air temperature (°C); *K* is the percentage of phase completed per useful degree of temperature and per day (% phase °C^{-1} day^{-1}).

2.4. Multiplicative photo-thermal model (MPT)

The MPT model has been applied to the emergence-flowering phase. It considers the influence of photoperiod in addition to temperature (Fig. 2 and Table 1). Photoperiod affects plant development by a well-known mechanism based on the reversibility of phytochrome between two states (red-far red). The amount

Table 1
Parameters and variables used in the three models and their units (* indicates that the parameter or variable is used by the model).

Symbol	Description	Units	NOAA	MPT	WSPM
Ds	Soil useful depth	mm	–	–	*
ETa	Actual evapotranspiration	mm day^{-1}	–	–	*
Etm	Maximum evapotranspiration	mm day^{-1}	–	–	*
ETr	Reference evapotranspiration	mm day^{-1}	–	–	*
FC	Water field capacity	mm$_{water}$ mm$_{soil}^{-1}$	–	–	*
fd	Factor of drought stress	Dimensionless	–	–	*
K	Percent of phase per useful GDD	% °C^{-1} day^{-1}	*	–	–
$K1$	Development coefficient	% °C^{-1} h^{-1} day^{-1}	–	*	–
Kc	Water consumption crop coefficient	Dimensionless	–	–	*
Mc	Critical moisture for stress	mm$_{water}$ mm$_{soil}^{-1}$	–	–	*
Ms	Soil moisture	mm$_{water}$ mm$_{soil}^{-1}$	–	–	*
N_{max}	Maximum phase length	Day	–	–	*
N_{min}	Minimum phase length	Day	–	–	*
P	Photoperiod	h	–	*	–
Pc	Critical photoperiod	h	–	*	–
PHI	Phenological index	Dimensionless	*	*	*
Q	Water reserve in soil	mm	–	–	*
$Rain$	Daily rainfall	mm day^{-1}	–	–	*
R_{se}	Rate of development sowing-emergence	% day^{-1}	*	–	–
R_{ef}	Rate of development emergence-flowering	% day^{-1}	–	*	–
R_{fm}	Rate of development flowering-maturity	% day^{-1}	–	–	*
Ru	Useful rain	mm day^{-1}	–	–	*
SI	Stress index	Dimensionless	–	–	*
Tb	Base temperature	°C	*	*	–
Tm	Daily mean air temperature	°C	*	*	–
T_{max}	Daily maximum air temperature	°C	*	*	–
T_{min}	Daily minimum air temperature	°C	*	*	–
Ts	Upper air temperature threshold	°C	*	*	–
WP	Wilting point	mm$_{water}$ mm$_{soil}^{-1}$	–	–	*

of phytochrome in the promoting flowering state is considered proportional to the dark period length of the day (D). Only the time exceeding a minimum critical value Dc, ($D − Dc$), is considered useful for the progress of development. If the dark period is less than Dc, the development is proportionally reversed. Because it is handier to use the photoperiod (P) instead of the dark period and $D = 24 − P$, then $Dc = 24 − Pc$, where Pc is the critical photoperiod. So, the useful dark period ($D − Dc$) can be substituted by ($Pc − P$). Pc is a parameter playing an important role in the adaptation of a species to the environment, and particularly to different latitudes.

Fig. 2. Relational diagram for MPT model as created by SEMoLa. See Table 1 for explanation of symbols.

In this model, the daily development rate emergence-flowering (R_{ef}) becomes:

$$R_{ef} = K1 \cdot (Tm − Tb) \cdot (Pc − P) \cdot (Tm > Tb) \cdot (P < Pc)$$

where $K1$ is the percentage of phase completed per useful degree of temperature, per hour of dark period and per day (% phase °C^{-1} h^{-1} day^{-1}).

The multiplicative combination of temperature and photoperiod effects was preferred to the additive one, where $R_{ef} = K1 \cdot (Tm − Tb) + K2 \cdot (Pc − P)$, because the multiplicative model has one parameter less, was as effective as the additive model in reducing the variability of residuals and, moreover, showed a less systematic error and best residuals distribution.

