Cardinal temperatures and thermal time requirements for germination of annual and perennial temperate pasture species

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Abstract

Cardinal temperatures (base (T_b), optimum (T_o) and maximum (T_m)) and thermal time (Tt) requirements for germination of 21 temperate annual and perennial grass, legume and weed species were calculated from incubator experiments. Cardinal temperatures were defined using an iterative broken-stick linear regression model of development rate against temperature. Species specific maximum germination rates were all > 80% except for the 60% attained by 'Pawera' red clover. The maximums were stable from 5 to 20 °C with the exception of 'Arrotas' arrowleaf clover, 'Advance' tall fescue and 'Vision' cocksfoot which had < 20% germination at 5 °C. T_o was approximately 26 °C for 'Woogenellup' subterranean, 'Mihi' Persian, alsike, red and strawberry clovers but ≤ 20 °C for white clover and the other annual clover species tested. A base temperature of 0 °C was found for all species except ripgut brome (T_b = 4.0 °C) and T_m was ≥ 35 °C. Thermal time requirements for germination were generally lower for annual than perennial clovers which may reflect adaptation to avoid out of season germination. Annual weed grasses, showed rapid germination which aids their competitive ability to invade establishing pastures. Vulpia hair grass seed germination was over 95% at 25 °C and below; barley grass declined with increasing temperatures from 5 to 35 °C.

Additional keywords: growing degree days, heat units, *Bromus* spp.*, Critesion glaucum, Trifolium* spp.*, Vulpia myuros*

Introduction

The rate and time of germination of seeds are modulated by changes in environmental conditions and differ among years and geographic locations. To quantify germination across environments, species specific cardinal temperatures (minimum or base (T_b), optimum (T_o) and maximum (T_m)) are calculated (Angus *et al.*, 1981). The base temperature is the lowest temperature at which germination occurs, while the optimum represents the temperature at which the rate of germination is fastest. The maximum temperature is that above which no seeds germinate. These cardinal temperatures represent species specific response profiles that in ecological terms could be expected to align the time of germination and

subsequent emergence to favourable conditions for seedling growth and development. Thus, the cardinal temperatures are associated with the environmental range of each species' adaptation (del Pozo and Aronson, 2000; Alvarado and Bradford, 2002). Temperate-adapted species typically have a T_b below 4 °C (Angus *et al.*, 1981). The cardinal temperatures of several common temperate perennial pasture species have been determined previously, including perennial ryegrass and white clover (Black *et al.*, 2006) but those for annuals species have not been reported.

Models which describe the pattern of germination against temperature are common and give satisfactory estimates of the thermal time requirements for a range of species (Angus *et al.*, 1981; Garcia-Huidoboro *et al.*, 1982). Thermal time (Tt) is a measure of thermal units, also known as heat units of growing degree days, accrued each day. Thermal time eliminates location-specific calendar day-based explanations. Thermal time requirements for germination have been reported for several temperate pasture legumes (Moot *et al.*, 2000; Black *et al.*, 2003; Boswell *et al.*, 2003; Lonati *et al.*, 2009). Overall, adventive annual species have a lower base temperature and/or a smaller thermal time requirement for germination than perennial species. In many cases adventive winter annual species have a lower optimum temperature than perennial species (Lonati *et al.*, 2009) which may inhibit germination of some of the seed population under warm, summer, conditions. This would prevent a 'false-break' which could generate a seedling population that subsequently dies in a dry autumn. Additional adaptations to avoid

out of season germination may include hard-seededness or dormancy where the final germination percent is decreased at high temperatures (Knight, 1965).

In this study the germination requirements of a range of commercially available annual and perennial species used in dryland pastures are compared with those of some economically important winter annual grass weeds.

Materials and Methods

Three replicates of 50 seeds per cultivar were placed on moist standard blotting paper in Petri dishes in unlit incubators at constant set temperatures from 5.0 to 35.0 °C (± 0.5 °C) in 5 °C increments (Table 1). Supplementary data for selected species were also gathered at other temperatures (4, 12, 22, 28 and 40 °C) using the same experimental procedures. Seed of commercial cultivars was sourced directly from retailers (Table 1) while the winter annual weed grass seed was from hand harvested plants from an experimental block at Lincoln University, Canterbury. Species and cultivars within species are referred to as species and indicative species responses are given unless individual cultivars produced different results.

