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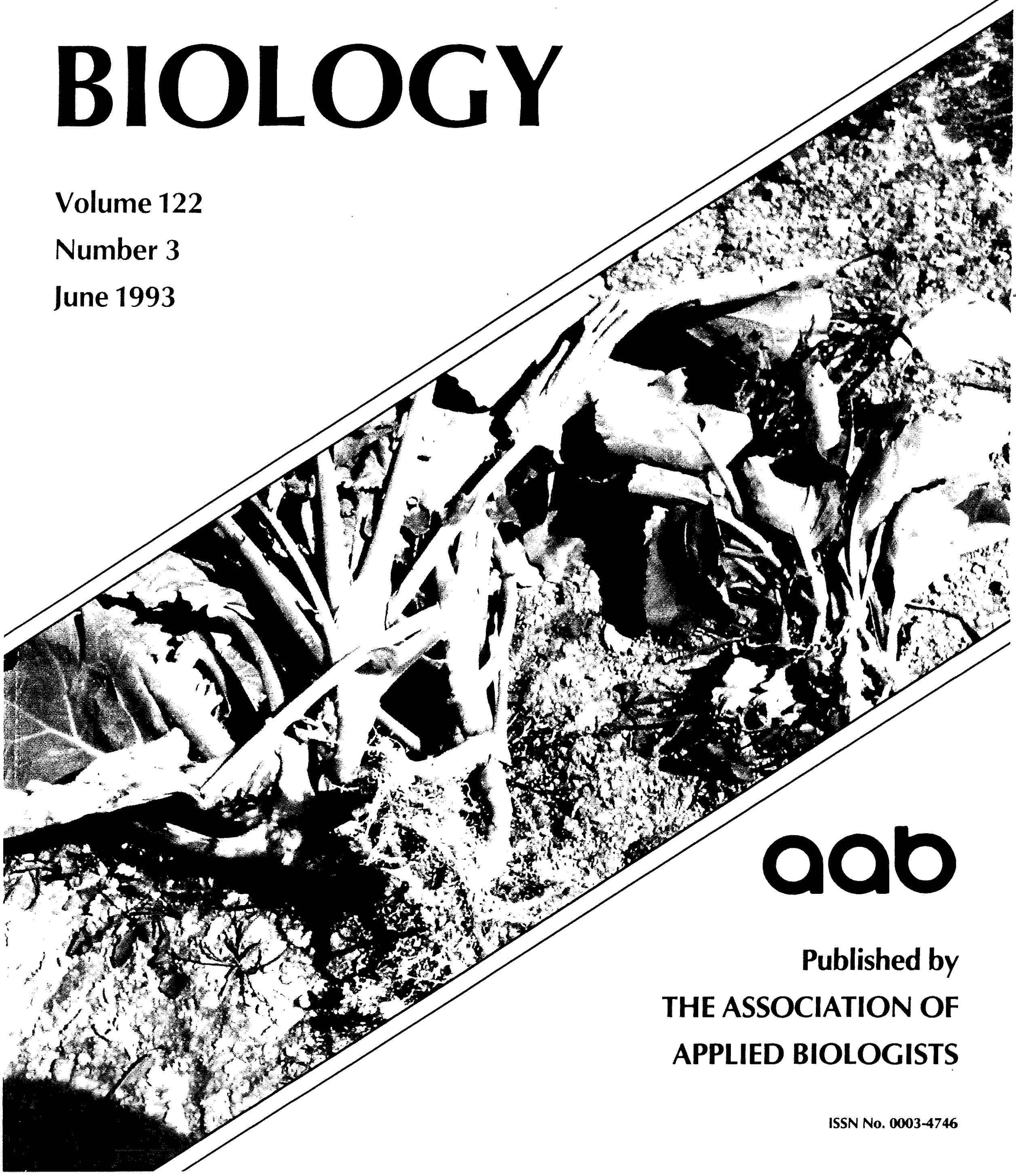

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By S. E. WEAVER[1], M. J. KROPFF* and R. COUSENS**

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A simulation model of *Avena fatua* L. (wild-oat) growth and development

By S. E. WEAVER[1], M. J. KROPFF* and R. COUSENS**

Agriculture Canada, Research Station, Harrow, Ontario, Canada N0R 1G0
**International Rice Research Institute, Agroecology Unit, P.O.B. 933, 1099*
Manila, Phillippines, and Department of Theoretical Production Ecology,
Agricultural University, P.O. Box 430, 6700 AK Wageningen, The Netherlands
***School of Crop Sciences, University of Sydney, New South Wales 2006,*
Australia

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Summary

An eco-physiological simulation model of the growth and development of *Avena fatua* was parameterised and tested. The model simulates growth of *A. fatua*, in kg dry matter ha^{-1} day^{-1}, from sowing to maturity as a function of irradiance, temperature and various species characteristics. Parameter values were derived from the literature and from field experiments, including both autumn and spring sowings of *A. fatua* over three years at two sites in southern England. With two exceptions, a single set of parameter values was sufficient to accurately simulate the emergence, growth and development of both autumn and spring cohorts over all years and sites. The two exceptions were the result of differences between autumn and spring cohorts of *A. fatua* in the rate of early leaf area growth and in the relationship between specific leaf area and developmental stage.

Key words: *Avena fatua*, wild-oat, simulation model

Introduction

Avena fatua is one of the most troublesome weeds worldwide (Holm, Plucknett, Pancho & Herberger, 1977). Crop yield losses due to *A. fatua* infestations have been abundantly documented, particularly for cereals (Bowden & Friesen, 1967; Wilson & Peters, 1982; Carlson & Hill, 1985). The ability of *A. fatua* to reduce crop yields is known to vary with weed and crop density, the time of emergence of the weed with respect to the crop, geographic location, soil type and climate (Peters & Wilson, 1983; Cousens, Brain, O'Donovan & O'Sullivan, 1987). In areas of the world with mild winters, *A. fatua* may occur as either a winter or summer annual. Several recent studies have documented the importance of the timing of morphological development, particularly with respect to height and light interception, in determining the outcome of competition between *A. fatua* and both winter and spring cereals (Cousens *et al.*, 1991; Cudney, Jordan & Hall, 1991; Morishita, Thill & Hammel, 1991). The rate of development of *A. fatua* is strongly influenced by temperature and photoperiod (Sharma & Vanden Born, 1978; Adkins, Loewen & Symons, 1987; Cudney, Jordan, Corbett & Bendixen, 1989; Rooney, Brain & Loh, 1989).

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[1] Corresponding author

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Cousens *et al.* (1992) previously quantified the relationship between temperature and photoperiod and *A. fatua* phenology and canopy development. In order to predict *A. fatua* competitive ability as a function of environmental conditions, a weather-driven, physiologically based simulation model of *A. fatua* growth and development was constructed.