In the MPT model, the Tb parameter can be used to rank species by their development rate sensitivity to temperature. In the same way, Pc allows species to be classified by their developmental sensitivity to photoperiod. After parameter estimation on phenological data, high Tb values denote high sensitivity to temperature and high Pc values correspond to low sensitivity to photoperiod. These assertions can be demonstrated considering the relative sensitivity of development rate (R_{ef}) to temperature (S_T) and photoperiod (S_P):

$$S_T = \frac{\partial R_{ef}}{\partial T} \cdot \frac{T}{R_{ef}}, \quad S_P = \frac{\partial R_{ef}}{\partial P} \cdot \frac{P}{R_{ef}}$$

Differentiating $\partial R/\partial T$ and $\partial R/\partial P$, substituting the MPT model for R_{ef} and rearranging the equations, we obtain the relative sensitivities as:

$$S_T = \frac{Tm}{Tm − Tb} \quad \text{for} \quad Tm > Tb \quad \text{and} \quad S_P = −\frac{P}{Pc − P}$$

Therefore, when Tb increases S_T increases and when Pc decreases, the absolute value of S_P increases.
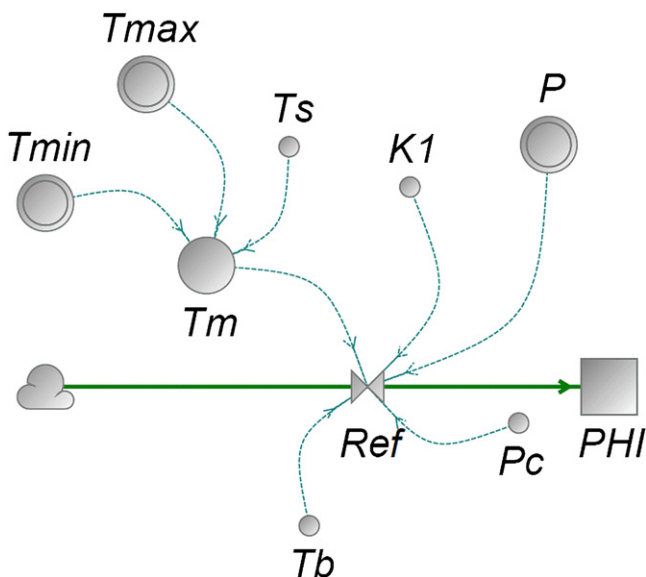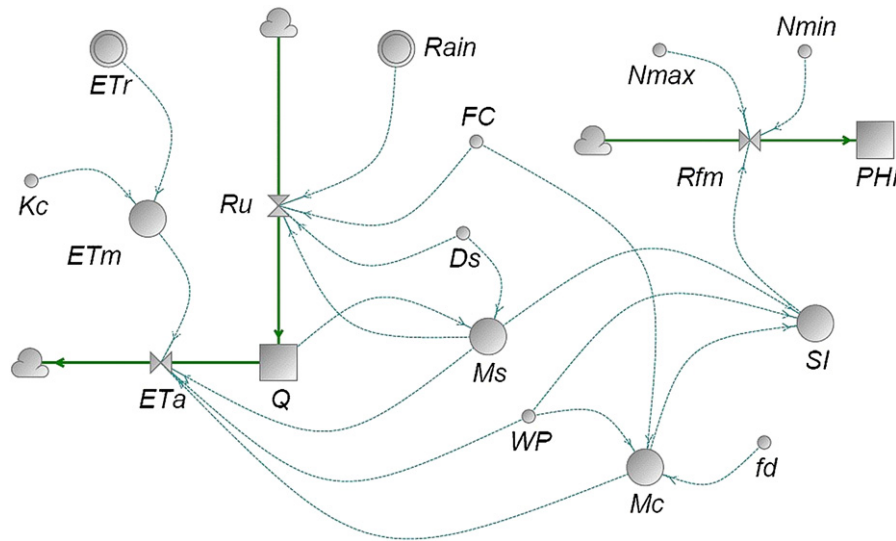
Fig. 3. Relational diagram for WSPM model as created by SEMoLa. See Table 1 for explanation of symbols.