None of the seeds were coated or treated except 'Bolta' balansa clover (*Trifolium michelianum* Boiss.), which had a lime-based coat. This was washed from the seed immediately before the experiment began. Actual incubator temperatures were recorded using a 'Hobo 4-Channel External' (Onset Computer Corporation) data logger calibrated against a reference thermometer prior to the experiment. Legumes were scarified between sheets

of 80-grit sandpaper, but no other pre-conditioning treatments were used. Distilled water was added as required to ensure moisture was non-limiting for germination. Petri dishes were re-randomised on a single incubator shelf after each count. Seeds were defined as germinated when the emerged radicle was twice the length of the testa. Germinated seeds were measured and removed once or twice daily for up to 19 days or until five days after the last seed in a dish had germinated. The number of days to reach 75% of final germination was derived from a generalised logistic curve, using Genstat Tenth Edition (10.1.0.72) (Lawes Agricultural Trust) (Equation 1).

Equation 1 $y = a + C/(-B^{(x \times - M)})$

Where y is germination percentage, a is the lower asymptote, C is the upper asymptote which represents the final germination percentage, B depends on the values of y(0), x is time after sowing and M is the point of inflection which represents the time of maximum germination rate when 50% of the final germination has been achieved. Curves were initially fitted to individual replicates but ANOVA of coefficients showed no significant differences so data were pooled and curves fitted across replicates.

In this paper, species and cultivars within species are treated as being indicative of species responses unless individual cultivars produced different results.

Data analysis

Data for each species were plotted as the reciprocal of the duration (in days) to 75% germination against temperature, where a linear relationship between the rate of germination and temperature indicated that use of the thermal time model was appropriate (Angus *et al.*, 1981). Broken stick linear regressions were performed using an iterative process (Draper and Smith, 1998) to find the point of inflection as an indication of the optimum temperature. Least squares regression analysis was then used for the positive linear portion of the line where:

Equation 2 $Rate = b_0 + b_1 x$

The regression coefficients b_0 and b_1 were related to T_b (base temperature) and Tt (thermal time), when $T_b \geq T \leq T_o$, by Angus *et al.* (1981) as:

Equation 3 $T_b = -b_0 / b_1$

Equation 4 $Tt = 1 / b_1$

Calculated T_b was considered to be different from 0 °C if the confidence interval (95%) did not include 0 °C. Thermal time was also calculated with $T_b = 0$ °C, by forcing the regression equations through the origin, to allow direct comparison among species (Moot *et al.*, 2000).

The maximum temperature at which germination occurred (T_m) was calculated as the x-axis intercept from a second linear regression for the decreasing portion of the regression at temperatures between the optimum (T_o), at which germination rate is the fastest, and T_m. Germination results were used to determine the final germination percentage and were analysed by ANOVA with means separated by least significant difference (5%).

Table 1: Species and cultivars evaluated and incubator temperatures used.

Functional Group	Common name	Botanical name	Cultivar	Temperatures	Source
Annual clovers	Arrowleaf	*Trifolium vesiculosum*	Arrowtas	5, 10, 15, 20, 25, 30, 35	DLF
	Balansa	*T. michelianum*	Bolta	5, 10, 15, 20, 25, 30, 35	Agricom
			Frontier	5, 10, 12, 15, 20, 22, 25, 30, 35	Agricom
	Persian	*T. resupinatum*	Laser	5, 10, 15, 20, 25, 30, 35	PGGW
			Mihi	5, 10, 15, 20, 25, 28, 30, 35, 40	PGGW
			Nitro	5, 10, 12, 15, 20, 22, 25, 30, 35, 40	PGGW
	Subterranean	*T. subterraneum*	Dalkeith	4, 5, 10, 15, 20, 25, 30	Lincoln University
			Leura	5, 10, 15, 20, 25, 30, 35	AgResearch
			Mt Baker	5, 10, 15, 20, 25, 30, 35	Lincoln University
			Woogenellup	5, 10, 15, 20, 25, 28, 30, 35	Lincoln University
Perennial clovers	Alsike	*T. hybridum*	MAI302	5, 10, 15, 20, 25, 30, 35	Lincoln University
	Red	*T. pratense*	Pawera	5, 10, 15, 20, 25, 30, 35	PPGW
	Strawberry	*T. fragiferum*	Onward	5, 10, 15, 20, 25, 30, 35	Lincoln University
	White	*T. repens*	Demand	5, 10, 15, 20, 25, 30, 35, 40	PGGW
			Nomad	5, 10, 15, 20, 25, 28, 30, 35	Lincoln University
Annual grass weeds	Barley grass	*Critesion glaucum*		5, 10, 15, 20, 25, 30, 35	Lincoln University
	Goosegrass	*Bromus mollis*		5, 10, 15, 20, 25, 30, 35	Lincoln University
	Ripgut brome	*Bromus diandrus*		5, 10, 15, 20, 25, 30, 35	Lincoln University
	Vulpia hair grass	*Vulpia myuros*		5, 10, 15, 20, 25, 28, 35	Lincoln University
Perennial grasses	Cocksfoot	*Dactylis glomerata*	Vision	5, 10, 15, 20, 25, 30, 35, 40	Lincoln University
	Perennial ryegrass	*Lolium perenne*	Commando	5, 10, 15, 20, 25, 30, 35	PGGW
	Tall fescue	*Schedonorus phoenix*	Advance	5, 10, 15, 20, 25, 28, 30, 35	PGGW
		syn. *Festuca arundinacea*	Flecha	5, 10, 15, 20, 25, 30, 35	PGGW