Process-oriented simulation models of crop growth have been developed for a number of species (Penning de Vries & van Laar, 1982; Weir, Bragg, Porter & Rayner, 1984; Spitters, van Keulen & van Kraalingen, 1989). Simulation models of weed-crop competition involving light, water, and nutrient resources were first introduced by Spitters & Aerts (1983), and further developed in subsequent studies (Kropff, 1988; Spitters, 1989; Graf *et al.*, 1990; Wilkerson, Jones, Coble & Gunsolus, 1990; Kropff & Spitters, 1992). The present study describes the parameterisation and testing of a simulation model for *A. fatua* grown in monoculture, based on the model of Spitters *et al.* (1989). A subsequent paper will show the application of the model to competition between *A. fatua* and winter wheat.

Model Description

A detailed description of the basic structure of the weed-crop model and a program listing were given in Spitters *et al.* (1989) and Spitters (1989). The model was adapted to simulate growth of *A. fatua*, in kg dry matter ha^{-1} day^{-1}, from sowing to maturity with a time step of one day. Dry matter accumulation is simulated as a function of irradiance, temperature and various species characteristics. For this application, soil moisture and nutrients were assumed to be adequately supplied. The effects of insects and diseases on *A. fatua* growth are not considered in the model. The most detailed and mechanistic part of the model concerns the distribution and absorption of light within the canopy. Plant development and dry matter partitioning are less well understood, and so are treated in a more descriptive fashion.

The model calculates light absorption within the canopy based upon the amount of incoming radiation, and the leaf area indices, vertical distribution of leaf area, and light extinction coefficients of the species. The horizontal distribution of leaf area is assumed to be homogeneous, and the vertical distribution of leaf area is assumed to be parabolic in shape. The model calculates leaf area in two ways. Prior to canopy closure, leaf expansion is assumed to be limited primarily by temperature rather than irradiance, and leaf area is calculated as a function of accumulated degree days. After canopy closure, leaf area is calculated as the product of leaf weight per unit area and the specific leaf area.

Instantaneous rates of CO_2 assimilation are calculated at different depths within the canopy, based on the amount of light intercepted and the photosynthetic rates of individual leaves, and are then integrated over the height of the canopy and over the day. The net daily growth rate, in kg dry matter ha^{-1} day^{-1}, is obtained by converting the assimilated CO_2 into carbohydrates (CH_2O) and subtracting the amount used for maintenance respiration. Integration of the daily growth rate over time gives the seasonal growth curve. The distribution of dry matter to the various plant organs and the growth in canopy height of the plants are simulated as an empirical function of developmental stage. Phenological development of *A. fatua* is simulated as an empirical function of accumulated degree days modified by photoperiod (Weir *et al.*, 1984).

Required inputs to the model include daily weather data (maximum and minimum temperature, global radiation, rainfall), site latitude, sowing density, date of sowing and biological parameters specific to the species. Parameter values of *A. fatua* were derived both from the literature and from field experiments. A listing of these parameters and the values used in the model is given in Tables 1 and 2.

Table 1. *Parameter values used in the model for* A. fatua

Description	Value[a]
Light interception and photosynthesis:	
Extinction coefficient for PAR	0.44 ha ha^{-1}
Initial light use efficiency	0.45 kg CO_2 ha^{-1} $h^{-1}/(Jm^{-2}$ $s^{-1})$
Maximum photosynthetic rate of individual leaves	40 kg CO_2 ha^{-1} h^{-1}
Maintenance respiration coefficients:	
Leaves	0.03 kg CH_2O kg^{-1} DM day^{-1}
Stems	0.015 kg CH_2O kg^{-1} DM day^{-1}
Roots	0.01 kg CH_2O kg^{-1} DM day^{-1}
Reproductive organs	0.01 kg CH_2O kg^{-1} DM day^{-1}
Assimilation requirements:	
Leaves	1.52 kg CH_2O kg^{-1} DM
Stems	1.55 kg CH_2O kg^{-1} DM
Roots	1.49 kg CH_2O kg^{-1} DM
Reproductive organs	1.42 kg CH_2O kg^{-1} DM
Crop height:	See Figure 1
Dry matter partitioned to the leaves:	See Figure 2
Leaf area growth prior to canopy closure:	See Figure 3
Specific leaf area:	See Figure 4
Relative death rate of leaves:	See Figure 5

[a]References: Gealy & Morrow, 1983; van Heemst, 1988; Penning de Vries & van Laar, 1982; Spitters 1989 (see text).

Table 2. *Parameter values used for phenological development of* A. fatua

Growth stage	Base temperature (°C)	Base photoperiod (h)	Accumulated degree days (°C days)
Phenological development:			
Sowing to emergence	1	—	148[a]
Emergence to stem extension	1	8	120[b]
Stem extension to anthesis	1	0	490[b]
Anthesis to maturity	1	—	642[a]

[a]Thermal time over i days calculated as:

$$\sum_{1}^{i}\left(\frac{T_{\max}+T_{\min}}{2}-T_{\text{base}}\right)$$

where $T_{\max}$, $T_{\min}$ and T_{base} are the daily maximum and minimum temperatures and the base temperature, respectively.

[b]Photothermal time over i days calculated as:

$$\sum_{1}^{i}\left[\left(\frac{T_{\max}+T_{\min}}{2}-T_{\text{base}}\right)\left(\frac{P_i-P_{\text{base}}}{24-P_{\text{base}}}\right)\right]$$

where P_i and P_{base} are the photoperiod on day i and the base photoperiod, respectively.

Experimental Design

Parameters describing phenology, leaf area development, canopy height and dry matter partitioning were based upon field experiments, conducted between 1986 and 1988, comprising four autumn sowings and three spring sowings of *A. fatua* grown in monoculture. Details of five of these sowings were reported previously by Cousens *et al.* (1992), and the

Table 3. *Dates of sowing, location, soil type and plant density for experiments used to parameterise the model*

Date of sowing	Location	Soil type	Plant density (# m^{-2})
18 September, 1986	Long Ashton	Sandy silt loam	267
14 April, 1987	Long Ashton	Sandy silt loam	264
12 May, 1987	Long Ashton	Sandy silt loam	265
22 September, 1987	Long Ashton	Sandy silt loam	281
14 March, 1988	Long Ashton	Sandy silt loam	249
17 October, 1988	Long Ashton	Sandy silt loam	203
26 October, 1988	Broom's Barn	Sandy loam	243

other two by Cousens *et al.* (1991). Data from all seven sowing dates were combined and reanalysed to derive the parameter values used in the model.

Dates of sowing, location, soil type, and plant density are summarised in Table 3. *A. fatua* seeds used in all experiments were taken from the same stock, collected in 1985, at Begbroke Hill, Oxford, and sieved to obtain a uniform sample in the range 1.5–2.0 mm. In five of the seven sowings the seeds were pricked with a needle before sowing to break dormancy. Seeds were sown at a depth of 5 cm in a regular grid pattern, with a spacing of approximately 7 cm between rows and 5 cm within rows. Plots were 1.2 m × 2.0 m in a randomised complete block design with four or six replicates. Other weeds were removed by hand. Nitrogen fertiliser, fungicides and insecticides were applied as required to meet the assumptions of the model that nutrients and pests did not limit plant growth (Cousens *et al.*, 1991, 1992).