2.5. Water stress phenological model (WSPM)

The WSPM model has been applied to the flowering-maturity phase. It assumes that the plant has a maximum phase length, shortened by a lack of water in the soil, while temperature and photoperiodic effect are not considered (see Appendix A, Fig. 3 and Table 1). This model is conceived to be applied only to the reproductive phase (flowering and seed development) because, in many species, water stress during the vegetative phase often causes phase lengthening (Giovanardi and Ceccon, 1987). This model has been developed and applied because, in our data, temperature and photoperiod were shown to be unable to explain the variations of the reproductive phase length.

The daily development rate (R_{fm}) is calculated from a water stress index (SI) as:

$$R_{fm} = \frac{100}{N_{max} \cdot (1 - SI) + N_{min} \cdot SI}$$

where N_{max} indicates the maximum length of the phase, without water shortage (days); N_{min} represents the minimum length of the phase (for soil moisture equal to or below wilting point). N_{min} has been considered equal to 1 day; SI is a water stress index representing the effect of water shortage on plant phenology:

$$SI = \left(1 - \frac{Ms - WP}{Mc - WP}\right) \cdot (Ms < Mc)$$

where WP is a soil parameter (moisture content at wilting point); Ms is the soil moisture ($mm_{water}\, mm_{soil}^{-1}$); Mc is the critical moisture below which the plant is stressed, it is considered a constant fraction of the available water and is obtained as

$$Mc = WP + fd \cdot (FC - WP) \quad (mm_{water}\, mm_{soil}^{-1}),$$

where FC is the soil moisture content at field capacity (mm) and fd is the fraction of available soil water not easily accessible by the plant.

The expression ($Ms < Mc$) gives 1 if it is true and 0 if it is false, preventing SI reaching meaningless, negative values. SI has a minimum of zero for $Ms \geq Mc$ and a maximum of 1 for $Ms \leq WP$, because Ms is always considered higher than or equal to WP. Ms can be measured or estimated by simulation models. In this paper, Ms has been estimated by a simple soil water model (see Appendix A).

2.6. Calibration

The calibration of the three models was done on the averaged data of five plants per plot.

The model parameters were estimated on phenological data obtained from all combinations (16) of different sowing times and years, separately for the two species and for the three models. Data from some sowing dates were not included in the elaboration because of low reliability due to plant damage by hares or difficulty in attributing a precise seed maturity date. The calibration was done with data from both years using the SEMoLa routine implementing the iterative Gauss–Newton method for the parameter estimation of non-linear models.

A "stage-wise iterative procedure" similar to the "stage-wise regression procedure" (Draper and Smith, 1981) was adopted to calibrate the water stress model. This procedure, unlike the least square estimation, maintains the hierarchical structure of the model. In our case, with the stress model (see Appendix A), parameters related to the soil water balance (Ds, useful soil depth for the plant; Kc, water consumption coefficient) were estimated first. Once calibrated, these parameters were held to constant values in order to estimate the values for fd and N_{max}. Then, holding fd and N_{max} at the previously calibrated values, Ds and Kc were recalibrated. The procedure was repeated until the parameter values converged. N_{min} has not been calibrated but considered, in every case, as equal to 1 day.

Concerning the validation, it should be taken into account that the modelling approach was used to highlight the ecophysiological differences between the two species, not aiming to create a predictive tool. Under these premises, therefore, classical empirical validation by comparison of simulation results with independent data is not required. Instead, we rely on the concept of "heuristic validation" (Carson et al., 1983; Oreskes et al., 1994) where a model is considered valid if it is able to increase the knowledge of the studied system.

2.7. Environmental conditions

The meteorological data were recorded at the weather station of the Experimental Farm. Fig. 4 shows the cumulated rainfall for the two years; Fig. 5 shows the photoperiod and temperature summation ($Tb = 10\,°C$) from March to October against the day of the
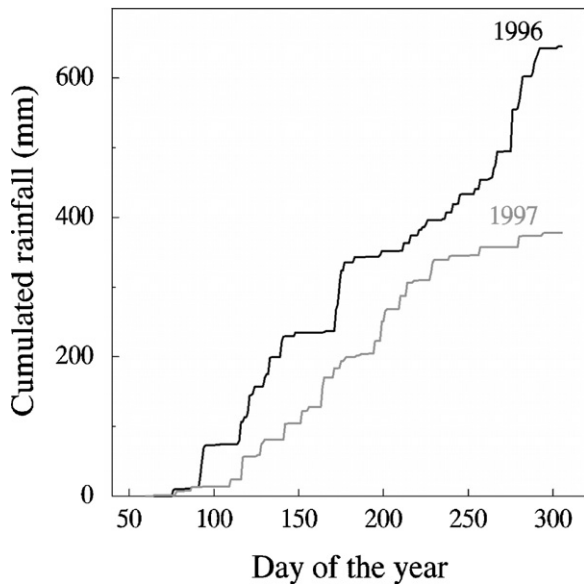
Fig. 4. Cumulated rainfalls from March to October in 1996 and 1997 at the experimental site (Legnaro, Italy).