Results

The rate and maximum cumulative germination percentage differed with temperature (Figure 1, 2). For annual legume species (Figure 2a), final germination percentage was constant between 5 and 20 °C and decreased to zero as temperatures increased. For example, the final germination percentage for 'Bolta' balansa clover (*Trifolium michelianum*) was 91 (± 2.5)% from 5 to 20 °C and then decreased linearly to 37% at 35 °C.
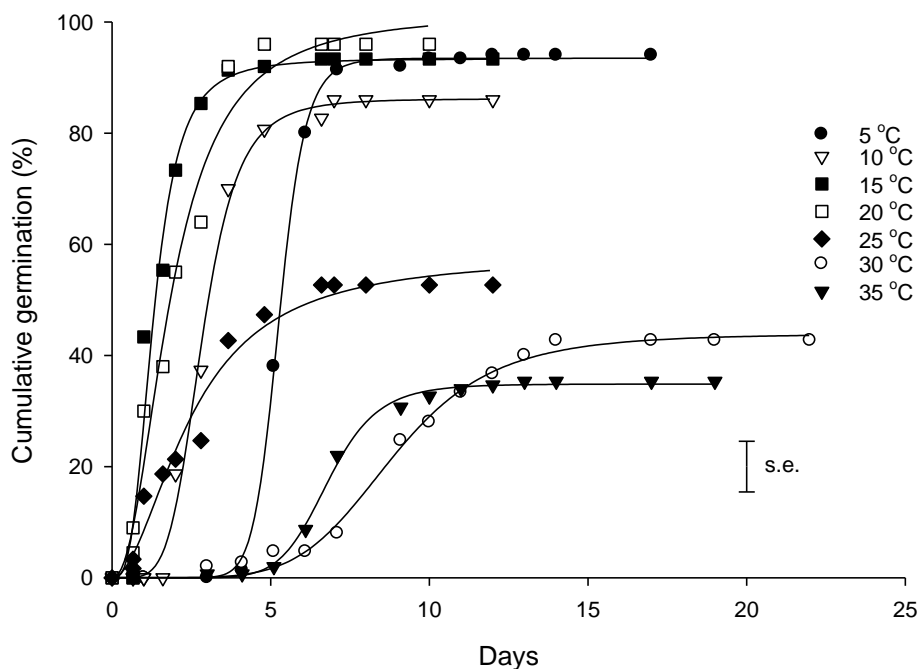

Figure 1: Cumulative germination of 'Bolta' balansa clover at 10 constant temperatures. Note: s.e. is maximum standard error for the final germination percent.

For perennial legumes (Figure 2b), the final germination percentage was constant across the entire temperature range and only declined at 35 °C. Maximum germination was only 65% for 'Pawera' red clover (*T. pratense* L.) compared with > 80% for all other species.

The maximum germination of the three annual grasses each responded differently to temperature (Figure 2c). The highest germination for barley grass (*Critesion glaucum* Steud.) was at 5 °C, it then decreased to 0% at 35 °C. For both vulpia hair grass (*Vulpia myuros* L.) and ripgut brome (*Bromus diandrus* Roth), the maximum germination percentage was > 90% from 5 to 25 °C, but declined above 25 °C in vulpia hair grass and 30 °C in ripgut brome.

The commercial perennial grasses all had their maximum germination at between 10 and 30 °C, but in 'Vision' cocksfoot (*Dactylis glomerata* L.) the maximum germination was only 60%.

The number of days to 75% germination differed among species and for temperatures (Figure 1). For

'Frontier' balansa clover, the time to 75% germination was less than five days at temperatures between 5 and 25 °C and more than six days at ≥ 30 °C (Figure 3).

The rate of germination increased as temperatures increased up to a temperature optimum and then decreased beyond that optimum (Figure 4). For 'Frontier', the germination rate increased linearly from approximately 20% germination per day at 5 °C, up to approximately 45% per day at 15 °C.

