Predicting broccoli development
I. Development is predominantly determined by temperature rather than photoperiod

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Accepted 8 November 1999

Abstract

Predictive models of broccoli (\textit{Brassica oleracea} L. var. \textit{italica} Plenck) ontogeny will aid farmers who need to forecast changes in crop maturity arising from variable climatic conditions so that their forward marketing arrangements can match their anticipated supply. The objective of this study was to quantify the temperature and photoperiod responses of development in a sub-tropical environment from emergence to floral initiation (EFI), and from floral initiation to harvest maturity (FIHM). Three cultivars, (‘Fiesta’, ‘Greenbelt’ and ‘Marathon’) were sown on eight dates from 11 March to 22 May 1997 and grown under natural and extended (16 h) photoperiods at Gatton College, south-east Queensland, under non-limiting conditions of water and nutrient supply. Climatic data, dates of emergence, floral initiation and harvest maturity were obtained. The estimated base (\(T_{\text{base}}\)) and optimum (\(T_{\text{opt}}\)) temperatures of 0 and 20°C, respectively, were consistent across cultivars, but thermal time requirements were cultivar specific. Differences in thermal time between cultivars during FIHM were small and of little practical importance, but differences in thermal time during EFI were large. Sensitivity to photoperiod and solar radiation was low in the three cultivars used. When the thermal time models were tested on independent data for five cultivars (‘Fiesta’, ‘Greenbelt’, ‘Marathon’, ‘CMS Liberty’ and ‘Triathlon’) grown as commercial crops over two years, they adequately predicted floral initiation and harvest maturity. © 2000 Elsevier Science B.V. All rights reserved.

Keywords: Broccoli; Ontogeny; Photoperiod; Temperature; \textit{Brassica oleracea}
1. Introduction

Development of predictive models for broccoli ontogeny will be useful for farmers. If they know in advance of a change of crop maturity arising from variable climatic conditions, their forward marketing arrangements can be modified accordingly, and thereby improve reliability of supply predictions (Tan et al., 1997).

Research on the effects of temperature has often assumed photoperiod does not modify floral initiation responses in broccoli (Marshall and Thompson, 1987; Thapa, 1994). However, plants grown at 17°C under 16 h photoperiod (light intensity not reported) formed floral primordia 1 week earlier than those under 8 h photoperiod (Fujime et al., 1988). Solar radiation was incorporated into thermal time models by some researchers (Marshall and Thompson, 1987; Wurr et al., 1991, 1992; Mourao and Hadley, 1998), but other workers claim that solar radiation had no effect on crop development (Pearson and Hadley, 1988; Fujime and Okuda, 1994).

Due to the difficulty of predicting the end of the juvenile stage, thermal time models have been used to predict floral initiation in broccoli (Diputado and Nichols, 1989; Fyffe and Titley, 1989; Pearson et al., 1994). The temperature response for crop development is often defined in terms of three cardinal temperatures: base ($T_{\text{base}}$), optimum ($T_{\text{opt}}$) and maximum ($T_{\text{max}}$). $T_{\text{base}}$ and $T_{\text{max}}$ are the temperatures below and above which the plant does not develop, while $T_{\text{opt}}$ is the temperature at which development proceeds most rapidly. Cardinal temperatures might have to change depending on phenological stage (Diputado and Nichols, 1989). There are variations in the reported cardinal temperatures from sowing to floral initiation. Some researchers used a standard $T_{\text{base}}$ of 4.5°C for all cultivars (Fyffe and Titley, 1989) while others calculated a $T_{\text{base}}$ of 1°C with a $T_{\text{opt}}$ of 21°C (Diputado and Nichols, 1989). There are also differences in the reported cardinal temperatures from floral initiation to harvest maturity. Reports of $T_{\text{base}}$ include 0°C (Wurr et al., 1991, 1992; Grevsen, 1998), 3°C (Diputado and Nichols, 1989) and 7°C (Pearson and Hadley, 1988; Dufault, 1997). The only $T_{\text{opt}}$ reported were 15°C (Wurr et al., 1991, 1992) and 17°C (Grevsen, 1998), and $T_{\text{max}}$ was 26.7°C for the duration from sowing to harvest (Dufault, 1997).

