Cardinal temperatures and thermal time requirements for germination of forage brassicas

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Abstract

Cardinal temperatures, base (T_b), optimum (T_{opt}) and maximum (T_m), and thermal time (Tt) requirements were defined for germination of nine forage brassica cultivars. Seeds were germinated at nine constant temperatures. Germination rate was described using linear and broken stick development models. Germination rate responses to temperature were more dependent on species than cultivars. Turnip (*Brassica rapa*) cultivars required 17°C days above a T_b of 3.6°C until 10°C, and 14°C days from 10°C until a T_{opt} of 31°C. Rape (*B. napus*) required 26.5°C days above a T_b of 3.3°C, and 'Aparima Gold' swedes required 34°C days above a T_b of -0.6°C, until a T_{opt} of 33°C. Kale and *Raphanobrassica* (*B. oleracea*) cultivars required 60°C days above a T_b of 0°C until a T_{opt} of 27°C. Estimates of T_m were 48°C for *B. rapa*, 38°C for *B. napus* and 35°C for *B. oleracea*. These cardinal temperatures were used to describe the daily Tt response to temperature of each species.

Additional keywords: development, growing degree days, linear models, phenology

Introduction

Forage brassicas are widely used as supplementary feed for grazing animals in New Zealand (de Ruiter *et al.*, 2009). They include kale (*Brassica oleracea* L. spp. *acephala*) and rape (*B. napus* L. spp. *biennis*), the bulb crops swedes (*B. napus* L. ssp. *napobrassica* (L.) Rchb.) and turnip (*B. rapa* L. spp. *rapa*) and leaf turnips such as 'Pasja' (*B. rapa*), a turnip-Chinese cabbage hybrid. There is also interest in *Raphanobrassica*, an intergeneric hybrid between *B. oleracea* and radish (*Raphanus sativus* L.) (Williams and Hill, 1986). Our aim was to accurately define the cardinal temperatures and thermal time (Tt) requirements for germination of these crops. These can then be used in later experiments to determine if they are consistent for other development phases.

In its simplest form, Tt is calculated by accumulating the mean daily temperature minus the base or threshold temperature (T_b) below which no development occurs (Angus *et al.*, 1981). A modification of this simple linear model is to include a linear decrease in the accumulated Tt above an optimum temperature (T_{opt}) down to zero, at the maximum temperature (T_m). These cardinal temperatures are derived from the relationship between temperature and development rate. Linear models have been used to quantify the T_b and Tt required for leaf development and yield in forage brassicas (Collie and McKenzie, 1998; Adams *et al.* 2005; Brown *et al.*, 2007), and to predict brassica yields in different locations (Scott and Pollock, 2004; Wilson *et al.*, 2004). For these studies T_b was between 0 and 4°C. Bilinear or broken stick models have been used to determine the cardinal temperatures and Tt requirements of several pasture species and cultivars (Black *et al.*, 2006; Lonati *et al.*, 2009), but there were few documented results on the cardinal and Tt requirements for development of forage brassicas.

A problem of estimating cardinal temperatures, especially T_b, from field experiments is that the data generated may have only a narrow temperature range. This can result in inaccurate cardinal temperatures (Bonhomme, 2000), in particular T_b. This occurs because low temperatures are not reached consistently in the field and therefore a large extrapolation to the x-axis is required to determine T_b. To overcome this, incubator and controlled environment experiments over a wide temperature range can be used to produce data physiologically more realistic (Angus *et al.*, 1981). These also enable the estimation of T_{opt} and T_m. Cardinal temperatures are then defined from the relationship between constant temperatures and development stage (Moot *et al.*, 2000; Black *et al.*, 2006; Lonati *et al.*, 2009;).

The objective of this paper was to determine cardinal temperatures and Tt requirements for germination of forage brassicas. Specific emphasis was placed on defining T_b and T_{opt} because of their importance in determining Tt requirements in the field. Two statistical models were tested to determine these cardinal temperatures, namely linear and broken stick methods.