Germination rate then decreased linearly to < 10 % per day at 40 °C. This pattern of linear increase and decrease in the rate of germination was uniform across species (except for 'Commando' perennial ryegrass (*Lolium perenne* L.) Figure 4) and was used to define the cardinal temperatures. Germination rate of 'Commando' increased from 4 to 10 °C but was then constant to 30 °C and 0 at 35 °C.
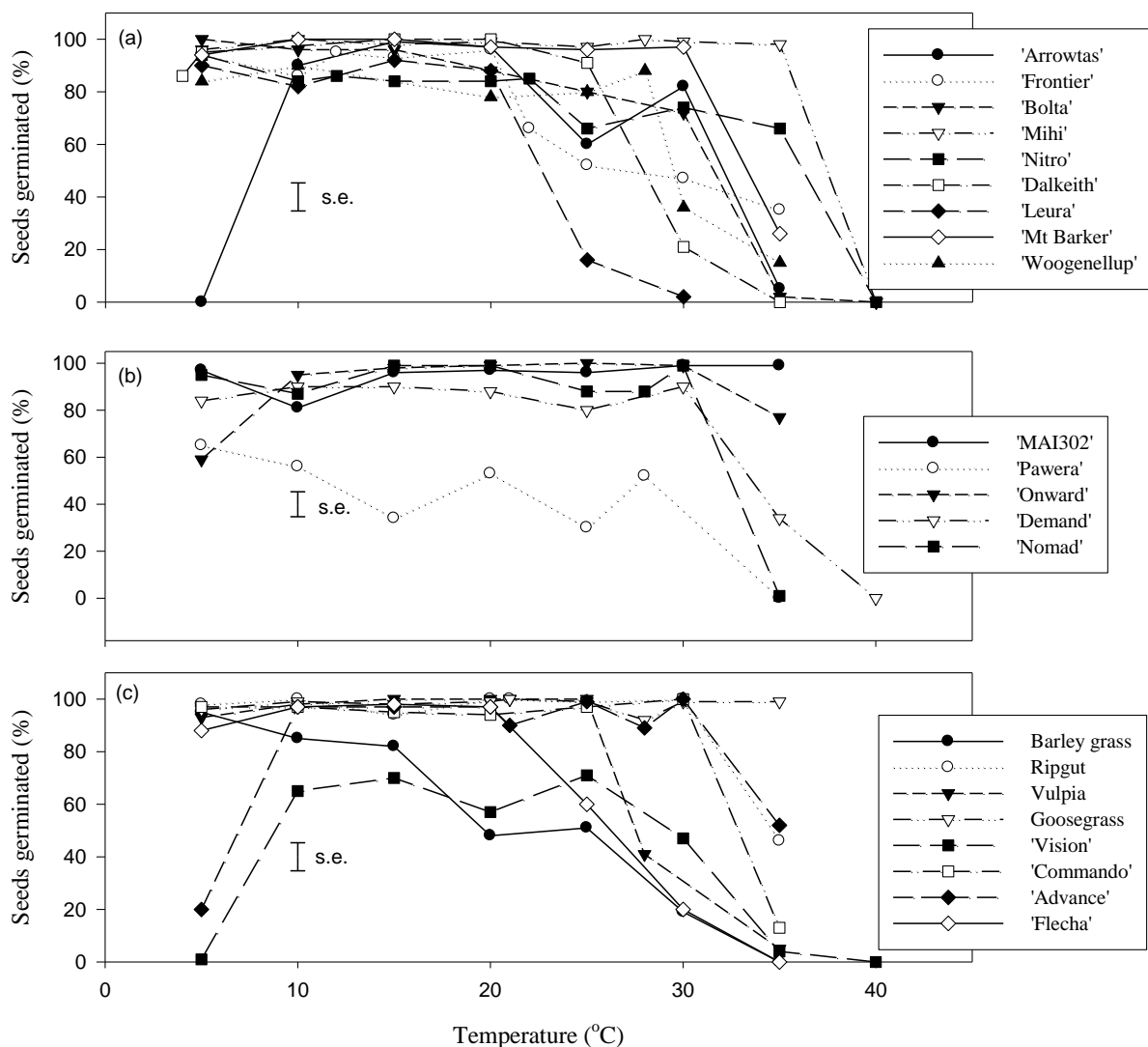

Figure 2: The maximum cumulative germination (%) of seeds from a range of temperate annual (a) and perennial (b) legumes and (c) grasses at different constant temperatures.

From regression analysis (Equation 2) the base temperature (T_b) for germination was not different from 0 °C (± 95% confidence intervals) (Table 2). The optimum temperature (T_o) for arrowleaf (*Trifolium vesiculosum* Savi), balansa, subterranean (*T. subterraneum* L.) and Persian (*T. resupinatum* L.) clovers was 12 to 20 °C except for 26 °C for 'Woogenellup' sub. clover and 25 °C for 'Mihi' Persian clover. For the perennial clovers, T_o was 18-20 °C for white clover (*T. repens* L.) and approximately 25 °C for the other three species. The T_o for ripgut brome was 10 °C compared with 16 °C for vulpia hair grass and 25-30 °C for barley grass and goosegrass (*Bromus mollis* L.).