Emergence was monitored daily until the main flush of germination had ceased. Destructive harvests were made at frequent intervals from emergence to anthesis, with sample sizes varying from 16 to 24 plants per sampling date. Sampling was conducted systematically from the ends of the plots, leaving guard rows around the outside border and between sampling dates, to avoid edge effects. Canopy height was measured from the ground to the highest point on the uppermost leaf. Plants were cut at soil level, and stem length, leaf area of green leaves, and dry weight of stems, green leaves and dead leaves were recorded. Stem length was measured from the crown node to the base of the developing panicle. The date of the beginning of stem extension was estimated by linear regression of the logarithm of stem length against thermal time. Heading, or panicle emergence, was recorded when the spikelets first appeared above the flag leaf. Anthesis was recorded when approximately 50% of the proximal spikelets had released pollen.

Estimation of Parameter Values

Photosynthesis and respiration

Characteristics describing photosynthesis and respiration (Table 1) were taken primarily from the literature. Where values for *A. fatua* were unavailable, those reported for cereals were used.

Values of the extinction coefficient for photosynthetically active radiation and the initial light use efficiency were chosen within the ranges previously reported for cereals (van Heemst, 1988; Spitters *et al.*, 1989). The maximum rate of photosynthesis of young, fully expanded leaves at light saturation (25°C) was taken from a growth chamber study of four

A. fatua ecotypes from the northwestern United States (Gealy & Morrow, 1983). The rate of photosynthesis did not differ among ecotypes, but declined as the plants aged. In the model, the maximum rate of photosynthesis remains at 40 kg CO_2 ha^{-1} h^{-1} from emergence to anthesis, and then declines linearly to 20 kg CO_2 ha^{-1} h^{-1} at maturity.

Maintenance respiration requirements used in the model were those reported for wheat at 25°C with $Q_{10} = 2$ (van Heemst, 1988; Penning de Vries & van Laar, 1982). Maintenance requirements decrease as the plants age in proportion to the fraction of the accumulated leaf weight that is still green (Spitters *et al.*, 1989). Requirements for growth respiration, or the conversion of carbohydrates into dry matter of the various plant organs, are values typical for cereals (van Heemst, 1988; Spitters *et al.*, 1989).

Phenological development

For the purposes of the simulation model, the life cycle of *A. fatua* was divided into four stages along a dimensionless scale, where 0 is emergence, 1 is the beginning of stem elongation, 2 is anthesis and 3 is maturity. These phenological stages were chosen to correspond to changes in the distribution of dry matter within the plant and the growth in canopy height. Emergence was simulated as a function of the mean number of accumulated degree days from sowing to 50% emergence. Development from emergence to anthesis depends upon both temperature and photoperiod, and so was simulated as a function of accumulated degree days modified by photoperiod (photothermal time) using the method of Weir *et al.* (1984) (Table 2). Development between anthesis and maturity was assumed to depend only upon temperature. Because the field observations of development did not extend beyond anthesis, data from the literature were used to determine the approximate length of time between anthesis and maturity (Thurston, 1959; Sharma & Vanden Born, 1978). Base temperatures and photoperiods used to calculate accumulated degree days or photothermal time for each developmental stage were derived by Cousens *et al.* (1992) and are shown in Table 2.

Canopy height and dry matter distribution

Cousens *et al.* (1992) demonstrated that the canopy height of *A. fatua* increases linearly with photothermal time from the beginning of stem extension until anthesis. The model treats canopy height as a function of developmental stage throughout the life cycle (Fig. 1). Canopy height increases from 1 to 15 cm between emergence and the beginning of stem extension, to 110 cm at anthesis, and then levels off. The model calculates daily canopy height by linear interpolation between these values. This is of course an approximation of what is more realistically an s-shaped curve, but with height declining slightly between anthesis and maturity. All sowings followed a similar pattern of growth in canopy height except the October, 1988, Long Ashton sowing. Height measurements for this sowing were, unfortunately, made to the top of the inflorescence rather than the top of the leaf canopy. Canopy height does not affect simulations in monoculture, because the growth of the population (kg ha^{-1}) rather than of individual plants is modelled, and the horizontal distribution of leaf area is assumed to be homogeneous for each species. The height of the canopy is an important parameter in simulating competition between plant species, however, because it influences the relative share of the incoming radiation that each receives.

The partitioning of dry matter to the leaves, stems, roots and reproductive organs is also treated as an empirical function of developmental stage. In the model, the total daily increment of dry matter is first divided between "shoots" and roots, and then the "shoot" fraction is further subdivided between leaves, stems and reproductive organs. These fractions

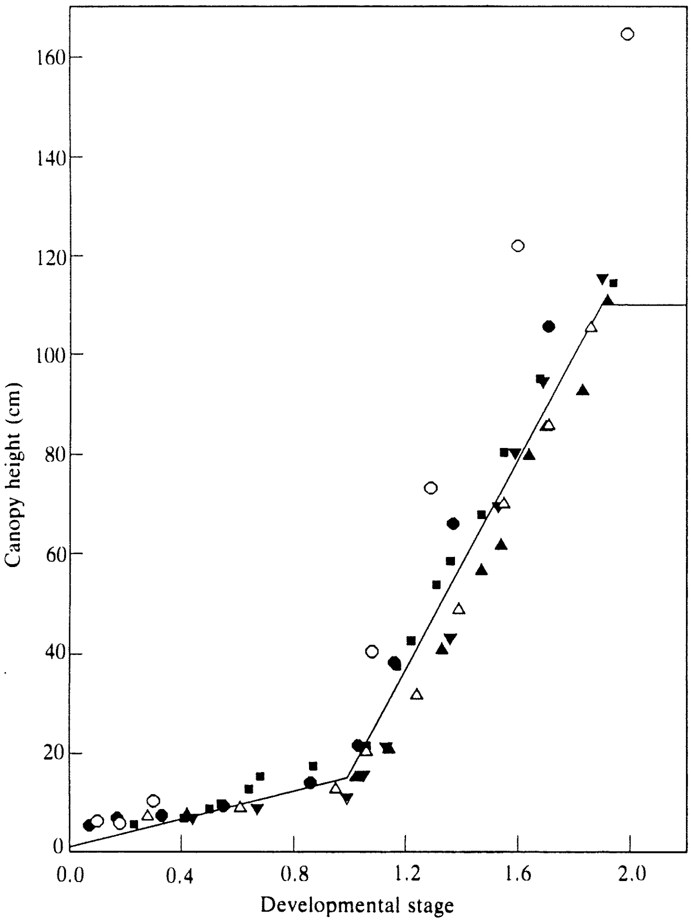

Fig. 1. Canopy height as a function of developmental stage for spring and autumn sowings of *A. fatua*: △, April 1987; ▲, May 1987; ▽, March 1988; □, September 1986; ■, September 1987; ○, October 1988; ●, October 1988, Broom's Barn. All sowings but the last were at Long Ashton. The solid line indicates the relationship used in the model.

are derived by calculating the proportion of new dry matter allocated to the various plant organs between two subsequent harvests. Roots were not harvested in the field experiments. The model assumes that 30% of new assimilates are allocated to the roots and 70% to the shoots between emergence and the beginning of stem extension, based on values reported for cereals (Weir *et al.*, 1984; van Heemst, 1988). Between stem extension and anthesis, the proportion allocated to the roots declines linearly to 0%, while the proportion going to the shoots increases to 100%. Assimilates partitioned to the shoots are divided between the leaves and the stems until shortly before anthesis. The fraction of new assimilates allocated to green leaf tissue as a function of developmental stage for all sowings is shown in Fig. 2. After anthesis, all new assimilates are allocated to the reproductive organs.