Materials and Methods

Seeds of nine forage brassica cultivars (Table 1) were germinated at constant temperatures (5, 10, 12, 15, 20, 25, 30, 35 and 38°C) in unlit incubators (Sanyo MIR 152, Sanyo Electric Co., Japan). Temperatures were monitored using a HOBO data logger (Onset Computer Corporation, Bourne, Massachusetts, USA) every 30 minutes. Target temperatures were used for all calculations once deviations in temperature were not significant. Fifty seeds were placed on filter paper, soaked with distilled water, in each of three Petri dishes per cultivar for incubation at each temperature. No preconditioning treatments were applied. Distilled water was added as required to ensure moisture was not limiting for germination.

Germinated seeds were counted and removed twice a day for 5-25°C treatments and three times a day for warmer temperatures. Seeds were considered germinated when the length of the radicle exceeded the diameter of the seed. Petri dishes were re-randomised after each count and counts continued until germination ceased.

Table 1: Cultivars and species of forage brassicas tested.

Cultivar	Species	Common name
Barkant	*Brassica rapa* spp. *rapa*	Turnip
Green Globe	*B. rapa* spp. *rapa*	Turnip
Pasja	*B. rapa* spp. *Rapa* × *B. rapa* spp. *pekeninensis*	Leafy turnip
Aparima Gold	*B. napus* spp. *napobrassica*	Swede
Goliath	*B. napus* spp. *biennis*	Rape
Titan	*B. napus* spp. *biennis*	Rape
Gruner	*B. oleracea* spp. *acephala*	Kale
Regal	*B. oleracea* spp. *acephala*	Kale
Raphanobrassica[1]	*B. oleracea* spp. *acephala* x *Raphanus sativus*	*Raphanobrassica*

[1]This seedlot was unnamed and is therefore referred to as '*Raphanobrassica*'.

Data analysis

Final germination percentage and number of days required to reach 75% of final germination (t_{75}) were determined by fitting a Gompertz curve (Seber and Wild 1989) to cumulative germination percentage G over time t for each Petri dish (Figure 1). The Gompertz function was:

$$G = a + ce^{-e^{-b(t-m)}} \qquad \text{Equation 1}$$

with asymptote a (set to zero), final germination percentage c, time in days t, and shape parameters b and m. The direction of the response was set to the right (c > 0 when b > 0). The Gompertz equation was differentiated as Equation 2 (Black *et al*., 2006) to find time to 75% of final germination (Figure 1) and germination rate was the reciprocal of t_{75}.

$$t_{75} = m - \frac{\ln\{-\ln(0.75)\}}{b} \qquad \text{Equation 2}$$

The linear and broken stick models were fitted to germination rates for each cultivar to quantify the influence of temperature T on development rate D. The linear model was:

$$D = (T - T_b)/q \qquad \text{Equation 3}$$

where q is Tt required to reach 75% of final germination. From linear regression:

$$T_b = \text{-intercept/slope} \qquad \text{Equation 4}$$

$$Q = 1/\text{slope} \qquad \text{Equation 5}$$

The broken stick model was:

$$D = (T - T_b)/q_1, \text{ when } T \leq T_{opt} \qquad \text{Equation 6}$$

$$D = (T_m - T)/q_2, \text{when } T \geq T_{opt} \qquad \text{Equation 7}$$

where q_1 and q_2 are the Tt required for germination below and above T_{opt} respectively. From broken stick regression Equations 8 and 9 are for the first line segment, Equations 10 and 11 for the second line segment and T_{opt} is the x-coordinate of the break point.

$$T_b = \text{-intercept/slope} \qquad \text{Equation 8}$$

$$q_1 = 1/\text{slope} \qquad \text{Equation 9}$$

$$T_m = \text{-intercept/slope} \qquad \text{Equation 10}$$

$$q_2 = 1/\text{-slope} \qquad \text{Equation 11}$$

The standard errors (SE) for T_b, T_{opt} and T_m were obtained from statistical derivatives in the linear and broken stick regression analyses. The SEs for q, q_1 and q_2 were calculated as:

$SE_{slope}/slope^2$ Equation 12

To enable direct comparisons of q between cultivars, the linear model was also fitted with T_b (and therefore the intercept) set to zero, and q and its SE were calculated as before.