Our working hypothesis is that broccoli development is influenced by temperature and photoperiod. Hence, development can be predicted using thermal time models calculated from estimated cardinal temperatures. The objective of this study was to quantify the temperature and photoperiod response of three broccoli cultivars (‘Fiesta’, ‘Greenbelt’ and ‘Marathon’) from emergence to floral initiation (EFI), and from floral initiation to harvest maturity (FIHM).
2. Materials and methods

2.1. Model

An optimisation program, DEVEL (Holzworth and Hammer, 1992), was used to determine the temperature and photoperiod responses of each cultivar for durations of EFI and FIHM. DEVEL contains a library of temperature and photoperiod functions, including linear, quadratic, logistic and polynomial functions, which can be used separately or in combination to examine the independent and interactive effects of temperature and photoperiod. The 2-stage broken linear response best explained both the temperature (Fig. 1a) and photoperiod (Fig. 1b) responses. A simplex optimisation method is used by DEVEL. This requires starting conditions (estimates of the parameters to be optimised) to be supplied. Numerous initial conditions were used to guard against the identification of local optima, and to assess whether they converged to the same global optimised values (Devlin, 1994).

Accumulated thermal time (°C day) for durations of EFI and FIHM (days, $i = 1 \cdots n$) were calculated using the estimated $T_{\text{base}}$ and $T_{\text{opt}}$ of 0 and 20°C (derived in this study) based on the equation

$$\text{Thermal time} = \sum_{i=1}^{n} \left[ \frac{T_{\text{Dmax}} + T_{\text{Dmin}}}{2} \right] - T_{\text{base}}, \quad (1)$$

where $T_{\text{Dmax}}$ is the daily maximum temperature and $T_{\text{Dmin}}$ the daily minimum temperature. All $T_{\text{Dmin}} < T_{\text{base}}$ were considered to be equal to 0°C, and all

![Diagram](image1.png)

Fig. 1. Schematic representative of (a) 2-stage broken linear temperature response and (b) 2-stage broken linear photoperiod response (adapted from Holzworth and Hammer, 1992).
$T_{D_{\text{max}}}$ > $T_{\text{opt}}$ were considered to be equal to 20°C (Barger System) (Arnold, 1974; Titley, 1987; Wurr et al., 1991). $T_{\text{max}}$ was not determined for durations of both EFI and FIHM for any cultivar as the range of temperatures experienced during the autumn and winter growing period was relatively narrow. There were few days with high temperatures (e.g. >25°C), and thus determination of $T_{\text{max}}$ was not possible. Typically, thermal time models have four parameters consisting of thermal time calculated from cardinal temperatures of $T_{\text{base}}$, $T_{\text{opt}}$ and $T_{\text{max}}$. Since $T_{\text{max}}$ was not determined, our EFI and FIHM thermal time models have three parameters; viz. (i) thermal time calculated from (ii) $T_{\text{base}}$ and (iii) $T_{\text{opt}}$ for the durations of EFI and FIHM, respectively.

Effective thermal time (ETT) (Scaife et al., 1987; Wurr et al., 1991) for each day was calculated using the following equation:

$$ETT^{-1} = TT^{-1} + aR^{-1},$$  \hspace{1cm} (2)

where TT is the thermal time (°C day) for the day, $R$ the total solar radiation (MJ m$^{-2}$) for the day, and $a$ a unitless constant defining the relative importance of solar radiation and temperature for the cultivar concerned. The best attribute (chronological time, thermal time, accumulated solar radiation duration or ETT) for predicting FIHM was determined by the attribute that minimised the sowing date $F$-value for each cultivar. The attribute should ideally be independent of sowing date.

2.2. Field experiment

A field experiment was conducted at the University of Queensland, Gatton College (latitude 27°33'S, longitude 152°20'E, altitude 89 m), located in the Lockyer Valley, approximately 80 km west of Brisbane, Queensland. Three broccoli ($Brassica oleracea$ L. var. *italica* Plenck) cultivars, ‘Fiesta’ (Bejo Zaden BV, Holland), ‘Greenbelt’ and ‘Marathon’ (Sakata, Japan), were sown on eight dates (11 March, 20 March, 1 April, 10 April, 21 April, 1 May, 12 May, 22 May 1997), (sowings #1–#8) under natural and extended (16 h) photoperiods. The natural photoperiods, including civil twilight (Jones and Kiniry, 1986), were calculated for the period from when there were four leaves >2 cm to harvest maturity, assuming the juvenile stage ended at the four leaves >2 cm stage (Wiebe, 1990). These photoperiods were 12.6, 12.4, 12.0, 11.8, 11.5, 11.4, 11.3 and 11.3 h for each sowing date, respectively. The soil type was a Black Earth (Blenheim Series) or Vertosol, typical of Lockyer Valley soils (Isbell, 1996).

