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MODELLING THE EFFECTS OF TEMPERATURE ON THE RATES OF SEEDLING EMERGENCE AND LEAF APPEARANCE IN LEGUME COVER CROPS

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SUMMARY

Simple models of the growth and development of legume cover crops in different environments may aid the selection of species and genotypes most suitable for particular farming systems. The effects of temperature and photoperiod on the daily rate of seedling emergence ($1/t_{50\%}$) and the rate of leaf appearance (leaves d^{-1}) were quantified for 12 diverse legume cover crop species. Six tropical or subtropical species were grown in 12 combinations of mean temperature (16.8, 21.8 and 26.8 °C) and photoperiod (11.5, 12.5, 13.5 and 14.5 h d^{-1}). Another six genotypes of temperate species were grown in nine combinations of mean temperature (16.8, 21.8 and 26.8 °C) and photoperiod (12.5, 13.5 and 14.5 h d^{-1}). Durations from sowing to 50% seedling emergence ($t_{50\%}$) were recorded and the number of leaves on the main stem counted during early vegetative growth. Photoperiod did not affect either $1/t_{50\%}$ or leaves d^{-1}. However, the effects of temperature, photoperiod response group (short-day or long-day response), genotype or species and their interactions were all significant. An optimal temperature between 21.8 and 26.8 °C for leaves d^{-1} was identified for *Vicia sativa*, *Vicia dasycarpa* and *Lupinus mutabilis*. Below the optimum temperature, $1/t_{50\%}$ and leaves d^{-1} were positive linear functions of temperature for all legume species except *Vicia dasycarpa*. Estimates of base temperature (T_b) and thermal time (θ) for $1/t_{50\%}$ and leaves d^{-1} were obtained for each legume cover crop from these functions. Common values of T_b were found within each photoperiod response group: 9 °C and 1 °C for $1/t_{50\%}$, and 10 °C and −2 °C for leaves d^{-1} for short-day and long-day species respectively. Differences among species were represented by variant estimates of θ. The practical consequences of the combined effects of these values of T_b and θ for selecting legume cover crops for particular farming systems are discussed.

INTRODUCTION

Increasing population pressures and associated efforts to intensify agriculture by long-term monocropping of subsistence cereal crops have depleted and degraded the natural resource base in many poorer regions of the world (Lal, 1997). Cover crops may provide a low-cost technology to rehabilitate degraded soils and combat problems such as soil erosion, decline in inherent soil organic matter and fertility in these regions, especially on hillsides in the tropics and subtropics (Yost and Evans, 1986; Balasubramanian and Blaise, 1993; Meelu *et al.*, 1994). Cover crops are usually legumes or grasses or a mixture of the two grown to

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improve and/or sustain the productivity of a given agricultural system. Although the terms 'cover crop' and 'green manure' have sometimes been used interchangeably (Smith *et al.*, 1987), they are recognized to be distinct (Lal *et al.*, 1991; Kiff *et al.*, 1996). The sole function of a green manure species is to enhance soil fertility and improve nutrient cycling. Cover crops fulfil additional functions such as weed suppression, pest and disease control, soil and water conservation, and the provision of food and animal feed.

Legume cover crops have been an important feature of farming systems both before and after the advent of chemical fertilizers (Pieters, 1917; Buckles, 1995). There are many examples of their wide-spread use in intensive agriculture (Stivers *et al.*, 1993; Reeves, 1994) and in increasing or sustaining the productivity of smallholder farming systems (Prinz, 1986). They have been particularly successful in combating soil degradation on sloping land; on land that was cleared and impoverished in slash and burn agriculture; and on land continuously cropped with cereals (Wilson *et al.*, 1982; Barber and Navarro, 1994). Recent initiatives to increase the use of legume cover crops in agricultural practices worldwide have been discussed by Swift *et al.* (1997). However, the lack of adequate information on the ecological adaptation of diverse legume cover crops has hampered their effective and efficient use in agricultural systems (Keatinge *et al.*, 1996).