Leaf area

Prior to canopy closure, the model calculates leaf area as an exponential function of accumulated degree days. In the *A. fatua* experiments, spring sowings had a significantly

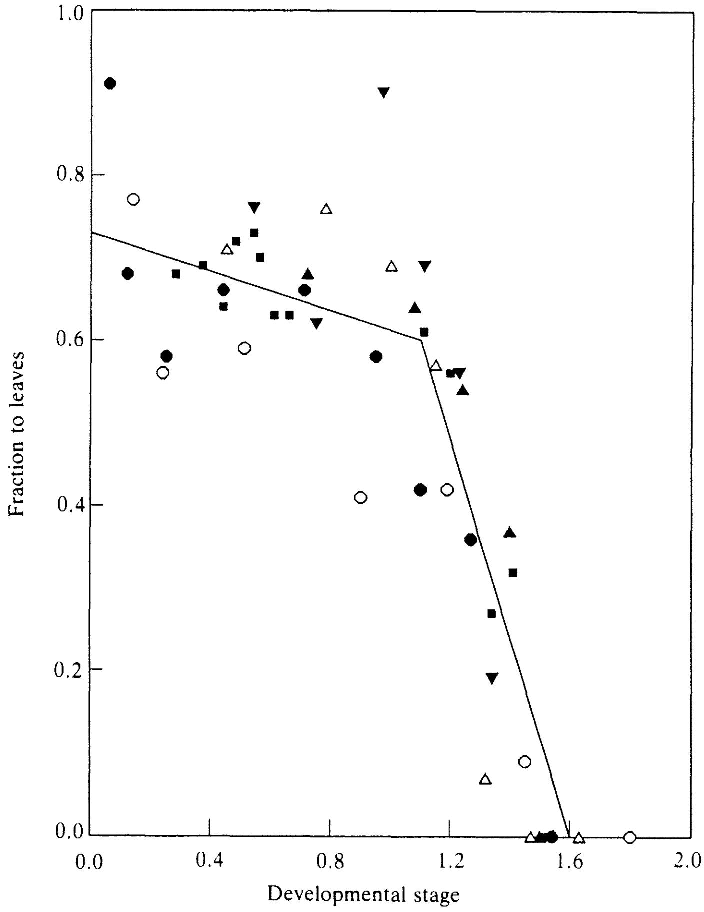

Fig. 2. The fraction of new "shoot" assimilates that are partitioned to the leaves as a function of developmental stage for spring and autumn sowings of *A. fatua*. Symbols are as in Fig. 1. The solid line indicates the relationship used in the model.

higher slope than autumn sowings (Fig. 3). Simulations using a single equation for autumn and spring sowings with an intermediate slope consistently overestimated growth of autumn sowings and underestimated growth of spring sowings. The effect of irradiance on early leaf area development of *A. fatua* is not clear. Cousens *et al.* (1992) reported a linear relationship between log (leaf area) and photothermal time, using a different base temperature and photoperiod than that required for development. They suggested that the rate of leaf appearance may depend upon photoperiod as well as temperature, but noted that it is difficult to disentangle the effects of photoperiod and irradiance. Rooney *et al.* (1989) reported a rate of leaf initiation dependent only upon temperature when plants were grown in growth chambers at constant photoperiod. In the absence of a quantitative understanding of the effects of irradiance on early leaf area development, separate functions were used for autumn and spring sowings in the model.

Similarly, the relationship between specific leaf area (SLA) and developmental stage varied for autumn and spring sowings of *A. fatua* (Fig. 4). The SLA of spring sowings tended to remain constant between emergence and anthesis, whereas the SLA of autumn

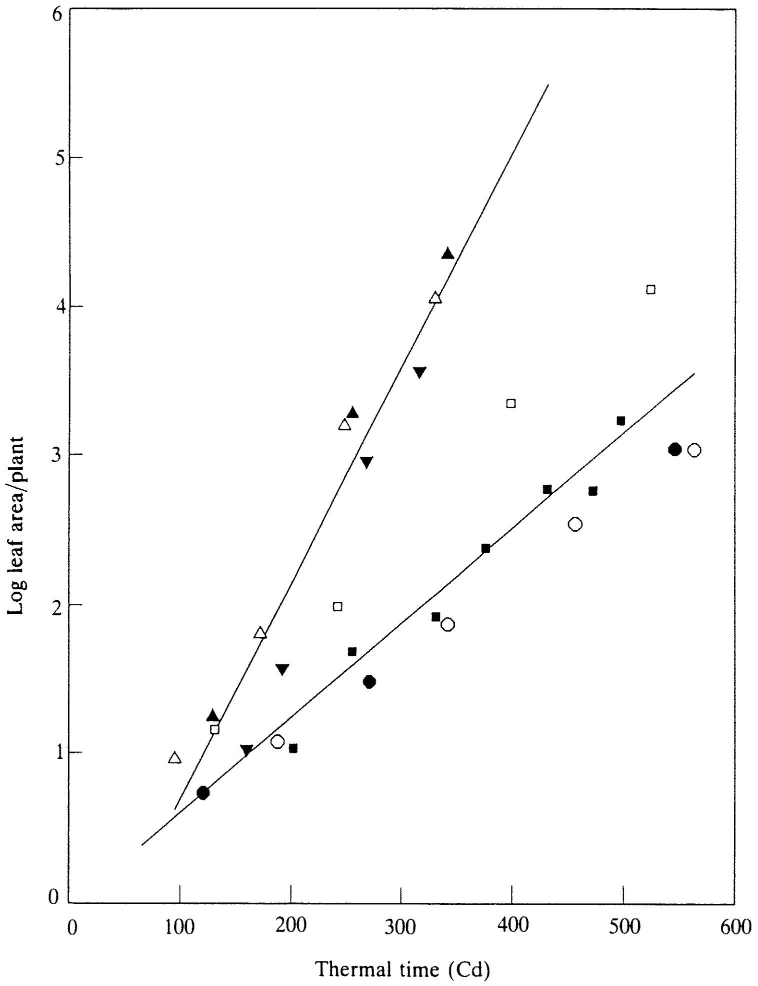

Fig. 3. The natural logarithm of leaf area per plant (cm^2) as a function of thermal time (T_{base} = 1 C) from emergence until an LAI of 1 for spring and autumn sowings of *A. fatua*. Symbols are as in Fig. 1. The solid lines represent fitted regression equations which are used in the model: spring, $Y = -2.64 + 0.014X$; autumn, $Y = -0.82 + 0.006X$.

sowings declined. All sowings showed marked fluctuations in SLA from one harvest to the next. The Broom's Barn (October, 1988) sowing generally had much lower SLA values than the other sowings from emergence through to stem extension. In the model, leaf area after canopy closure is calculated as the product of leaf dry weight and SLA, with SLA determined as a function of developmental stage. The relationship between SLA, irradiance, temperature and development of *A. fatua* is not well understood, and so separate functions were used for autumn and spring sowings.