When T_b was set to 0 °C, thermal time requirements for germination for the annual clovers arrowleaf, balansa and Persian ranged from 18-31 °Cd and the subterranean clovers ranged from 41-62 °Cd (Table 3). The perennial clovers ranged from 35-48 °Cd. For germination of the weed grasses, ripgut brome required 29 °Cd, vulpia hair grass 39 °Cd and barley grass, 77 °Cd.
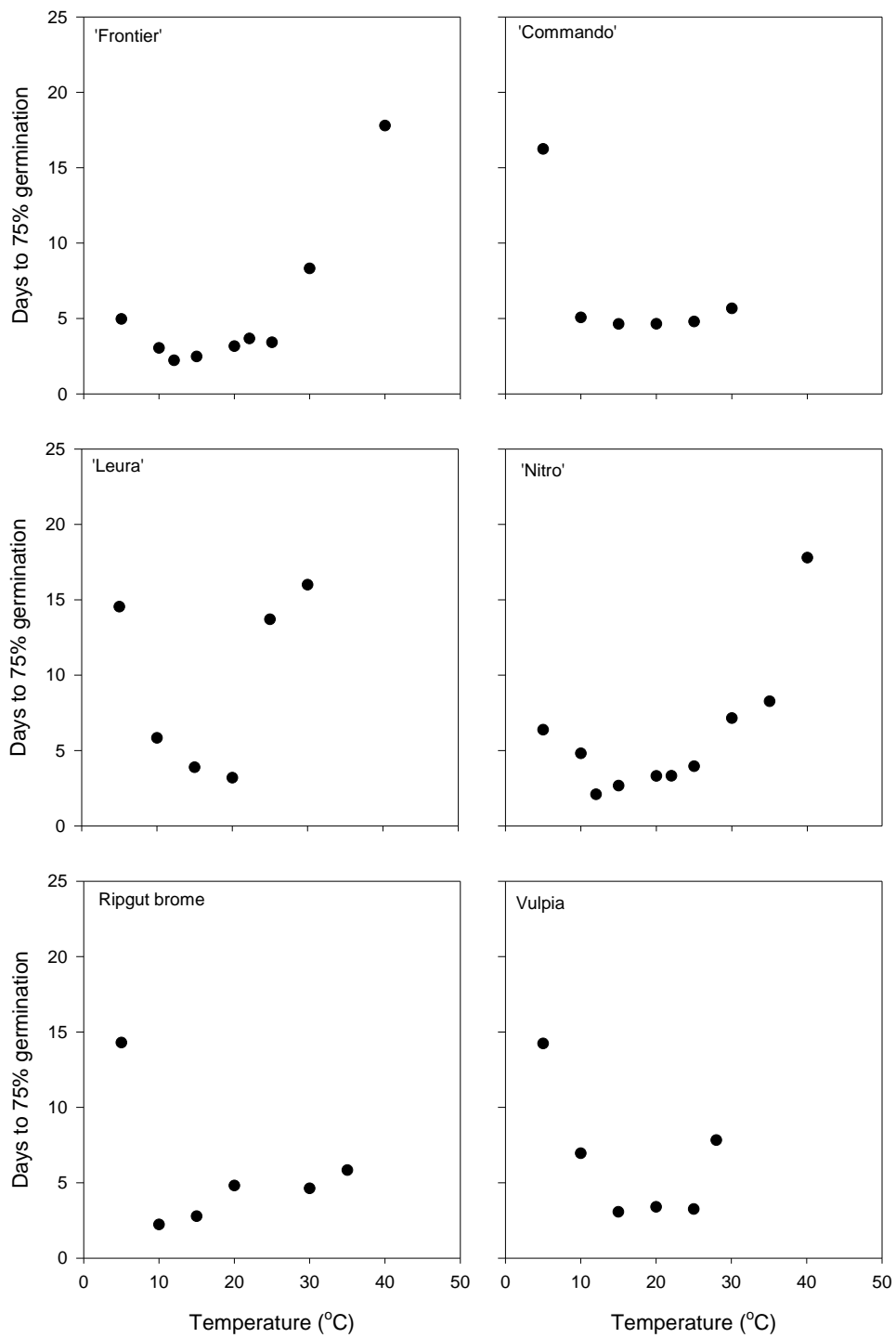
Figure 3: Days after sowing to 75% of final germination for 'Frontier' balansa clover, 'Commando' perennial ryegrass, 'Leura' subterranean clover, 'Nitro' Persian clover, ripgut brome and vulpia hair grass at different temperatures.