The models were fitted and data analysed in GenStat (version 14, VSN International Ltd, UK). Treatment effects on final germination percentage were analysed using an analysis of variance (ANOVA) which dealt with the pseudo-replicate Petri dishes within temperatures. Differences in mean estimates of cardinal temperatures and Tt requirements between the linear and broken-stick models, and between species groups (*B. rapa*, *B. napus* and *B. oleracea*; Table 1) within models, were analysed using t tests and pooled SEs.

The cardinal temperatures were used to calculate the daily Tt for each cultivar or species group based on a broken stick (Olsen *et al*., 1993) threshold model:

$Tt = 0$, when $T<T_b$ Equation 13

$Tt = T - T_b$, when $T_b \leq T \leq T_{opt}$ Equation 14

$Tt = (T_m - T)/q_2$, when $T_{opt} \leq T \leq T_m$ Equation 15

$Tt = 0$, when $T>T_m$ Equation 16

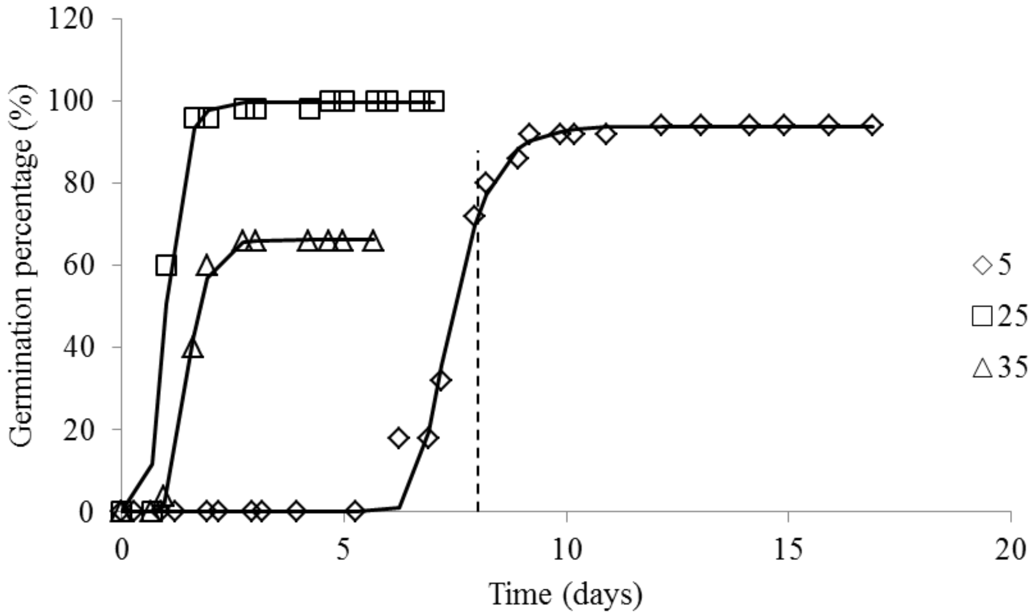

Figure 1: Cumulative germination of one replicate of 'Aparima Gold' swede incubated at three temperatures: points are observed data; solid lines are Gompertz curves; vertical dashed line is time to 75% of final germination at 5°C.

Results

Germination percentage

The cumulative germination percentages over time were accurately described by the Gompertz curves (average R^2=98), as shown in Figure 1 for one replicate of 'Aparima Gold' swede at three temperatures.

The final germination of each cultivar differed across temperatures (Table 2). Germination was between 90 and 100% from 5 to 30°C for 'Aparima Gold', from 10 to 35°C for 'Barkant', 'Green Globe', 'Pasja' and 'Goliath', and from 12 to 30°C for 'Titan'. It was above 79% from 5 to 30°C for 'Gruner' (except at 15°C) and from 5 to 25°C for 'Regal', but for *Raphanobrassica* it was 76-87% from 12 to 25°C. At 5°C germination was only 29-45% for 'Barkant', 'Green Globe', 'Titan' and *Raphanobrassica*. At 35°C it was less than 15% for 'Gruner', 'Regal' and *Raphanobrassica,* and at 38°C there was little or no germination for all cultivars except 'Barkant', 'Green Globe' and 'Pasja'.