A split split-plot experimental design with three replicates was used. Photoperiod treatment was the main plot, sowing date the sub-plot, and cultivar the sub-sub-plot, each randomised within the next higher level. Three rows, 0.35 m apart and 8 m long (6 plants per m$^2$), were sown for each cultivar on raised beds for each sowing date. Photoperiod extension to 16 h was achieved by
installing two rows of two lights (Philips RO 80 lights of output 100 W with reflective backs), the rows of lights being 3 m apart over the appropriate sub-plot. Spill of light into neighbouring plots where the crop was grown under natural photoperiod conditions was prevented by the angle of downward projection of the light and a 3 m wide guard between the main plots. Irrigation and nutrients were supplied at rates to ensure that non-limiting conditions were maintained. Insect pests and weeds were controlled as required.

2.3. Commercial farm crops for testing the model

Crop ontogeny data to test the EFI and FIHM thermal time models was obtained from a commercial farm (latitude 27°39' S, longitude 151°21' E, altitude 364 m), located near Brookstead on the Darling Downs, approximately 200 km west of Brisbane. There were 60 sowings (Table 1) of five cultivars (‘Fiesta’, ‘Greenbelt’, ‘Marathon’, ‘CMS Liberty’ (Petoseed, USA) and ‘Triathlon’ (Sakata, USA)) over two growing seasons (1997 and 1998). Seeds were sown in double rows 0.25 × 0.25 m (8 plants per m²) on beds 1.0 m apart. The soil type was a fertile black, self-mulching cracking clay (Black Earth or Vertosol) typical

<table>
<thead>
<tr>
<th>Cultivar</th>
<th>Sowing date</th>
<th>Month</th>
<th>Year</th>
</tr>
</thead>
<tbody>
<tr>
<td>Fiesta</td>
<td>26, 3, 7, 14, 24</td>
<td>February</td>
<td>1997</td>
</tr>
<tr>
<td></td>
<td>1, 7, 11, 14, 21, 29</td>
<td>March</td>
<td></td>
</tr>
<tr>
<td></td>
<td>2, 13, 15, 23, 29</td>
<td>April</td>
<td></td>
</tr>
<tr>
<td></td>
<td>25, 26</td>
<td>June</td>
<td></td>
</tr>
<tr>
<td></td>
<td>4, 11, 18, 25, 27</td>
<td>March</td>
<td>1998</td>
</tr>
<tr>
<td></td>
<td>1, 3, 6, 14, 20, 21</td>
<td>April</td>
<td></td>
</tr>
<tr>
<td></td>
<td>1, 2, 13, 14, 27</td>
<td>May</td>
<td></td>
</tr>
<tr>
<td>Greenbelt</td>
<td>24, 28</td>
<td>February</td>
<td>1997</td>
</tr>
<tr>
<td></td>
<td>5, 8, 12, 20, 29</td>
<td>March</td>
<td></td>
</tr>
<tr>
<td>Marathon</td>
<td>17, 26</td>
<td>March</td>
<td>1997</td>
</tr>
<tr>
<td></td>
<td>4, 16, 24</td>
<td>April</td>
<td></td>
</tr>
<tr>
<td></td>
<td>12, 23</td>
<td>May</td>
<td>1998</td>
</tr>
<tr>
<td></td>
<td>30</td>
<td>May</td>
<td></td>
</tr>
<tr>
<td>CMS Liberty</td>
<td>27</td>
<td>February</td>
<td>1998</td>
</tr>
<tr>
<td></td>
<td>2, 9, 13, 16, 23</td>
<td>March</td>
<td></td>
</tr>
<tr>
<td>Triathlon</td>
<td>20, 21, 29, 30</td>
<td>April</td>
<td>1998</td>
</tr>
</tbody>
</table>
of Darling Downs soils (Isbell, 1996). Vigorous crop growth was assured by appropriate application of fertiliser, furrow irrigation and insecticides.