Figure 4: Germination rate of 'Frontier' balansa clover, 'Commando' perennial ryegrass, 'Leura' subterranean clover, 'Nitro' Persian clover, ripgut brome and vulpia hair grass at different temperatures.
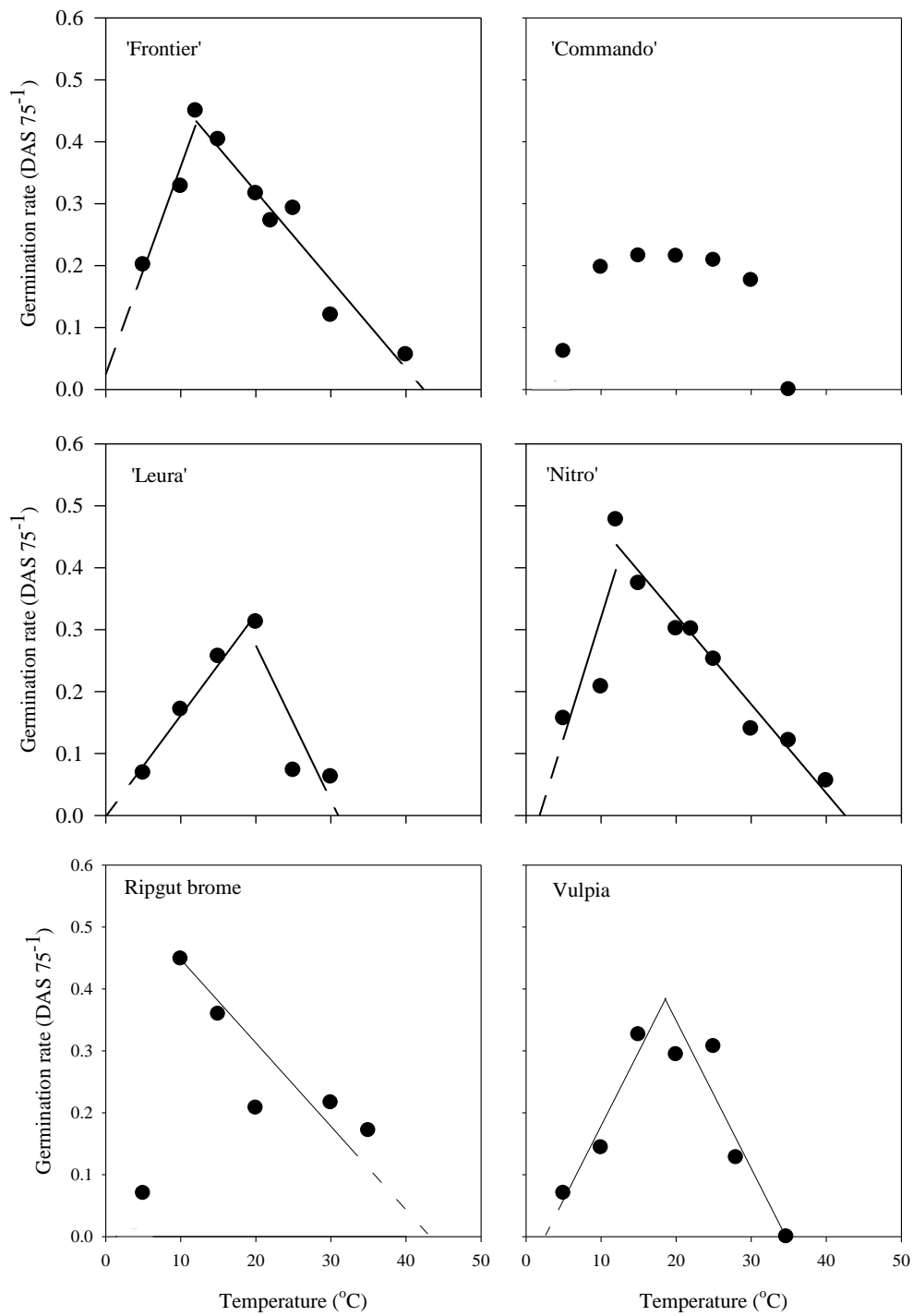
Table 2: Estimates of base (T_b), optimum (T_o) and maximum (T_m) temperature and total thermal time (Tt) requirement for germination of a range of temperate pasture species.