Table 2: Final germination percentages of nine cultivars of forage brassica incubated at different temperatures (T) at Lincoln University, Canterbury: means of predicted data from the Gompertz curves; bold values are ≥85% of the maximum final germination obtained for each cultivar within temperatures; SED=4.37.

T (°C)	Barkant	Green Globe	Pasja	Aparima Gold	Goliath	Titan	Gruner	Regal	*Raphano.*
5	28.9	45.0	61.9	**92.4**	**85.7**	30.2	**79.3**	**83.8**	42.0
10	**91.4**	**96.2**	**96.0**	**97.0**	**98.7**	**86.5**	**85.8**	**85.9**	66.2
12	**99.3**	**96.1**	**98.4**	**98.0**	**99.3**	**94.2**	**88.2**	**85.8**	**76.2**
15	**99.9**	**99.8**	**98.2**	**97.7**	**98.3**	**92.6**	68.2	**93.1**	**86.5**
20	**100.0**	**100.0**	**96.4**	**99.0**	**99.8**	**96.1**	**85.2**	**89.0**	**77.7**
25	**99.4**	**99.4**	**97.2**	**96.3**	**100.0**	**94.4**	**84.5**	**79.8**	**77.8**
30	**98.9**	**99.4**	**96.5**	**95.6**	**98.5**	**90.1**	**81.2**	71.3	45.4
35	**98.6**	**97.4**	**94.4**	59.3	**91.5**	79.6	11.2	5.9	14.5
38	73.6	65.9	76.0	0.0	5.6	0.0	1.3	2.0	5.4

Germination rate

The germination rate (1/days to 75% final germination) increased linearly as temperature increased from 5 to approximately 25-30°C, but then decreased as temperature increased to 35/38°C (Figure 2). At 35 and 38°C the germination rate was recorded as zero for cultivars with 15% or less germination (Table 2).

The temperature range used for the linear model differed among cultivars (Table 3 and Figure 2). The 35 and 38°C temperatures were excluded from all linear analyses, 30°C was excluded for 'Aparima Gold' and 'Titan', and 25 and 30°C were excluded for 'Barkant', 'Pasja', 'Gruner', 'Regal' and *Raphanobrassica*, because they were all above the linear range (Figure 2). When these results were removed, the linear model gave a reasonable fit (R^2=86-99) and suggested that the Tt required from sowing to 75% final germination was generally similar between cultivars of each species, but it was lower for *B. rapa* than *B. napus,* which required less Tt than *B. oleracea* ($P<0.05$). The mean T_bs for *B. rapa* (1.1°C) and *B. oleracea* (3.6°C) cultivars were not significantly different, but 'Aparima Gold' had a lower ($P<0.05$) T_b (1.2°C) than 'Titan' (4.6°C) within *B. napus*.