Keatinge *et al.* (1998) quantified the effects of temperature and photoperiod on the times to flowering and maturity of 12 legume cover crops. Such relationships can be used to identify which legume cover crops may be adapted to particular agro-ecological environments or cropping systems provided that long-term climatic records are available. Many of the potential benefits of cover crops rely on the rapid establishment of the crop leaf canopy in order to provide ground cover. The objective of this paper is to examine the early vegetative growth of diverse legume cover crops. In particular, we aim to quantify the effects of temperature and photoperiod on the rates of seedling emergence and leaf appearance in 12 legume cover crops in order to provide simple quantitative models of these processes essential to leaf canopy development.

MATERIALS AND METHODS

Plant material

Twelve tropical, subtropical and temperate legumes of proven performance as cover crops (Price, 1985; Sarrantonio, 1992), including two genotypes of *Vicia faba* from different ecological backgrounds in the Andes (Bolivia) and the Himalayas (Nepal), were selected (Table 1).

Environmental conditions

Twelve photothermal environments were created using controlled-environment glasshouses each with separate day and night compartments to form an orthogonal factorial design of three mean diurnal air temperatures (16.8, 21.8 and 26.8 °C) and four photoperiods (11.5, 12.5, 13.5 and 14.5 h d^{-1}). Each diurnal

Table 1. Information on the 12 multi-purpose legume cover crops selected for this investigation.

Assumed photoperiod response†	Species	Common name	Origin of genotype	100-seed weight (g)	*Rhizobium* inoculant type
SDP	*Canavalia ensiformis* L.	Jack bean	Honduras	178	M(CB756)
	Crotalaria juncea L.	Sunn hemp	Brazil	5	M(CB756)
	Dolichos lablab L.	Lablab bean	Honduras	35	J(CB1024)
	Mucuna pruriens L.	Velvet bean	Honduras	73	M(CB756)
	Pueraria phaseoloides (Roxb.) benth.	Tropical kudzu	Brazil	1.3	M(CB756)
	Stylosanthes hamata (L.) Taub.	Green stylo	India	0.2	CB1650
LDP	*Lupinus mutabilis* Sweet	Tarwi	Bolivia	21	G(WU425)
	Trifolium resupinatum L.	Persian clover	Lebanon	0.5	O(CC2483g)
	Vicia faba L. (Bolivia)	Broad bean (Cochabamba)	Bolivia	126	FABA BEAN
	Vicia faba L. (Nepal)	Broad bean (Kathmandu)	Nepal	79	FABA BEAN
	Vicia sativa L.	Common vetch	Cyprus	7	E(SU303)
	Vicia dasycarpa Roth‡	Woolly pod vetch	West Asia	4	E(SU303)

†SDP is short-day plant and LDP is long-day plant. For further details of SDP and LDP, see Roberts and Summerfield (1987) and Keatinge *et al*. (1998); ‡*Vicia dasycarpa* is also known as *Vicia villosa* ssp. *dasycarpa*.

photothermal regime had a thermoperiod of 11.5 h at the warmer temperature during natural daylight followed by 12.5 h in the cooler night compartments (from which natural light was completely excluded). Photoperiods longer than 11.5 h d^{-1} were provided by artificial lights within the night compartments using 100 W tungsten incandescent bulbs. Air temperatures were recorded at 10 min intervals using screened and aspirated thermocouples positioned above the leaf canopy in each photothermal regime. The actual mean air temperatures for the appropriate period of the investigation were calculated from these measurements and used in all analyses.

Plant husbandry and culture

Germination tests were conducted at a constant temperature of 26 °C on all seed stocks. More than 90% of seeds of each species germinated. Uniform seeds were selected for all species and seeds of *Crotalaria juncea*, *Pueraria phaseoloides*, *Vicia sativa*, *Vicia dasycarpa* and *Trifolium resupinatum* were scarified mechanically before sowing. All species were inoculated with a slurry containing the appropriate species of Rhizobia (Table 1) the day before sowing.