Table 2
Averaged and cumulated values of meteorological variables (from March to October) observed in the years 1996 and 1997 at Legnaro (Lat 45° N), Padova (Italy).

Variable	Unit	1996	1997
Mean minimum daily temperature	°C	11.9	11.9
Mean maximum daily temperature	°C	22.7	24.4
Total rainfall	mm	645	378
Temperature summation (base 10 °C)	°C day	1921	2046

year. It can be seen that 1996 had lower temperatures and higher rainfall than 1997, especially at the end of summer-beginning of autumn. The average minimum temperatures during the growing season were the same in both years (about 12 °C, Table 2), while average maximum temperatures differed, mainly due to a warm dry period in September–October 1997.

The photoperiod was calculated as proposed by Keisling (1982), considering the astronomic daylength.
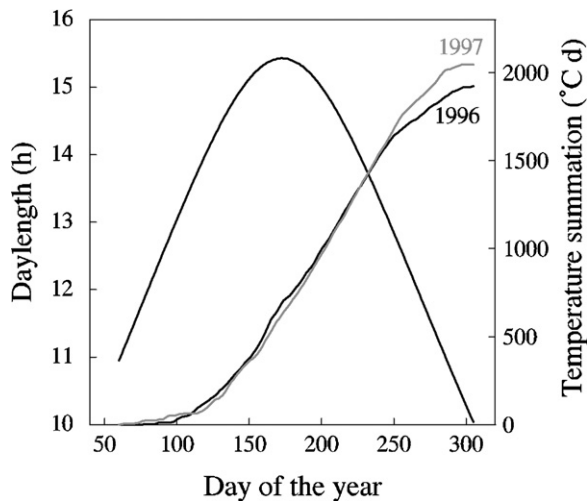

Fig. 5. Photoperiod (h) and temperature summation (°C day, base 10 °C) from March to October in 1996 and 1997 at Legnaro (Italy).
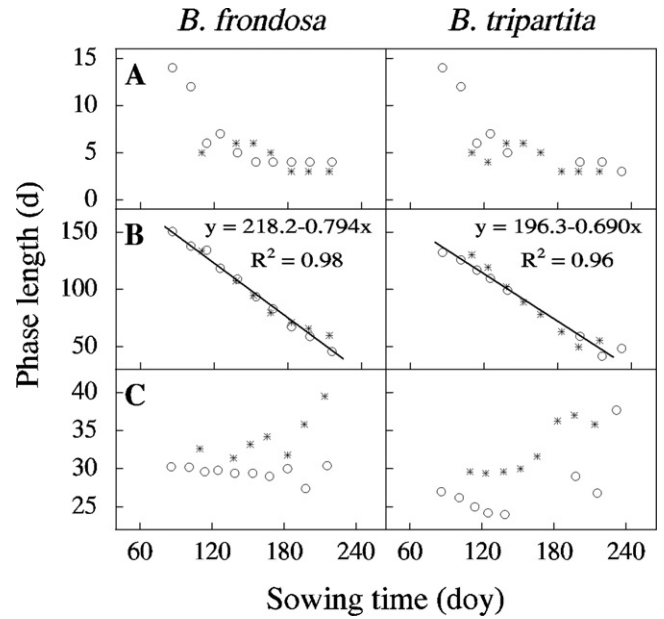

Fig. 6. Length of phases sowing-emergence (A), emergence-flowering (B) and flowering-maturity (C) in relation to sowing time (doy = day of the year). * = 1996, ○ = 1997.

Wilting point (WP) and field capacity (FC) were determined by the Richards apparatus, at soil moisture corresponding to water matric potential of 15 bar and 0.3 bar, respectively.