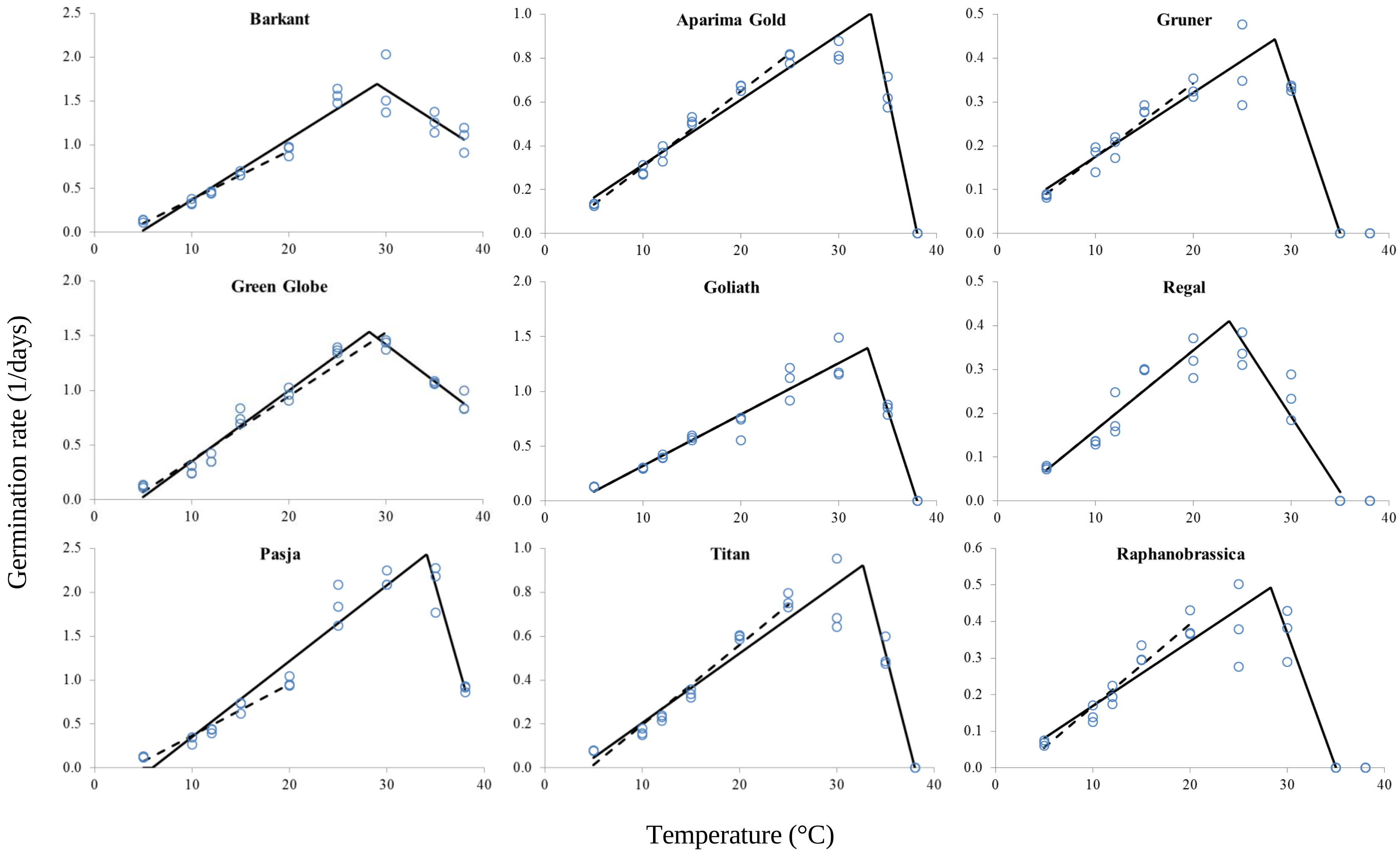

Figure 2: Germination rates of nine cultivars of forage brassica incubated at different temperatures: points are observed data; dashed lines are linear models, solid lines are broken stick models.

Table 3: Estimates ±SE of the base temperature (T_b) and thermal time requirements (q, also with T_b set to zero) from the linear model for the germination rate of nine forage brassica cultivars, within the linear temperature range.

Cultivar	T range (°C)	R^2 (%)	T_b	q	q (T_b=0)	R^2 (T_b=0) (%)
Barkant	5-20	97.9	3.2±0.41	18.2±0.70	23.4±0.82	92.6
Green Globe	5-30	95.4	3.8±0.75	17.1±0.84	21.0±0.75	91.6
Pasja	5-20	95.8	3.7±0.77	17.1±0.96	22.9±1.06	88.7
Aparima Gold	5-25	98.5	1.2±0.44	29.0±0.87	31.0±0.46	98.1
Goliath	5-30	93.6	3.1±0.92	21.3±1.25	25.2±0.89	91.2
Titan	5-25	96.6	4.6±0.54	27.4±1.26	37.3±1.72	88.7
Gruner	5-20	93.7	-0.4±1.82	59.5±4.10	58.0±1.41	94.1
Regal	5-20	85.8	1.1±1.34	54.9±5.93	59.6±2.58	86.1
Raphanobrassica	5-20	93.9	2.6±0.75	44.3±3.03	54.0±2.05	90.8
B. rapa			3.6±0.66	17.5±0.83	22.4±0.87	
B. napus spp. *biennis*			3.9±0.77	24.4±1.12	31.2±1.27	
B. oleracea			1.1±1.37	52.9±4.52	57.2±2.07	