To account for leaf senescence, a relative death rate of leaves (RDRL) was calculated as a function of developmental stage (Fig. 5). RDRL is obtained by dividing the increment in dead leaf tissue between two subsequent harvests by the leaf dry weight at the beginning of the interval. The net growth rate of leaves is obtained by subtracting the leaf death rate from the growth rate of new leaf tissue. Based on the field experiments, the relative death rate of *A. fatua* leaves was estimated to increase linearly from 0 at emergence to 0.007 kg

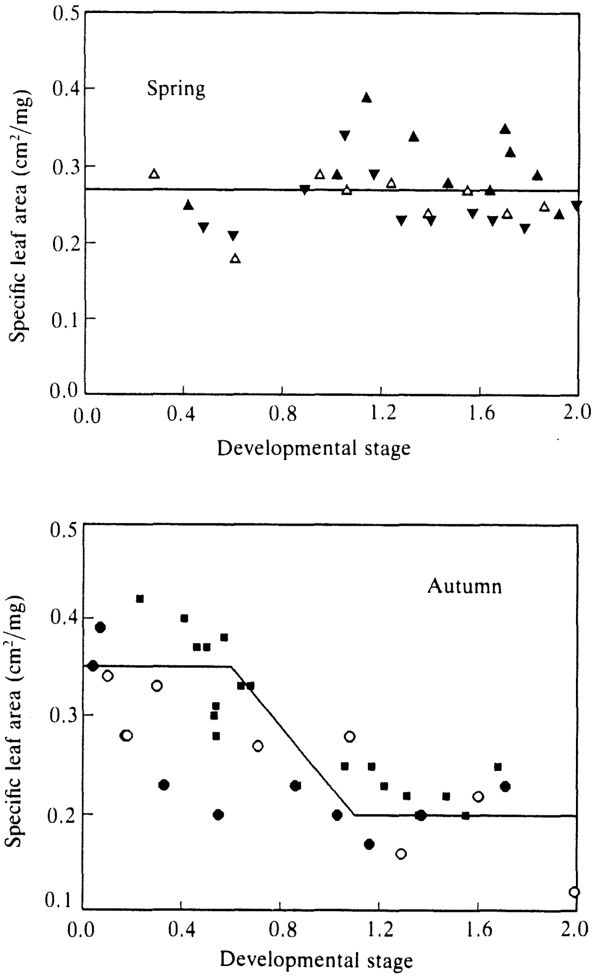

Fig. 4. Specific leaf area as a function of developmental stage for spring and autumn sowings of *A. fatua*. Symbols are as in Fig. 1. The solid lines indicate the relationships used in the model.

ha^{-1} day^{-1} shortly after the beginning of stem extension, to 0.02 kg ha^{-1} day^{-1} at anthesis. The relative death rate of stems was assumed to be 0, because the weight of stem tissue lost during tiller death is very small compared to the weight of leaf tissue lost. These rates reflect ontogenetic development, and neglect senescence due to shading or extreme temperatures. Establishing the relationship between RDRL and temperature will be an important improvement to the model, because it is evident from Fig. 5 that leaf death began earlier in the autumn sowings than in the spring sowings and earlier in the October sowings than in the September sowings.

Model Performance

Simulation runs with the model were conducted in two ways. First, the model was run using a single set of parameter values for all seven sowing dates, but with observed leaf areas from sequential harvests for each sowing as input, in order to evaluate the carbon

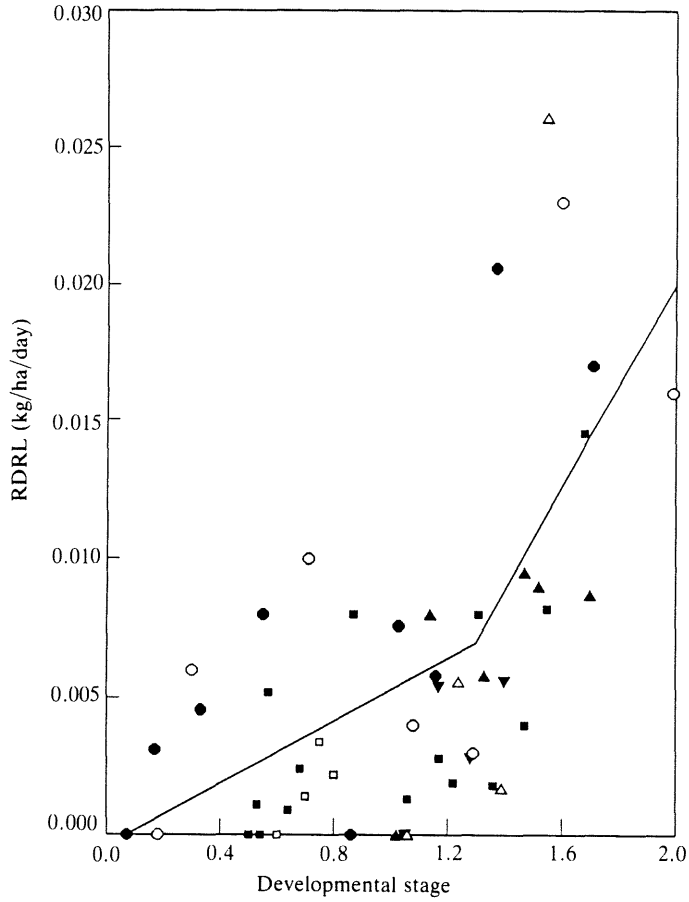

Fig. 5. The relative death rate of leaves (RDRL) as a function of developmental stage for spring and autumn sowings of *A. fatua*. Symbols are as in Fig. 1. The solid line indicates the relationship used in the model.

balance section of the model. Secondly, runs were conducted in which leaf area was simulated, again using a single set of parameter values with the exception of separate functions for autumn and spring sowings to describe early leaf area growth and specific leaf area. This allowed the analysis of model behaviour with respect to morphological processes. The performance of the model was evaluated based on its ability to accurately simulate *A. fatua* growth for each of the seven sowings. These runs do not represent a true "validation" of the model with an independent data set, because model performance was assessed against the same data sets from which the parameter values were derived. However, the parameter values are based on data from multiple years, sites and times of emergence, rather than a single experiment. This demonstration therefore serves as an indication of how well the model simulates growth of *A. fatua* on the basis of physiological responses to a range of environments.