3. Results

3.1. Sowing-emergence phase

The average length of the sowing-emergence phase was similar in both species and decreased with the advancing of sowing time. The maximum duration (about 14 days) was observed for the end of March sowings and the minimum (3–4 days) for the July sowings (Fig. 6A). Among the different tested phenological models using air temperature as predictive variable, the NOAA model showed the best behaviour in terms of variability of the residues, physiological significance of the parameters and simplicity. The estimated values of parameters K and Tb are reported in Table 3. The two species do not substantially differ in the emergence phase: the temperature sum required to complete emergence was 76 °C d with a base temperature (Tb) of about 4.5 °C. The coefficient of variation (CV) of residuals was wide, being in the order of 20–23%: this can probably be attributed to the relatively long measurement interval (1 day) with respect to the phase length. However, the model allowed the CV to be more than halved with respect to that based on the duration expressed in days.

3.2. Emergence-flowering phase

The average length of the emergence-flowering phase was 93 days for *B. frondosa* and 87 for *B. tripartita*. Phase length in *B. frondosa* ranged from a minimum of 46 days (sowing on 4 August) to a maximum of 150 (sowing on 27 March); for *B. tripartita* the minimum and maximum duration was 42 and 132 days, respectively. In both species and years, the length of this phase linearly decreased with the advance of sowing time, as shown by the regressions in Fig. 6B. Year-to-year differences within species were not significant ($P > 0.05$), but there were significant differences between species ($P < 0.05$), so data for the two years were regressed together to derive separate equations for each species. The slopes of the

Table 3
Sowing-emergence phase. Values for the parameters K and Tb of the NOAA model, obtained by calibration on the two-year data.

Parameter	Unit	Bidens frondosa		Bidens tripartita		Both species	
		Value	Standard error	Value	Standard error	Value	Standard error
K	% phase °C^{-1} day^{-1}	1.32	0.17	1.31	0.20	1.31	0.123
Tb	°C	4.61	1.49	4.51	1.72	4.56	1.095
Mean absolute err.	% phase	16.7		19.2		17.90	
CV (RMSE)	%	20.5		23.2		21.87	
N. obs.		17		16		33	

The CV of the length of the sowing-emergence phase (days) was 54% for B. frondosa and 56% for B. tripartita.

regressions, representing the reactivity of each species to sowing time, were significantly different ($P < 0.05$), being −0.794 and −0.690 for B. frondosa and B. tripartita, respectively. For each day's delay in sowing, the phase lengths of B. frondosa and B. tripartita shortened by about 0.8 days and 0.7 days, respectively.

The multiplicative photothermal model gave the best adaptation, with a CV of the residuals of about 10%. It emerged from the calibrations that while parameter Pc is estimated with a low error, Tb is affected by a relatively high error. It was also seen that $K1$ was very similar in both species, so it was considered worthwhile to recalibrate the model considering a common $K1$ and maintaining it constant at 0.083. Table 4 reports the results of the calibration with two parameters. It should be noted that Pc was always easily estimated with good accuracy. This allows safe discrimination between the two species. The values obtained for Pc were 15 h 29 min (15.49 h) for B. frondosa and 15 h 53 min (15.88 h) for B. tripartita.

The MPT model gave better results when soil temperature instead of air was considered as the predictive variable (CV of the residues 5.8 and 8.4 for B. frondosa and B. tripartita, respectively) but these results are not reported because soil temperature data are often not available from weather data records.

3.3. Flowering-maturity phase

The flowering-maturity phase was very short, around 32 days for B. frondosa and 29 days for B. tripartita (two-year average, eliminating the last sowing in 1997 because of difficulty in attributing a precise seed ripening date) (Fig. 6C). The thermal and photo-thermal models tested were difficult to calibrate and the phenological indexes calculated did not appear to be more stable than the observed phase length. However, the flowering-maturity phase was always longer in 1996 than in 1997, for the corresponding sowing times, suggesting a water stress effect. Using the WSPM model, that linearly links water stress to the development rate R, the parameters in Table 5 were estimated, simultaneously, with a stage-wise iterative method. The procedure was repeated with different combinations of the parameters Ds and Kc (see Appendix A). The combination that gave the lowest CV of the residuals (maintaining realistic values) was $Ds = 450$ mm and $Kc = 0.3$. With this model the maximum length of the phase without water stress N_{max} was

found to be 35.2 days for B. frondosa and 36.3 days for B. tripartita. The effect of stress on the shortening of the phase is represented by the parameter fd. Although the similar value of N_{max} between the two species indicates that, in non-limiting water conditions, the rate of progress towards maturation is similar, the higher value of fd in B. tripartita seems to indicate a higher sensitivity to water stress, i.e. a faster response in the cycle shortening because of water stress.