2.4. Data collection

Daily maximum and minimum temperatures (°C) and total solar radiation (MJ m$^{-2}$, Kipp & Zonen\textsuperscript{16} CM11 pyranometer) were obtained from a standard weather station located approximately 100 m from the experimental site at Gatton College. Temperatures at Gatton College ranged from 0 to 37°C during the experiment. Temperatures and total solar radiation at Brookstead were obtained from an on-farm automatic weather station. Time of emergence was recorded when 50% of the seedling hypocotyls had emerged from the soil. Floral initiation was determined from three randomly selected plants, removed at 3-day intervals starting 35 days after emergence. The apices were dissected under a stereoscopic light microscope (×100) and their morphological stage compared with standard electron micrographs (Tan et al., 1998). The assessment continued until the apices rated 4 on a scale of 1–7. Floral initiation was recorded when the graph of apex rating against time from emergence reached 3 (Tan et al., 1997, 1998). All broccoli heads were harvested when 50% of the heads in each sub-sub-plot had reached an inflorescence diameter of 100 mm (Dufault, 1997). The total number of leaves present was also recorded at floral initiation.

Analysis of variance (ANOVA) was completed for chronological time, thermal time, and solar radiation (accumulated daily radiation) duration of EFI and FIHM to test the independent and interactive effects of photoperiod extension, sowing date and cultivar, using the general linear model (GLM) procedure of SAS version 6.12. Regressions were calculated using SAS. Pearson correlation coefficients between accumulated solar radiation and thermal time were determined using SAS to test the independence of the predictors.

3. Results

3.1. Photoperiod, cultivar and sowing date effects

Table 2 shows that the most notable interaction was between cultivar and sowing date which was significantly different ($P < 0.01$) for both chronological time (Fig. 2a) and total leaf number (Fig. 2b). All cultivars showed a general trend of longer chronological duration of EFI when they were sown later in autumn (except for #8). For ‘Greenbelt’ and ‘Marathon’, total leaf number decreased with later sowings while for ‘Fiesta’, total leaf number decreased initially (#1–#4) but became relatively constant in later sowings (#4–#8).

The extended photoperiod treatment resulted in a delay ($P < 0.05$) of 1 day in floral initiation for all cultivars in #5 and #6 only (Fig. 2c). This suggests a very
slight short-day photoperiod response in broccoli. Further analysis using DEVEL was carried out to explain this response. Photoperiod extension did not affect the duration of FIHM when assessed by DEVEL, though significant responses were found by analysis of variance (Table 3). These significant responses are confounded by different environmental conditions affecting the chronological

Table 2
Main and interactive effects of photoperiod extension (PP), sowing date (SD) and cultivar (CV) on the chronological time (days), thermal time (°C day) and accumulated solar radiation (MJ m⁻²) during the interval from emergence to floral initiation, and total leaf number in broccoli

<table>
<thead>
<tr>
<th>Effect</th>
<th>PP</th>
<th>SD</th>
<th>CV</th>
<th>PP × SD</th>
<th>PP × CV</th>
<th>SD × CV</th>
<th>PP × SD × CV</th>
</tr>
</thead>
<tbody>
<tr>
<td>Chronological time</td>
<td>n.s.</td>
<td>*</td>
<td>*</td>
<td>*</td>
<td>**</td>
<td>*</td>
<td>n.s.</td>
</tr>
<tr>
<td>l.s.d. (P = 0.05)</td>
<td>–b</td>
<td>0.86</td>
<td>0.47</td>
<td>1.26</td>
<td>0.78</td>
<td>1.39</td>
<td>–b</td>
</tr>
<tr>
<td>Thermal time</td>
<td>n.s.</td>
<td>**</td>
<td>*</td>
<td>*</td>
<td>**</td>
<td>*</td>
<td>n.s.</td>
</tr>
<tr>
<td>l.s.d. (P = 0.05)</td>
<td>–</td>
<td>12.31</td>
<td>6.77</td>
<td>17.60</td>
<td>10.34</td>
<td>19.90</td>
<td>–b</td>
</tr>
<tr>
<td>l.s.d. (P = 0.05)</td>
<td>–b</td>
<td>10.42</td>
<td>5.65</td>
<td>15.05</td>
<td>8.99</td>
<td>16.70</td>
<td>–b</td>
</tr>
<tr>
<td>Total leaf number</td>
<td>n.s.</td>
<td>**</td>
<td>*</td>
<td>n.s.</td>
<td>n.s.</td>
<td>**</td>
<td>n.s.</td>
</tr>
<tr>
<td>l.s.d. (P = 0.05)</td>
<td>–b</td>
<td>0.62</td>
<td>0.26</td>
<td>–b</td>
<td>–b</td>
<td>0.86</td>
<td>–b</td>
</tr>
</tbody>
</table>

* P < 0.05.
** P < 0.01.
a Not significantly different (P = 0.05).
b No l.s.d. was calculated as the F-test was not significant at P = 0.05.