The model generally performed well for both autumn and spring sowings of *A. fatua* when observed leaf areas were input to the model (Figs. 6, 7). However, dry matter growth was underestimated by the model for the harvest just prior to anthesis in the October, 1988, Long Ashton and Broom's Barn sowings. The model slightly overestimated dry matter

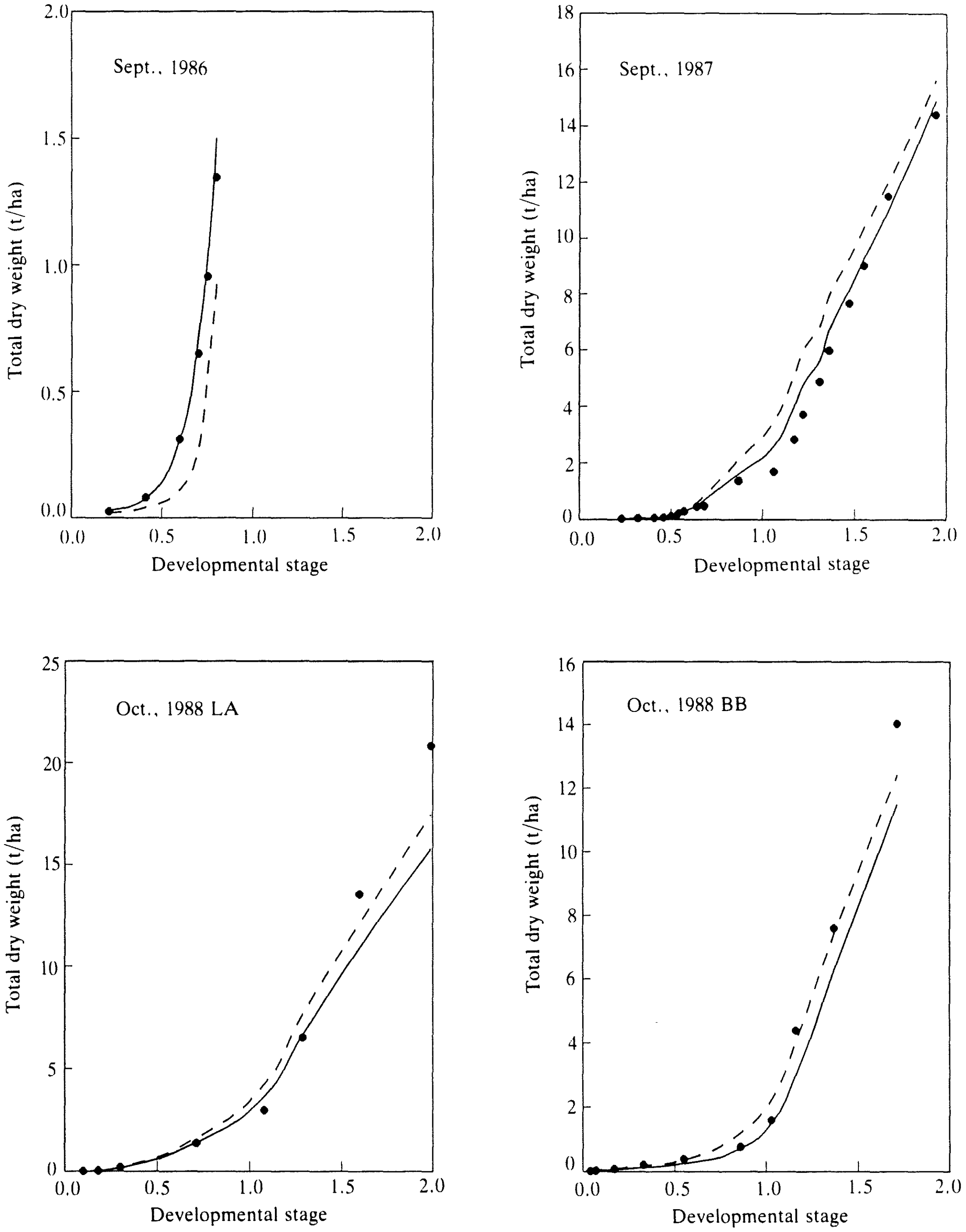

Fig. 6. Simulated (lines) and observed (●) total above-ground dry weight of autumn sowings of *A. fatua* as a function of developmental stage. The solid lines represent model runs with observed LAI values as input; the dashed lines represent model runs with simulated LAI.