Six seeds of each species were hand-sown on 2 April 1996 in plastic pots (0.23 m in diameter, 7 L capacity) with basal drainage holes. Three pots (replicates) were used for each species within each photothermal regime. The long-day plants were not sown at the 11.5 h d^{-1} photoperiod. Thus, there were only nine treatment combinations for these species. The growth medium comprised vermiculite (grade size DM), coarse washed sand, crushed (6 mm) gravel, and multi-purpose compost mixed in a ratio of 4:2:4:2 v/v, respectively. All medium components except for vermiculite were steam sterilized at 96 °C and 300 kPa for between 10 and 20 min before sowing. Pots were filled with growth medium, soaked with tap water and then left to drain the day before sowing.

When seedlings in the various photothermal regimes reached the first trifoliate leaf stage, they were thinned to one plant per pot for *Canavalia ensiformis*, *Mucuna pruriens* and *Dolichos lablab* and three uniform plants per pot for the other species. Using a complete nutrient solution containing 10 mg L^{-1} inorganic nitrogen (Summerfield *et al*., 1977), individual pots were then irrigated automatically twice each day for 5 min (but subsequently more frequently) to return the pots to field capacity. Plants were supported by bamboo canes as and when required. Biological control of red spider mites (*Tetranychus urticae*) and thrips (*Frankiniella* spp.) was practised using Spidex (containing *Phytoseiulus persimilis*) and Thripex (containing *Amblyseius cucumeris*) respectively applied at 7-d intervals (Koppert Biological Systems UK Ltd, UK).

Observations

Individual pots were inspected daily to record the number of seedlings that had emerged. Then, one representative plant in each pot was chosen for subsequent leaf counts on the main stem.

Leaf counting started 14 d after sowing at the coolest temperature and at 7 d after sowing at the other two temperatures and was continued for 28 d. All leaves which appeared after the cotyledons were counted. A leaf was defined as appeared when separate leaflets were first seen (except *Crotalaria juncea* which produced only simple leaves, all other legume species produced compound leaves on the main stem). For *V. sativa* and *V. dasycarpa*, nodes were more distinguishable than the leaves on the main stem, and so it was the nodes which were counted rather than leaves. The area of the third leaf on the main stem of each replicate plant of all legume species grown at 26.8 °C under 14.5 h d^{-1} was measured at 35 d after sowing using a leaf area meter (Delta-T Devices Ltd). The third leaf of all species was fully expanded by this time.

Data analysis

From the counts of seedlings that had emerged, the duration in days from sowing to 50% seedling emergence ($t_{50\%}$) and the daily rate of seedling emergence ($1/t_{50\%}$) were estimated for each cover crop in each environment. The daily leaf appearance rate (leaves d^{-1}) was calculated as the slope of the linear regression between the number of leaves on the main stem and days after sowing using the three replicate plants for each photothermal regime. The effects of photoperiod response group (short-day or long-day plants), legume species (or genotype of *V. faba*) within each photoperiod response group and photoperiod on $1/t_{50\%}$ and leaves d^{-1} were analysed by comparing the effects of these variables on the relationship between either $1/t_{50\%}$ or leaves d^{-1} and mean temperature. The intercept (a) and slope (b) regression coefficients of each of these linear relationships were used to calculate the base temperature ($T_b = -a/b$, when $1/t_{50\%}$ or leaves $d^{-1} = 0$) and the thermal time ($\theta = 1/b$). The standard error (s.e.) of T_b was calculated using the method of Wheeler (1990), where:

$$\text{s.e.} = \{[\text{var}(a) - (2*\text{k}*\text{covar}(a \text{ and } b)) + \text{k}^2*\text{var}(b)]/b^2\}^{0.5}$$

where $\text{k} = +a/b$, var(a) is the variance of coefficient a, covar(a and b) is the covariance of a and b, and var(b) is the variance of coefficient b.

To test whether a common value of T_b for all short-day or all long-day species was justified, the relationship between $1/t_{50\%}$ or leaves d^{-1} and temperature was fitted for all short-day or long-day species with T_b constrained to a common value for each group. The common value of T_b was changed in 0.5 °C increments, and the best common estimate of T_b was then selected on the basis of the minimal residual sum of squares. The variance accounted for (r^2) by the relationship with a common T_b was then compared with that when individual relationships were used for each species. All regression equations were fitted and tested using GENSTAT V (GENSTAT V Committee, 1987).