The linear model with T_b adjusted to zero had R^2=86-98 within the linear temperature range and estimated Tt requirements for germination which were consistent with the first linear model (Table 3).

The complete temperature range (5 to 38°C) was used for the broken stick model for most cultivars (Table 4 and Figure 2). For *B. oleracea*, the 38°C temperature was excluded from the broken stick analyses because germination rate was already zero at 35°C. The broken stick model (R^2=86-97) estimated similar T_b and Tt values to those found by the linear model for *B. napus* and *B. oleracea*. However, the Tt required for *B. rapa* was 14°C days above a T_b of 5.1°C based on the broken stick model compared with 22°C days above 3.6°C from the linear model ($P<0.05$). Germination rates of *B. rapa* at 5°C were underestimated by the broken stick model, but they were accurately predicted by the linear model, and the two models intersected at about 10°C (Figure 2). Therefore, the broken stick model was modified for *B. rapa* to consider the linear model as a third line segment when T≤10°C.

The mean T_b for the *B. rapa* cultivars (5.1°C) was higher ($P<0.05$) than the mean for *B. oleracea* cultivars (-0.1°C), and 'Aparima Gold' had a lower ($P<0.05$) T_b (-0.6°C) than 'Goliath' (3.1°C) and 'Titan' (3.5°C) based on the broken stick model (Table 4).

The broken stick model suggested T_{opt} was similar at 32°C for *B. rapa*, *B. napus* and 'Aparima Gold', but lower ($P<0.05$) for *B. oleracea* at 27°C (Table 4). The Tt required for germination at supra-optimum temperatures (q_2) was lowest ($P<0.05$) for *B. napus* and highest for *B. oleracea* (Tables 3 and 4).

Daily thermal time

The response of daily Tt to temperature was calculated for each species group based on the mean cardinal temperatures derived from the broken stick development models (Figure 3), except for 'Aparima Gold' that had a separate model. For *B. rapa*, Tt increased linearly from T_b until 10°C at a rate of 0.77°C days/°C and then at 1.0°C days/°C until the mean T_{opt} of 32°C, before dropping to zero again at a mean T_m of 48°C. For *B. napus* spp. *biennis*, 'Aparima

Gold' and *B. oleracea*, Tt increased by 1.0°C days/°C from T_b until the T_{opt} of 32 and 27°C respectively, and then decreased to zero at T_m of 38 and 35°C respectively.

Table 4: Estimates ±SE of the base (T_b), optimum (T_{opt}) and maximum (T_m) cardinal temperatures and thermal time requirements above (q_1) and below (q_2) the T_{opt} from the broken stick model for the germination rate of nine forage brassica cultivars.

Cultivar	*T* range (°C)	R^2 (%)	T_b	T_{opt}	T_m	q_1	q_2
Barkant	5-38	92.0	4.7±0.91	29.1±0.90	52.9±3.99	14.4±1.11	14.1±2.99
Green Globe	5-38	96.5	4.6±0.55	28.3±0.57	51.1±2.16	15.4±0.72	14.9±1.89
Pasja	5-38	94.0	5.9±0.77	34.1±0.36	40.3±0.52	11.6±0.66	2.6±0.33
Aparima Gold	5-38	96.4	-0.6±0.93	33.3±0.24	38.0±0.10	33.7±1.64	4.7±0.33
Goliath	5-38	94.9	3.1±0.85	33.0±0.33	38.0±0.19	21.4±1.15	3.6±0.33
Titan	5-38	91.6	3.5±1.02	32.7±0.46	38.0±0.26	31.6±2.08	5.8±0.71
Gruner	5-35	91.6	-2.0±1.63	28.3±0.45	35.0±0.32	68.4±6.27	15.1±1.38
Regal	5-35	88.0	1.1±1.47	23.7±0.71	35.6±0.69	54.9±6.54	29.1±2.90
Raphanobrassica	5-35	86.0	0.4±1.79	28.3±0.60	35.0±0.45	56.6±6.53	13.6±1.72
B. rapa			5.1±0.76	30.5±0.65	48.1±2.64	13.8±0.85	10.5±2.05
B. napus spp. *biennis*			3.3±0.94	32.9±0.63	38.0±0.50	26.5±1.30	4.7±0.72
B. oleracea			-0.1±1.64	26.8±0.60	35.2±0.51	59.9±6.45	19.3±2.10