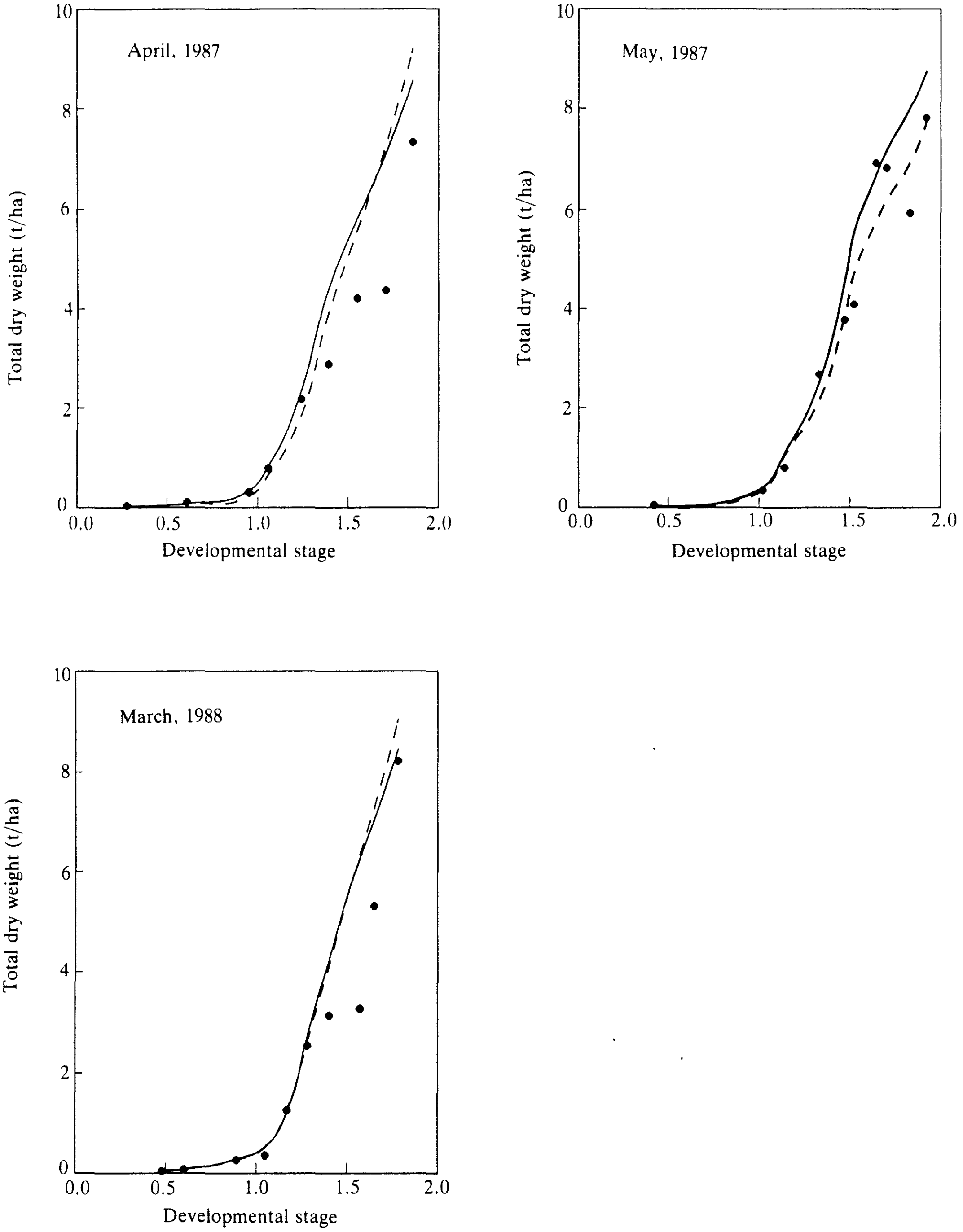

Fig. 7. Simulated (lines) and observed (●) total above-ground dry weight of spring sowings of *A. fatua* as a function of developmental stage. The solid lines represent model runs with observed LAI values as input; the dashed lines represent model runs with simulated LAI.

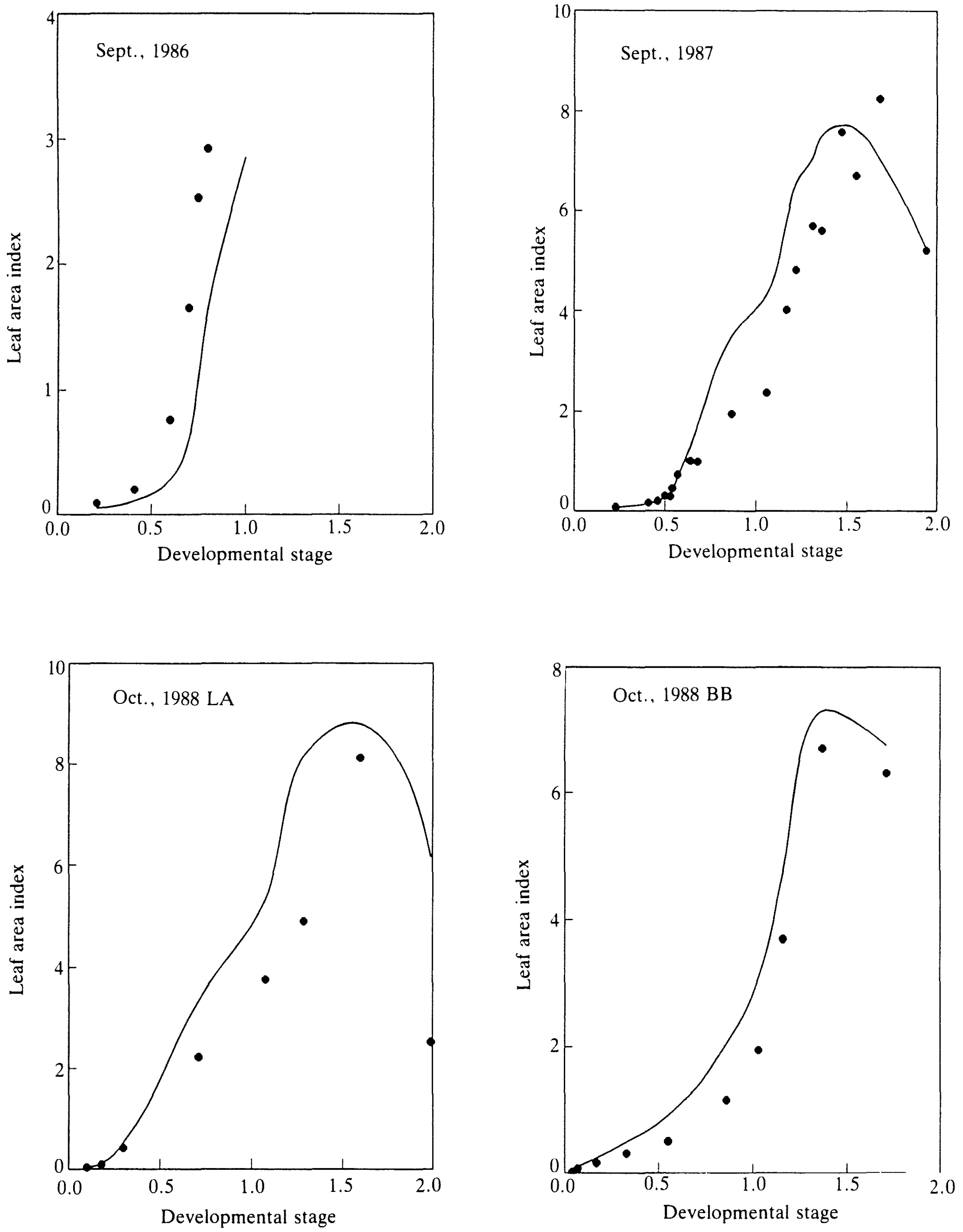

Fig. 8. Simulated (—) and observed (●) leaf area index as a function of developmental stage for autumn sowings of *A. fatua*.

growth for intermediate harvests in the April 1987, September 1987, and March 1988 sowings. The performance of the model when leaf area was simulated was similar to that when leaf areas were input. Over- or underestimations of dry matter by the model for simulated leaf areas corresponded to an over- or underestimation of LAI (Figs. 8, 9). The inability of the model to accurately simulate LAI in all cases is a reflection of the unexplained variation among sowings in specific leaf area and dry matter partitioning in relation to developmental stage. Deviations between simulated and observed leaf areas were greater than for simulated and observed dry matter, which may also reflect the greater error involved in the measurement of leaf area. Accurate simulation of LAI is less important for modelling the dry matter growth of monocultures with closed canopies, than for mixtures of plant species in which the amount and position of leaf area determines the relative amount of light interception.

Differences between autumn and spring sowings in the pattern of accumulation of dry matter and leaf area were simulated accurately by the model. Autumn sowings accumulated more dry matter (15–16 t ha^{-1}) and had greater leaf areas ($LAI = 4 - 6$) at anthesis than spring sowings ($8 - 10$ t ha^{-1} dry matter, $LAI = 3 - 4$), reflecting the longer growing period. In all sowings, leaf area peaked and then began to decline just before anthesis. The precipitous decline in LAI observed in the October, 1988, Long Ashton sowing, in the 3 week period prior to anthesis, was not observed in the other sowings and may have been anomalous.

Observed data after anthesis were not available. However, simulated seed yields at maturity, assuming a seed weight of 12 mg $seed^{-1}$ (Thurston, 1959), ranged from 125 to 255 seeds per plant, with seed production declining with date of sowing from September to May. Comparisons with the literature suggest that these are realistic values for *A. fatua* monocultures at these densities (Thurston, 1959; Sharma & Vanden Born, 1978).