Sensitivity analysis of the phenological index (PHI) to parameters showed that the model response is very sensitive to the N_{max} and fd parameters. On the contrary, sensitivity towards the parameters FC, WP and Ds is low, while for Kc it is very low. So, when applying the model N_{max} and fd are to be accurately estimated, while a good estimation for FC, WP, Ds and Kc can be considered less critical.

4. Discussion

The modelling approach adopted allows the adaptation differences between the two species to be evidenced through model parameters estimation.

The description of the phenological behaviour of Bidens required different models for each phenological phase. However, the best adaptation was obtained with the same model for both species.

The sowing-emergence phase has been described well by a thermal model (NOAA) and the two species showed the same parameter values. With this model the phase ends when an average of 76 useful degrees has been accumulated.

The different weather conditions in the two years did not affect the duration of emergence-flowering, while the flowering-maturity phase was shorter in 1997, with a reduction from 2–3 days in early sown plants to 10–11 days in late sown ones. Applying the MPT model to the entire biological cycle, with the parameters estimated on the basis of the 1997 data and applied to 1996 conditions, underestimated the 1996 phenological data. This appears to be due to water shortage and seems to explain why the MPT model gave better estimates of the emergence-flowering phase length when soil temperature instead of air was used as input variable. The estimates also appear to be much more reliable the greater the depth of temperature measurement. The effects of the soil water level are

Table 4
Emergence-flowering phase. Values for parameters $K1$, Tb and Pc of the MPT model, obtained by calibration on the two-year data.

Parameter	Unit	Bidens frondosa		Bidens tripartita	
		Value	Standard error	Value	Standard error
$K1$	% phase °C^{-1} h^{-1} day^{-1}	0.083	–	0.083	–
Tb	°C	10.77	0.893	12.38	0.779
Pc	h	15.49	0.083	15.88	0.108
Mean absolute error	% phase	8.08		8.97	
CV (RMSE)	%	10.31		10.46	
N. obs.		17		16	

The CV of the length of the emergence-flowering phase (days) was 34% for B. frondosa and 36% for B. tripartita.

Table 5
Flowering-maturity phase. Values for parameters N_{max} and fd of the WSPM model obtained by calibration on the two-year data. WSPM simulations were done adopting $Ds = 450$, $Kc = 0.3$ and $N_{min} = 1$.

Parameter	Unit	Bidens frondosa		Bidens tripartita		Both species	
		Value	Standard error	Value	Standard error	Value	Standard error
N_{max}	Day	35.20	1.000	36.31	3.130	35.280	1.120
fd	Dimensionless	0.58	0.029	0.63	0.086	0.592	0.032
Mean absolute error	% phase	4.57	–	8.31	–	6.71	–
CV (residuals)	%	5.81	–	10.10	–	8.37	–
N. obs.		16		16		32	

The CV of the phase length, expressed in days, was 10% for *B. frondosa* and 16% for *B. tripartita*.

felt in some way, giving lower soil temperatures in the presence of high moisture content.

Both species behaved like short day plants: flowering occurred in response to photoperiod, and this sharply reduced the length of the vegetative phase of late emerging plants, especially in *B. frondosa*. Plants emerging in late August can flower in less than 50 days, i.e. one third of the time required by plants emerging in early April.

The MPT model calibration allows *B. frondosa* to be identified as a more short day plant (greater sensitivity to photoperiod) as it has a lower critical photoperiod value (Pc) than *B. tripartita* (15 h 29 min against 15 h 53 min). With a photoperiod of 14 h, for example, the sensitivity of the development rate in the vegetative phase (S_P) is 9.4 for *B. frondosa* and 7.4 for *B. tripartita*. This means that a variation of 8.4 min (1% in the 14-h photoperiod) corresponds to a variation of the development rate (R) of 9.4% and 7.4% for *B. frondosa* and *B. tripartita*, respectively.