Table 3
Main and interactive effects of photoperiod extension (PP), sowing date (SD) and cultivar (CV) on the chronological time (days), thermal time (°C day), accumulated solar radiation (MJ m⁻²), and effective thermal time (ETT) during the interval from floral initiation to harvest maturity (FIHM) in broccoli

<table>
<thead>
<tr>
<th>Effect</th>
<th>PP</th>
<th>SD</th>
<th>CV</th>
<th>PP × SD</th>
<th>PP × CV</th>
<th>SD × CV</th>
<th>PP × SD × CV</th>
</tr>
</thead>
<tbody>
<tr>
<td>Chronological time</td>
<td>n.s.</td>
<td>**</td>
<td>*</td>
<td>n.s.</td>
<td>**</td>
<td>n.s.</td>
<td>**</td>
</tr>
<tr>
<td>l.s.d. (P = 0.05)</td>
<td>–b</td>
<td>2.10</td>
<td>0.78</td>
<td>–b</td>
<td>–b</td>
<td>2.76</td>
<td>3.11</td>
</tr>
<tr>
<td>Thermal time</td>
<td>n.s.</td>
<td>**</td>
<td>*</td>
<td>n.s.</td>
<td>**</td>
<td>*</td>
<td>**</td>
</tr>
<tr>
<td>l.s.d. (P = 0.05)</td>
<td>–b</td>
<td>27.13</td>
<td>10.67</td>
<td>–b</td>
<td>36.64</td>
<td>42.67</td>
<td></td>
</tr>
<tr>
<td>Solar radiation</td>
<td>n.s.</td>
<td>**</td>
<td>*</td>
<td>n.s.</td>
<td>**</td>
<td>*</td>
<td>**</td>
</tr>
<tr>
<td>l.s.d. (P = 0.05)</td>
<td>–b</td>
<td>28.88</td>
<td>11.27</td>
<td>–b</td>
<td>38.87</td>
<td>45.07</td>
<td></td>
</tr>
<tr>
<td>ETT</td>
<td>n.s.</td>
<td>**</td>
<td>*</td>
<td>n.s.</td>
<td>n.s.</td>
<td>**</td>
<td>*</td>
</tr>
<tr>
<td>l.s.d. (P = 0.05)</td>
<td>–b</td>
<td>24.52</td>
<td>9.45</td>
<td>–b</td>
<td>–b</td>
<td>37.81</td>
<td></td>
</tr>
</tbody>
</table>

* P < 0.05.
** P < 0.01.
a Not significantly different (P = 0.05).
b No l.s.d. was calculated as the F-test was not significant at P = 0.05.
duration of EFI. Since results of the DEVEL analysis were unaffected by this confounding factor, they were used in further analyses.

3.2. Temperature response

$T_{\text{base}}$ and $T_{\text{opt}}$ of 0 and 20°C were found for all three cultivars, these temperatures falling within the 10% confidence interval for the individual cultivars for duration of both EFI and FIHM (Tables 4 and 5). $T_{\text{base}}$ and $T_{\text{opt}}$ were consistent across cultivars for both EFI and FIHM. Thermal time requirement was specific to each cultivar. Thermal time durations of EFI for ‘Fiesta’, ‘Greenbelt’,
Table 4
Optimum rate of development (expressed as rate of progress (per day), and chronological time (days)) and thermal time (TT °C day, mean ± S.E.) duration with estimated base and optimum temperatures of 0 and 20°C during the time from emergence to floral initiation for three broccoli cultivars (‘Fiesta’, ‘Greenbelt’ and ‘Marathon’) grown at Gatton College

<table>
<thead>
<tr>
<th>Cultivar</th>
<th>Optimum rate of development (per day)</th>
<th>10% confidence interval</th>
<th>Minimum chronological duration (days)</th>
<th>TT (°C day) (mean ± S.E.)</th>
<th>r²a</th>
<th>nᵇ</th>
</tr>
</thead>
<tbody>
<tr>
<td>Fiesta</td>
<td>0.026</td>
<td>0.026–0.026</td>
<td>38</td>
<td>670 ± 3.36</td>
<td>0.89</td>
<td>16</td>
</tr>
<tr>
<td>Greenbelt</td>
<td>0.028</td>
<td>0.027–0.028</td>
<td>36</td>
<td>612 ± 5.43</td>
<td>0.70</td>
<td>16</td>
</tr>
<tr>
<td>Marathon</td>
<td>0.026</td>
<td>0.026–0.026</td>
<td>38</td>
<td>627 ± 5.90</td>
<td>0.53</td>
<td>16</td>
</tr>
</tbody>
</table>