Functional Group	Species	Cultivar	T_b (°C)	± 95% CI	T_o (°C)	R^2 (%) (≤T_o)	T_m (°C)	± 95% CI	R^2 (%)(≥T_o)	Tt (°Cd)
Annual legumes	Arrowleaf	Arrowtas	3.7	6.6	14	96	30.3	7.1	72	12
	Balansa	Bolta	1.4	4.9	14	95	38	6.5	84	26
		Frontier	-0.7	14.2	12	95	42.4	6.4	92	30
	Persian	Mihi	0	9.1	25	92	34.2	4.3	88	22
		Nitro	1.8	16.4	12	66	41.9	6.3	97	26
	Subterranean	Dalkeith	0.7	1.1	19	100	31.9	8.1	93	39
		Leura	0.1	3.9	20	98	31	13.4	78	61
		Mt Baker	0.4	4.6	20	98	41.6	18.9	76	45
		Woogenellup	1.3	2.2	26	99	>35	-	-	52
Perennial legumes	Alsike	MAI302	0	7.1	~25	90	~40	-	92	35
	Red	Pawera	2.4	8.7	25	87	>28	-	99	46
	Strawberry	Onward	1.1	6.6	26	94	>35	-	86	47
	White	Demand	-0.6	6.6	20	93	43	3.4	99	49
		Nomad	0.2	8.1	18	93	31.5	3.7	96	38
Annual weed grasses	Barley Grass		1	14.2	~25	72	~35	-	-	95
	Goosegrass		-3.7	9.7	>30	94	>35	-	-	72
	Ripgut brome		4	0.2	10	100	43.9	29.9	79	13
	Vulpia hair grass		3.4	7.6	16	94	34.3	17	73	52
Perennial grasses	Cocksfoot	Vision	-0.8	6.5	18	96	48	14.7	89	181
	Perennial Ryegrass	Commando	3.2	5.9	10-30	87	>30	-	-	52
	Tall fescue	Advance	-	-	15-30	-	>35	-	-	-
		Flecha	4.6	6.2	17	80	35.8	3.8	97	38

Note: '-' = insufficient data to allow derivation, CI is confidence interval for the x-axis intercept. R^2 = coefficient of variation for linear regression.

Table 3: Summary of thermal time to 75% germination for temperate climate species at sub-optimal temperatures when $T_b = 0°C$.

Functional Group	Species	Cultivar	Tt (°Cd)	Minimum R^2 (%)
Annual legumes	Arrowleaf clover		18	86
	Balansa clover		29	95
	Persian clover	Mihi	20	89
		Nitro	31	64
	Subterranean clover		50	98
Perennial legumes	Alsike clover		35	98
	Red clover		48	87
	Strawberry clover		47	93
	White clover		40	91
Annual weed grasses	Barley grass		77	68
	Goosegrass		63	89
	Ripgut brome		29[1]	80
	Vulpia hair grass		39	87
Perennial grasses	Cocksfoot		167	95
	Perennial ryegrass		66	82
	Tall fescue		60	69

Note: [1]Ripgut brome had no statistical justification (95% CI) for re-analysis using $T_b = 0 °C$. R^2 = coefficient of variation for linear regression (sub-optimum temperatures).

Discussion

The germination rate increased linearly as temperature rose from T_b until reaching a maximum at T_o (Figure 4). The thermal time concept summarised the time from sowing to germination at different temperatures between T_b and T_o to be expressed as a single coefficient. Base temperatures for all cultivars were $\leq 4.7 °C$ and, except for ripgut brome, none were different from 0 °C. This, and previous work (Moot *et al.*, 2000; Lonati *et al.*, 2009) suggests that, without evidence to the contrary, future work with temperate pasture species could assume a Tb of 0 °C for germination.

As temperatures rose above T_o, germination rate decreased linearly to zero at T_m. The strong linear relationships confirm the appropriateness of using the linear response models when estimating thermal time at sub- and supra-optimal temperatures (Lonati *et al.*, 2009). Of note, 'Commando' perennial ryegrass and 'Advance' and 'Flecha' tall fescue had an 'optimum temperature range' for germination which had a plateau across several temperatures. These responses were in line with the expected physiological response to temperature (Angus *et al.*,

1981). The linear portions on either side of the range were used to calculate the thermal time requirements for germination and therefore may not conform to results seen in the field.

The thermal time requirements calculated here for germination of the control grass species perennial ryegrass and cocksfoot were 20% shorter than those previously published (Moot *et al.*, 2000). This reflects the time for shoot initiation as defined by the different methodologies. Moot *et al.* (2000) followed the International Seed Testing Association (ISTA) descriptions of germination with normal seedling development requiring a shoot and root compared with radicle-only observations used here.

The observed differences in germination rate among cultivars of Persian clover were unexpected. In most cases germination rate is genetically determined and, without specific selection pressure, uniform within a species (Moot *et al.*, 2000). However, it is possible that these cultivars may be different sub-species. 'Nitro' Persian clover (*Trifolium resupinatum* var. *resupinatum*) had a maximum germination rate of 0.47 and is derived from the prostrate, hard seeded sub-species *resupinatum* (Wurst *et al.*, 2004). Other cultivars from this sub-species include 'Prolific' and 'Kyambro'. 'Mihi' had a maximum germination rate of 1.2 and is believed to have been selected from the erect, later flowering subspecies *majus*. These cultivars could act as adventives and be over-sown in hill and high country environments or areas with brief germination windows to colonise a site that may not be accessible to slower germinating species.