RESULTS

Seedling emergence rate ($1/t_{50\%}$)

Seedling emergence was greater than 80% for all 12 cover crops under all photothermal conditions. For 11 cover crops, $t_{50\%}$ decreased curvilinearly with increase in air temperature with no visible differences among photoperiods, for example, *M. pruriens* and *V. sativa* (Fig. 1). Linear relationships between $1/t_{50\%}$ and temperature were found for all six short-day species and for five of the six long-day ones (solid lines in Fig. 2 and 3 respectively). The effects of photoperiod response group, legume genotype, and their interactions on the relationships between $1/t_{50\%}$ and temperature were significant, but the effect of photoperiod was not. Estimates of $1/t_{50\%}$ for *V. dasycarpa* were not affected by temperature (Fig. 3d). The fitted relationships shown in Fig. 2 and 3 are given in Table 2 together with the calculated values of T_b and θ.

Individual simple linear relations for the six short-day species combined to account for 97.3% (d.f. = 60) of the total variation in $1/t_{50\%}$ (solid lines in Fig. 2). These relationships fitted with the best-fit estimate of T_b common to all these species of 9 °C, but with different slopes (Table 2), accounted for 97.1%

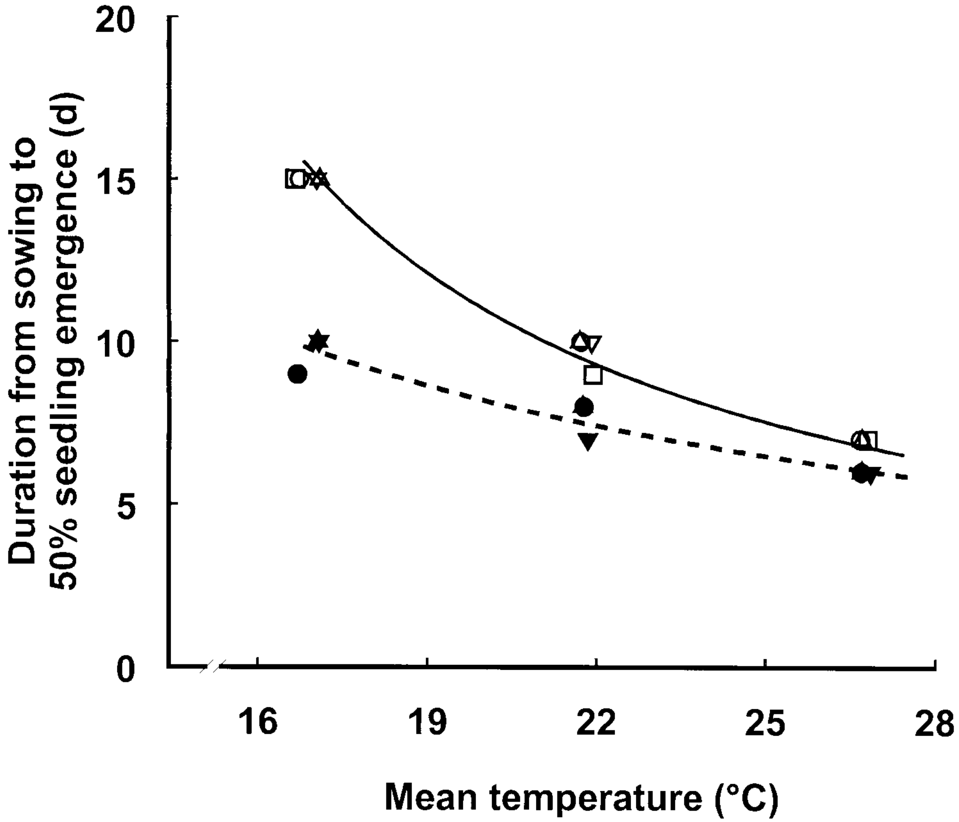

Fig. 1. Relationship between duration from sowing to 50% seedling emergence ($t_{50\%}$) and mean air temperature for *Mucuna pruriens* (open symbols) and *Vicia sativa* (solid symbols) at photoperiods of 11.5 (□, ■), 12.5 (○, ●), 13.5 (△, ▲) and 14.5 h d^{-1} (▽, ▼). The solid lines fitted are $1/t_{50\%} = a + bT$ with the values of *a* and *b* presented in Table 2.