The critical photoperiod (Pc) of *B. frondosa* resulted as being close to the maximum day length at the trial's latitude (at 45° N the maximum day length is about 15 h 26 min), i.e., moving northwards the daily development rate of *B. frondosa* will be zeroed for a longer period around the summer solstice, when the photoperiod P is higher than the critical photoperiod Pc. In other words, at northern latitudes plants emerged before the solstice will not be able to reduce the duration of the emergence-flowering phase, while

B. tripartita, because of 24 min longer Pc should result as more 'flexible', up to a latitude of about 48° N.

In terms of response to temperature, *B. tripartita* showed more macrothermal behaviour because of the higher value of base temperature in the emergence-flowering phase and the higher sensitivity to temperature in terms of variation of R with respect to Tm. For instance, at 20 °C, the sensitivity of the development rate in the vegetative phase (S_T) is 2.17 for *B. frondosa* and 2.62 for *B. tripartita*. The potential effect of global warming on the dynamics of invasion is recognised by some authors (Mooney and Hobbs, 2000; Richardson et al., 2000), but *B. tripartita*, despite being more macrothermal than *B. frondosa*, does not seem to benefit from a temperature increase, at least in a partially controlled environment (Verlinden and Nijs, 2010).

The overall result of the different sensitivities to different factors is shown in Fig. 7, which reports the time course of the phenological index of both species during the emergence-flowering phase. *B. frondosa* sown early in the season starts flowering later than *B. tripartita*, while in the later sowings it starts at the same time. In other words, the later in the season *B. frondosa* emerges the greater is its ability to shorten the phase duration and to always reach flowering, almost independently of sowing time.

Plant heights differed at harvest: *B. frondosa* was always taller than *B. tripartita*, especially in early sown plants (data not shown), while differences are smaller in late sown plants, when the phase length is similar in both species.

5. Conclusion

The parameters estimation of the tested phenological models highlighted the differences in the adaptation behaviour of the two congeneric species.

The capacity of *B. frondosa* to delay reproductive development when emerging early in the season permits greater vegetative growth, therefore, although competitive ability was not explored in this experiment, it seems likely that *B. frondosa* would be more competitive, as shown by Oliver (1979) in *A. theophrasti*. Furthermore, the seed production potential is higher in taller plants, increasing the spreading capacity of a species.

On the other hand, the later and shorter period of flowering, and therefore seed ripening, of *B. frondosa* could be a disadvantage in an agricultural habitat, where disturbances like crop harvesting could impede or reduce the seed return to the soil (Huang et al., 2000). The flowering-maturity phase was the most difficult to model. Daylength was less relevant than expected for short day plants like the studied species: this phase was very short (35 days maximum) and started almost in the same period of the year (September) for all sowing dates, because of the plasticity of the previous phase.

The best model found for the flowering-maturity phase was that based on water stress, which shows that *B. tripartita* is able to complete the cycle more quickly and ripen the seeds first if there is a shortage of water in the soil. This result supports the conclusions of Bendova and Gruberova (1999a): their study showed that
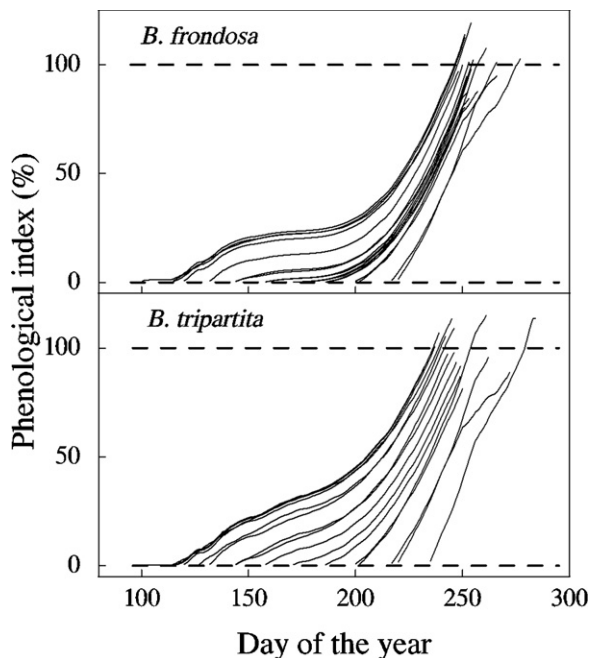

Fig. 7. Time course of the phenological index for the phase emergence-flowering (*PHI*) obtained with the model MPT for *B. frondosa* and *B. tripartita* for all the sowing times of the two years. Each curve represents a sowing time.