The maximum germination percentage of the annual legumes began to decline at lower temperatures than for the perennial legumes. The typical lifecycle of these annual legumes starts with germination in autumn as moisture increases. Vegetative growth continues through winter and spring before reproductive structures are formed and seed is set in spring/summer. Annual legumes avoid the drought conditions of their native environment as seed (Sulas *et al.*, 2000). The decline in germination percent at higher temperatures (> 20 °C) was consistent with previous reports (Lonati *et al*. 2009), and may be an ecological adaptation to limit seedling losses due to out of season germination (false break) when moisture is insufficient to sustain growth. This adaptation is referred to as high temperature dormancy (Knight, 1965) and, along with other strategies such as hard seed coats, may be a more important mechanism in hot dry environments such as Australia or the Mediterranean, than in New Zealand. At Lincoln University, in the dry (660 mm average annual rainfall) coastal region of Canterbury, maximum daily soil surface temperatures peak in February at approximately 38 °C, with average daily soil temperatures of 22 °C (Wilson *et al.*, 1995). Current estimates show mean air temperatures rising 3 to 4°C in the next 50 years (Salinger, 2003). This will potentially compromise germination of these annual species. Cultivars such as 'Dalkeith', with relatively low temperature onset for high temperature dormancy, reach their maximum germination potential later in the autumn, when temperature had decreased to 25 °C and below. The implications for future cultivar

suitability, requires analysis of temperature and rainfall responses under different climate change scenarios.

The perennial legumes did not show the same decline in final germination percent as the annual legumes until temperature were > 30 °C. Perennial legumes, by definition, persist throughout the summer and use other drought avoidance mechanisms such as tap roots (Thomas, 2003). As such, selection pressure within a population for summer germination avoidance may have been reduced or dealt with via other mechanisms such as hard seed.

The annual grasses germinate in the autumn and vegetative growth occurs through winter and spring before seed is set in spring/summer to avoid drought. Barley grass showed a steady decline in germination percent from 95% at 5 °C to no germination at 35 °C. Ultimate germination and seedling populations of barley grass would therefore be limited by warmer summer temperatures. Of the perennial grass species, only 'Flecha' tall fescue showed a drop in germination below 30 °C.

Among the legumes, tetraploid 'Pawera' red clover and subterranean clover had higher thermal time requirements for germination than the other legumes with lighter seeds. Larger seeds, within a species seed lot have a competitive advantage as seedlings because they are able to utilise a greater supply of stored carbohydrate in the endosperm to promote initial leaf development (Black, 1957). However, among species, smaller seeds tend to germinate more rapidly (Murali, 1997; Norden *et al.*, 2009) and at lower temperatures compared with heavier seeds (Easton and Kliendorfer, 2008).

Lighter seeded species may be adapted to environments where there is only a brief period when conditions are suitable for germination (Norden *et al.*, 2009). Arrowleaf, balansa and Persian clovers are native to the Mediterranean region, including Iran, Turkey and Israel, where autumn rainfall can be brief and sporadic (del Pozo and Aronson, 2000; Dear, 2003). Rapid germination in this environment may allow these species to establish before the perennial species and confer a competitive advantage. However, germination prior to consistent autumn moisture can lead to a 'false strike', where seedlings do not receive sufficient rain to survive (Taylor *et al.*, 1984), and crop failure in winter annuals such as balansa clover (Monks *et al.*, 2008).

Of the annual weed grasses, ripgut brome required the least thermal time for germination. For example, with a mean daily temperature of 10 °C, ripgut brome would fulfil the 13 °Cd ($T_b = 4$ °C) requirement for germination in a little over two days. The germination rate of ripgut brome at 10 °C was 0.45. That is, 45% of agronomic germination (75% of seed germinated) occurred per day at 10 °C. The germination rate of ripgut brome, and vulpia hair grass (39 °Cd), was double that of 'Commando' perennial ryegrass, 'Flecha' tall fescue and 'Vision' cocksfoot, which required between 58 and 167 °Cd. These annual weed species would therefore germinate more rapidly than perennial grasses and are on a par with the small seeded annual legumes.

The potential to germinate rapidly in a pasture system gives weed species a competitive advantage at establishment, populating the bare space and capturing

incoming radiation. This would, in turn, compromise the establishment of other autumn sown or re-establishing species. It may also explain how they can quickly invade pastures after summer drought. Cultural and chemical management that reduce these grass weed seed populations at establishment may be required to enable control particularly for slow establishing dryland pasture species like cocksfoot and tall fescue.

Conclusion

A base temperature of 0 °C was found for all species except ripgut brome (T_b = 4.0 °C). Thermal time requirements were generally lower in annual than perennial clovers which may reflect adaptation to avoid out of season germination. Of the weed grasses, ripgut brome and vulpia hair grass both germinated as quickly as perennial ryegrass which means they are likely to compete at establishment for limited resources so pre-emergence control is recommended.

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