Discussion

Most parts of the general model structure have been thoroughly evaluated previously through sensitivity testing and model analysis (Penning de Vries & van Laar, 1982; Spitters *et al.*, 1989). The model has been used to simulate the growth of a number of crop and weed species in monoculture and in competition with one another (Spitters & Aerts, 1983; Kropff, Vossen, Spitters & de Groot, 1984; Kropff, 1988; Lotz, Kropff & Groeneveld, 1990; Kropff, 1992*a*; Weaver, Kropff & Groeneveld, 1992; Kropff *et al.*, 1992*b*). We have demonstrated that the model can accurately simulate the emergence, growth and development of both autumn and spring cohorts of *A. fatua* grown in monoculture, based on calculations of the amount of light intercepted by the canopy and known relationships between development, dry matter partitioning, and temperature and photoperiod. A single set of parameter values was sufficient to describe phenology, dry matter distribution and canopy height for both autumn and spring sowings. Differences in early leaf area development and specific leaf area between autumn and spring cohorts remain unexplained. Deviations between observed and predicted growth of *A. fatua* were largely attributable to under- or overestimation of leaf area index. The ability of autumn cohorts to produce more dry weight and leaf area than spring cohorts has been reported elsewhere (Thurston, 1959). Further testing of the model is required for *A. fatua* monocultures grown at more extreme densities or under more adverse weather conditions.

There are a number of improvements which could be made to the model, particularly to the sections involving empirical relationships. A clearer understanding of the processes which affect specific leaf area and dry matter partitioning within the plant would improve

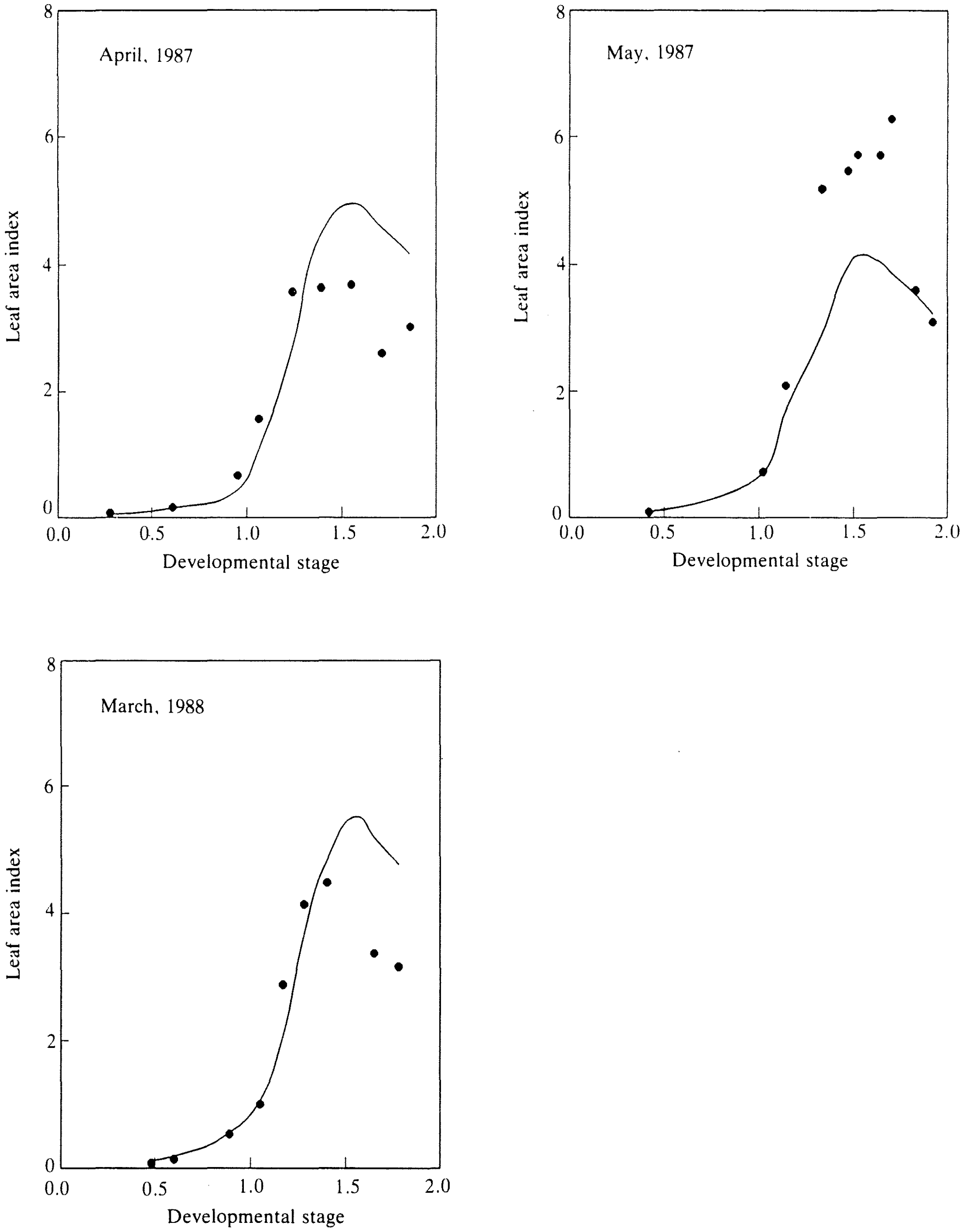

Fig. 9. Simulated (—) and observed (●) leaf area index as a function of developmental stage for spring sowings of *A. fatua*.

the ability of the model to accurately simulate leaf area. In this version of the model, the vertical distribution of leaf area has been assumed to be parabolic, but Cudney *et al.* (1991) have shown that leaf area distribution changes during the life cycle. Leaf death rates must clearly be made a function of temperature and possibly shading as well as developmental stage. Autumn germinating *A. fatua* may be killed or lose some or all of their leaves during episodes of freezing temperatures in winter. The redistribution of assimilates after leaf or stem mortality is not well understood for *A. fatua*, and has not been accounted for in the model.

Application of the model to *A. fatua* populations in other geographic areas would require an independent derivation of at least some parameter values. *A. fatua* populations are known to vary morphologically and physiologically throughout the species range (Thurston, 1957; Miller, Nalewaja & Mulder, 1982; Rooney, 1991). Developmental response to temperature and photoperiod varies with latitude of origin (Whalley & Burfitt, 1972; Somody, Nalewaja & Miller, 1984). Furthermore, some populations of *A. fatua* have shown a vernalisation response with respect to time of flowering (Paterson, Boyd & Goodchild, 1976; Darmency & Aujas, 1986).

Simulation models can be used as research tools to highlight aspects of growth and development which are not well understood. Previous studies have demonstrated the importance of morphological development and the rate of increase in leaf area in determining the outcome of competition between species (Kropff, 1988; Cousens *et al.*, 1991; Cudney *et al.*, 1991; Rooney, 1991). The pronounced differences between autumn and spring cohorts of *A. fatua* in leaf area development is a clear example of the as yet poorly understood effects of environmental factors on growth characteristics that can influence competitive interactions.

Acknowledgements

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