B. tripartita requires higher site moisture than *B. frondosa*. The non-native species grows well and occurs in a wider variety of site moisture conditions than the native species.

In conclusion, the study showed that the two species are not so different in terms of phenological development, although the models highlighted some differences in terms of response to temperature, photoperiod and soil water availability. *B. frondosa* seems to be generally more plastic than *B. tripartita*, as it is able to regulate the vegetative phase length better, perhaps acquiring greater competitivity and a higher seed production potential.

The phenological differences showed in this study, together with other differential traits reported by Kock (1988), Bendova and Gruberova (1999a, 1999b) and Brandel (2004), like higher growth rate and dry matter production, higher reproductive capacity and greater ease of spread by epizoochory (in particular for the central achenes that are morphologically better adapted for dispersal by animals), support the observed higher invasive capacity of *B. frondosa* in comparison with the congeneric species *B. tripartita*. The role of these differences in determining the invasive ability of the two species can only be hypothesised and can vary greatly with the environment, especially in agricultural habitats characterised by a high variability of type and timing of disturbances.

The modelling approach and the information obtained in the study are anyway a basic requirement for the construction of more comprehensive models of *Bidens* growth and population dynamics and for developing risk assessment systems for screening likely invasive plants (Bernez et al., 2006; Dahler et al., 2004).

Acknowledgements

Appendix A. Water stress phenological model (WSPM)

Considering a maximum phase length (N_{max}) existing for a plant, being determined by genotype, we assume that this phase is shortened by the soil water content below a critical value (Mc).

The effect of water shortage is represented by a stress index (SI) linearly related to water content and assuming values between 0 (at Mc or higher moisture) and 1 (at wilting point, WP). The duration of the phase N goes from N_{max} to a minimum value N_{min}, at WP.

$$N = N_{max} \cdot (1 - SI) + N_{min} \cdot SI$$

So, we can calculate the daily development rate (R_{fm}) as:

$$R_{fm} = \frac{100}{N_{max} \cdot (1 - SI) + N_{min} \cdot SI}$$

Soil moisture (Ms) during the plant cycle is calculated from the amount of water in the soil (Q) and from the useful soil depth for the plant (Ds): $Ms = Q/Ds$ ($mm_{water}\ mm_{soil}^{-1}$). No gravel has been assumed.

Q is obtained daily for each day t of the phase by applying the following water balance:

$$Q_t = Q_{t-1} + Ru - ETa \quad (mm),$$

where Ru is the useful rainfall (mm per day), corresponding to the amount of daily rainfall ($Rain$) that can be held by the matric strength of the soil:

$$Ru = Rain \qquad \text{if } Rain \leq Ds \cdot (FC - Ms)$$
$$Ru = Ds \cdot (FC - Ms) \quad \text{if } Rain > Ds \cdot (FC - Ms)$$

ETa is the actual evapotranspiration ($mm\ day^{-1}$), obtained by the following equations:

$$ETa = ETm \cdot (Ms - WP)/(Mc - WP) \quad \text{for } WP < Ms < Mc$$
$$ETa = 0 \qquad\qquad\qquad\qquad\qquad\ \text{for } Ms \leq WP$$
$$ETa = ETm \qquad\qquad\qquad\qquad\ \ \text{for } Ms \geq Mc$$

where Etm is the maximum evapotranspiration, obtained as $Etr \cdot Kc$. ETr is the reference evapotranspiration and Kc is a water consumption crop coefficient. The values adopted for Ds and Kc were 450 mm and 0.3, respectively, and obtained by iterative calibrations. At the experimental site (Legnaro), the measured values of FC and WP were 0.36 and 0.14 ($mm_{water}\ mm_{soil}^{-1}$).

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