ᵃ Coefficient of determination for the EFI thermal time model from DEVEL analysis.
ᵇ Number of observations.
Table 5

Duration (mean ± S.E.) from floral initiation to harvest maturity, expressed as chronological time (days), thermal time (°C day), accumulated solar radiation (MJ m⁻²), and effective thermal time (ETT) for three broccoli cultivars (‘Fiesta’, ‘Greenbelt’ and ‘Marathon’) grown at Gatton College

<table>
<thead>
<tr>
<th>Duration</th>
<th>Cultivar</th>
<th>Mean ± S.E.</th>
<th>F-valueᵇ</th>
<th>Mean ± S.E.</th>
<th>F-valueᵇ</th>
<th>Mean ± S.E.</th>
<th>F-valueᵇ</th>
</tr>
</thead>
<tbody>
<tr>
<td>Chronological</td>
<td>Fiesta</td>
<td>49 ± 0.62</td>
<td>11.1</td>
<td>49 ± 0.62</td>
<td>22.6</td>
<td>50 ± 0.56</td>
<td>10.45</td>
</tr>
<tr>
<td>Thermal time</td>
<td>Greenbelt</td>
<td>664 ± 5.50</td>
<td>1.5</td>
<td>660 ± 5.05</td>
<td>4.2</td>
<td>678 ± 6.96</td>
<td>7.73</td>
</tr>
<tr>
<td>Solar radiation</td>
<td>Marathon</td>
<td>619 ± 12.60</td>
<td>26.5</td>
<td>601 ± 10.97</td>
<td>49.0</td>
<td>617 ± 9.54</td>
<td>22.15</td>
</tr>
<tr>
<td>ETT</td>
<td></td>
<td>633 ± 5.21</td>
<td>1.3</td>
<td>633 ± 4.82</td>
<td>4.1</td>
<td>487 ± 4.45</td>
<td>3.85</td>
</tr>
</tbody>
</table>

ᵃ Thermal time was calculated using base and optimum temperatures of 0 and 20°C. ETT was calculated using estimated a values of 0.045, 0.039 and 0.354 for ‘Fiesta’, ‘Greenbelt’ and ‘Marathon’, respectively.
ᵇ F-value for sowing date for each cultivar. In this assessment, a low F-value indicates constant value of the appropriate attribute over sowing dates.

and ‘Marathon’ were 670, 612, and 627°C day, respectively. The thermal time model explained 89, 70 and 53% of the variation during EFI for ‘Fiesta’, ‘Greenbelt’ and ‘Marathon’, respectively (Table 4). Thermal time durations of FIHM for ‘Fiesta’, ‘Greenbelt’, and ‘Marathon’ were 664, 660, and 678°C day, respectively, for all sowing dates (Table 5). The thermal time model explained 90, 80 and 36% of the variation during FIHM for ‘Fiesta’, ‘Greenbelt’ and ‘Marathon’, respectively (data not presented). ‘Marathon’ had a consistently poor fit to the thermal time models due to greater within-cultivar variation as demonstrated by a higher coefficient of variation in thermal time than other cultivars (data not presented).

Thermal time for duration of EFI for ‘Fiesta’ was greater (P < 0.01) than for ‘Marathon’, which in turn was, greater (P < 0.01) than for ‘Greenbelt’ (Table 2). Thermal time duration of FIHM for both ‘Fiesta’ and ‘Greenbelt’ was not significantly different (P > 0.05) from each other (Table 3), but thermal time duration for ‘Marathon’ was slightly greater (P < 0.05). Differences in thermal time in FIHM between cultivars were small and of little practical importance, but differences in thermal time in EFI were large. The longer crop duration of ‘Fiesta’ was mainly due to the high thermal time requirement during EFI.

3.3. Photoperiod response during EFI

Inclusion of photoperiod in the analysis by DEVEL accounted for an additional 6, 2 and 4% of the variation for ‘Fiesta’, ‘Greenbelt’ and ‘Marathon’, respectively, in EFI, calculated from the difference in coefficient of determination for the combined temperature and photoperiod model, and the temperature model
Due to the very low photoperiod sensitivity detected, the effect of photoperiod was ignored in further analyses. The limited photoperiod response was confirmed by the lack of any effect of extending photoperiod on total leaf number in all sowings (Table 2).