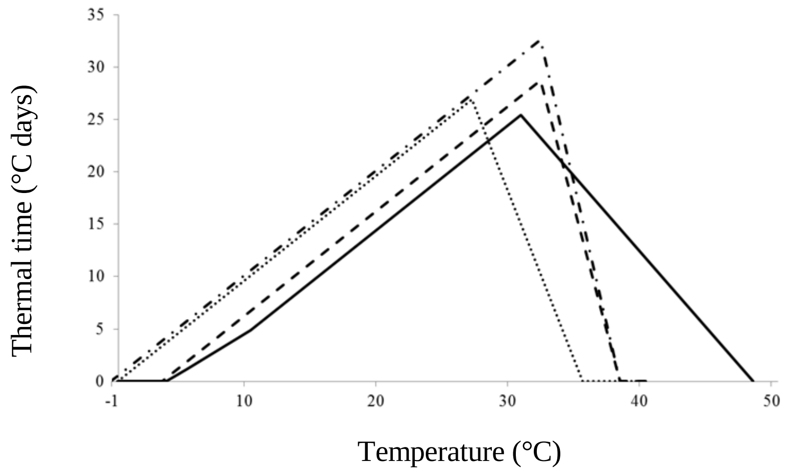

Figure 3: Response of daily thermal time to temperature for the development of *B. rapa* (solid line), *B. napus* (dashed line), *B. oleracea* (dotted line) and 'Aparima Gold' (dash-dot line).

Discussion

The germination responses to temperature of most of the forage brassicas used in this study were species-dependent rather than cultivar, subspecies or hybrid-dependent, except for 'Aparima Gold'. The species by temperature interaction was evident in the final germination (Table 2), but was most obvious in germination rates (Figure 2). The wide range of temperatures that produced final germinations greater than 85% (Table 2) shows the potential germination of all cultivars was high. As temperatures moved from the optimum some cultivars still produced final germination percentages greater than 75%. However, germination rates were lower which indicates that final germination percentage was not a good indicator of germination rates.

Germination at optimal temperatures was fastest for the turnips and leaf turnip (*B. rapa*), intermediate for the swede and rapes (*B. napus*), and slowest for the kales and *Raphanobrassica* (*B. oleracea*) (Figure 2). However, germination at 5°C was slow for all cultivars, and at higher temperatures (35 and 38°C) cultivars of *B. rapa* germinated, but there was little or no germination from *B. napus* spp. *biennis*, 'Aparima Gold' and *B. oleracea* cultivars. The intermediate germination rates from the swede and rape cultivars could have been expected because *B. napus* is a cross between *B. rapa* and *B. oleracea*. These species rather than cultivar effects were consistent with previous results for other temperate and tropical forage species (Angus *et al*., 1981; Moot *et al*., 2000). Thus, these results highlight a wide range of optimum temperatures that were species rather than cultivar specific.