### 3.4. Total solar radiation

Incorporation of solar radiation in the calculation of ETT did not improve the thermal time model for duration of EFI. This suggests that broccoli development is not sensitive to solar radiation during EFI, within the range of solar radiation received in the experiment at Gatton College. The low Pearson correlation coefficient (0.24, \( n = 144 \)) between the predictors, accumulated solar radiation and thermal time indicates that these two predictors were largely independent in
this study. Although ETT (Fig. 3d) estimated FIHM of each cultivar among the sowing dates with a lower F-value than either chronological time (Fig. 3a) or accumulated solar radiation (Fig. 3c), F-values were almost the same as for thermal time in ‘Fiesta’ and ‘Greenbelt’, and only marginally lower than for thermal time in ‘Marathon’ (Fig. 3b, Table 5). The thermal time model would describe duration of FIHM adequately since ETT only reduced F-values marginally.

3.5. Total leaf number

There was a significant linear relationship ($P < 0.01$) between total leaf number and average temperature for each cultivar (Fig. 4). There was also a

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Fig. 4. Effect of average temperature (°C) (open symbols) and thermal time (°C day) (closed symbols) from emergence to floral initiation (EFI) on the total leaf number at floral initiation in three broccoli cultivars, ‘Fiesta’ (circles (a,b)), ‘Greenbelt’ (squares (c,d)), and ‘Marathon’ (triangles (e,f)) at Gatton College.
significant linear relationship ($P < 0.01$) between thermal time duration of EFI and total leaf number for ‘Greenbelt’ and ‘Marathon’ but not ‘Fiesta’ ($P > 0.05$) (Fig. 4).

### 3.6. Evaluation of model against independent farm data

Coefficient of determination for predicted values of chronological duration of EFI from independent farm data at Brookstead using estimated temperature coefficients, accounted for 64% of the variation in observed data for the pooled analysis with five cultivars (‘Fiesta’, ‘Greenbelt’, ‘Marathon’, ‘CMS Liberty’ and ‘Triathlon’) (Fig. 5). Most predicted EFI durations fall close to the 1:1 line. The RMSD for the pooled data was 1.8 days, representing approximately 4% of overall mean EFI. Our model provided satisfactory prediction for the chronological duration of EFI ranging from 40 to 55 days.

Coefficient of determination for predictions of chronological duration of FIHM from independent farm data using estimated temperature coefficients, accounted for 80% of the observed data for the pooled analysis using all five cultivars (Fig. 6). Predicted values are close to the 1:1 line and RMSD for the pooled data was 2.9 days, representing approximately 5% of overall mean FIHM. The model provided good prediction for the chronological duration of FIHM ranging from 44 to 64 days.

Fig. 5. Comparison between predicted and observed duration (days) from emergence to floral initiation for independent data from five broccoli cultivars (‘Fiesta’ (●), ‘Greenbelt’ (■), ‘Marathon’ (▲), ‘CMS Liberty’ (▼), and ‘Triathlon’ (◆)) grown on a commercial farm in Brookstead in 1997 and 1998. Predicted duration based on thermal time was calculated using base and optimum temperatures of 0 and 20°C, respectively.
4. Discussion

4.1. Estimated temperature coefficients

The $T_{\text{base}}$ and $T_{\text{opt}}$ of 0 and 20°C for the duration of EFI determined from the present study are consistent with a thermal time study in New Zealand (Diputado and Nichols, 1989) where $T_{\text{base}}$ and $T_{\text{opt}}$ of 1 and 21°C were derived. The estimated $T_{\text{base}}$ of 0°C also agrees with other results (Marshall and Thompson, 1987). The estimated $T_{\text{base}}$ and $T_{\text{opt}}$ of 0 and 20°C for the duration of FIHM is similar to estimated temperatures for that of EFI. The estimated $T_{\text{base}}$ of 0°C also agrees with other reports (Marshall and Thompson, 1987; Wurr et al., 1991, 1992; Grevsen, 1998), but is lower than the $T_{\text{base}}$ of 3°C reported (Diputado and Nichols, 1989). There appears to be no need to use different $T_{\text{base}}$ for the various developmental intervals. No support was found in the present study for the higher $T_{\text{base}}$ of 7°C reported (Pearson and Hadley, 1988; Dufault, 1997). The $T_{\text{opt}}$ of 20°C in this study is higher than the values of 15 and 17°C reported for temperate broccoli cultivars growing in the UK (Wurr et al., 1991) and Denmark (Grevsen, 1998), respectively.

Lack of fit in both EFI and FIHM thermal time models for ‘Marathon’ was mainly due to within-cultivar variation. ‘Marathon’ is not well adapted to environmental conditions in south-east Queensland (Jauncey, P., personal communication), and the gradual replacement by ‘Triathlon’ and ‘Decathlon’
(Sakata, USA), which are superior versions of ‘Marathon’ bred by Sakata, is fully justified. Our EFI and FIHM thermal time models are robust as they predicted chronological durations of EFI and FIHM for independent data of commercial field-grown broccoli (60 crops) in a different location over two growing seasons. Hence, they can be readily used with confidence by farmers and researchers. Since estimated temperature response coefficients were the same across the range of cultivars, it is reasonable to use these temperatures as initial estimates of $T_{\text{base}}$ and $T_{\text{opt}}$ for EFI and FIHM in other broccoli cultivars.

4.2. Photoperiod response

The minimum irradiance (2 W m$^{-2}$, equivalent to an additional 0.06 MJ m$^{-2}$ per day, since lights were on daily for 8 h) in our work exceeded 1.5 W m$^{-2}$ (Friend, 1969) which was found to be sufficient to saturate the photoperiod response of oilseed brassica ($B. \text{campestris}$ L. cv ‘Ceres’). Thus, we contend there was sufficient irradiance to detect a photoperiod response. However, photoperiod sensitivity was very low. In no case was there evidence of earlier floral initiation, as suggested by Fujime et al. (1988), in our 16 h photoperiod treatment. Our results agree with a recent study in the UK which also showed no evidence for photoperiod sensitivity in three commercial cauliflower cultivars (‘Plana’, ‘Kathmandu Local’ and ‘Snowball-16’) grown under different photoperiods (9, 12, 15, and 18 h per day) (Thapa, 1994).

4.3. Solar radiation response

Inclusion of solar radiation did not improve the precision of the EFI model. This agrees with the literature since there is no report of any solar radiation effect for the duration of EFI (Miller et al., 1985; Wurr et al., 1995; Mourao and Hadley, 1998). The equation relating ETT to thermal time during FIHM reveals that the value of parameter $a$, which quantifies sensitivity to solar radiation, was very low. ‘Marathon’ had a higher value of $a$, and hence is slightly more sensitive to solar radiation than ‘Fiesta’ or ‘Greenbelt’. Recent work on broccoli head growth in Aarlev, Denmark (latitude 15°18’N) showed that inclusion of solar radiation did not improve the accuracy of thermal time models for practical purposes (Grevsen, 1998). Hence, thermal time models can be effectively applied to broccoli growing areas in temperate zones at higher latitudes, as well as in warmer areas.

4.4. Leaf number

The linear relationship between total leaf number and temperature for our data is consistent with the literature reports (Miller et al., 1985). At lower temperatures, broccoli plants flower at a lower node, and thus have fewer leaves
than when temperatures are higher. There was also a significant linear relationship between thermal time duration of EFI and total leaf number at floral initiation for ‘Greenbelt’ and ‘Marathon’, as in cauliflower (Salter, 1969) but not in ‘Fiesta’. Thus, total leaf number of ‘Fiesta’ is not very responsive to temperature.

In our work, higher temperatures (mean temperatures close to 20°C) tended to shorten chronological EFI and FIHM. We did not have to estimate the end of the juvenile phase, as used in studies of vernalisation, which is imprecise and may add to the error (Pearson et al., 1994). Higher rates of development at higher temperatures may be related to an increased total leaf number and carbohydrate supply for floral initiation and development (Fontes and Ozbun, 1972). The present work confirms our hypothesis that thermal time models calculated using estimated cardinal temperatures can accurately predict broccoli development since development is predominantly determined by temperature rather than photoperiod.

Acknowledgements

We thank David Heath of Matilda Fresh Foods for technical support, and Phillip Jauncey of the same company and the Horticultural Research and Development Corporation for funding this project. Thanks are due to the University of Queensland, Gatton College, for provision of field resources and equipment. We gratefully acknowledge Allan Lisle for statistical advice, Max Heslehurst for advice on thermal time calculations, Donald Irving for advice on the manuscript, and Dallas Williams, Yu Sha Li and Xiu Zhen Su for assistance in collection of field data.

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