Summarising results into repeatable coefficients required the broken stick development model. This enabled the definition of cardinal temperatures and Tt requirements for each cultivar and species (Table 4). For example, the Tt required for germination at sub-optimum temperatures (q_1) was only a constant 14°C days for *B. rapa* and 60°C days for *B. oleracea*, but Tt accumulation ($T - T_b$) was slower for *B. rapa* up to T_{opt} because of a higher T_b. Therefore, germination rate was similar for both species at 5°C (about 0.1/day), but it was higher for *B. rapa* at optimum temperatures (approximately 1.9 compared with 0.5/day), which was also due to its slightly higher T_{opt} (31 compared with 27°C). Similarly, the Tt required at supra-optimum temperatures was less for *B. rapa* than *B. oleracea* (q_2), but Tt accumulation (T_m - T) was faster for *B. rapa* due to its higher T_m (48 compared with 35°C), which meant it germinated faster. *B. napus* spp. *biennis* and 'Aparima Gold' were intermediate in response mainly because they required more Tt for germination (26.5 and 33.7°C days, respectively) than *B. rapa* and less Tt than *B. oleracea* up to T_{opt}, but also due to their similar T_b and T_m to *B. oleracea*, highest T_{opt} (33°C) and lowest Tt requirement above T_{opt}.

The linear model described the species effects on the temperature response, but over a narrow temperature range. It was applied from 5 to 20, 25 or 30°C, depending on the cultivar (Table 3), because the germination rates appeared to deviate from the linear Tt assumption (Angus *et al*., 1981) at warmer temperatures (Figure 2). In contrast the broken stick model was more appropriate because it estimated T_{opt} and T_m on the basis that the response was approximately linear both below and above the T_{opt}. This assumption of a linear relationship between temperature and development rate has been a criticism of the Tt approach (Angus *et al*., 1981; Streck *et* *al*., 2008). However, the linear approach is useful because it quantifies each temperature response as a single Tt requirement for the range of temperatures that forage brassicas are likely to experience in the field.

Similar estimates of T_b and Tt requirements were obtained by both models for *B. napus* and *B. oleracea*, but the Tt required for *B. rapa* was higher for the linear model (Tables 3 and 4). Furthermore, the T_b for *B. rapa* was 3.6°C for the linear model and 5.1°C for the broken stick model. Although this difference was not significant, the broken stick model did not account for germination observed at 5°C (Figure 2) and thus its estimations of T_b and Tt require further investigation. The linear model estimated T_b and Tt from the fitting of a smaller range of temperatures and therefore explained the nonlinear behaviour of the response at suboptimal temperatures (Wilson *et al*., 1995). Figure 2 shows there was a difference in the rate of increase in germination from T_b up to 10°C and from 10°C to T_{opt} for *B. rapa* cultivars. The broken stick model was therefore modified to consider the linear model as a third line segment when temperatures were ≤10°C (Figure 3).

The T_b and Tt requirements estimated in this study showed that *B. rapa* (turnips) required the least Tt, followed by *B. napus* spp. *biennis* (rape) and 'Aparima Gold', while *B. oleracea* (kale) cultivars had the highest Tt requirement to reach 75% of final germination. The next step is to determine if the cardinal temperatures defined in this study are appropriate for other stages of vegetative development of brassica cultivars, and evaluate the performance of the daily Tt models proposed here.

Conclusions

(1) Cultivars of the same species, or related to the same species through crossings, had similar cardinal temperatures and Tt requirements for germination, except 'Aparima Gold'.

(2) The broken stick model was the most appropriate to estimate cardinal temperatures and Tt requirements and to develop a daily Tt model for germination of brassicas species, although minor changes were made to the model for *B. rapa.*

(3) Turnip (*B. rapa*) cultivars required 17°C days above a T_b of 3.6°C until 10°C, and 14°C days from 10°C until a T_{opt} of 31°C for germination.

(4) Rape (*B. napus* spp. *biennis*) cultivars required 26.5°C days above a T_b of 3.3°C, and 'Aparima Gold' swedes required 34°C days above a T_b of -0.6°C for germination, until a T_{opt} of 33°C.

(5) Kale and *Raphanobrassica* (*B. oleracea*) cultivars required 60°C days above a T_b of 0°C for germination until a T_{opt} of 27°C.

(6) Estimates of T_m were 48°C for *B. rapa*, 38°C for *B. napus* spp. *biennis* and 'Aparima Gold', and 35°C for *B. oleracea*.

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