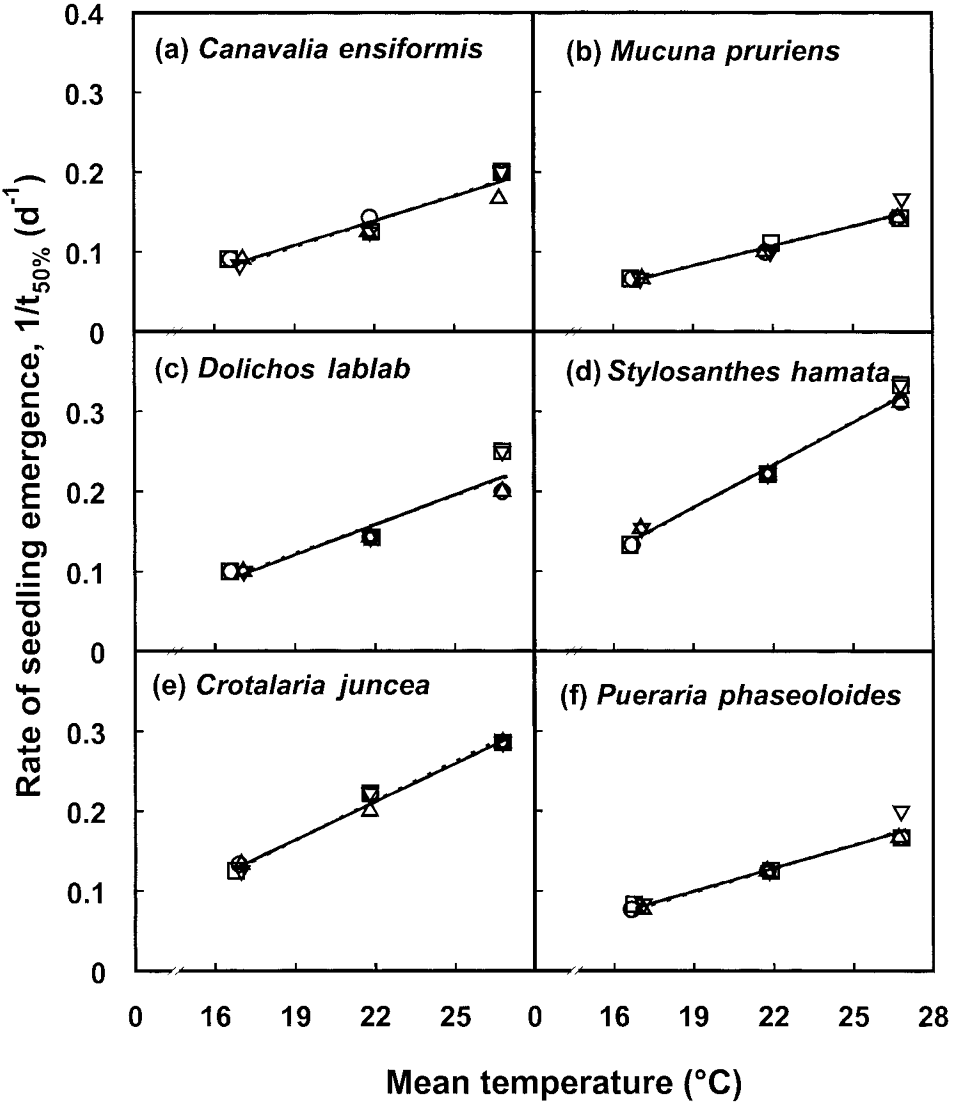

Fig. 2. Relationship between rate of progress from sowing to 50% seedling emergence ($1/t_{50\%}$) and mean air temperature for six short-day species at photoperiods of 11.5 (□), 12.5 (○), 13.5 (△) and 14.5 h d^{-1} (▽). The solid lines fitted are $1/t_{50\%} = a + bT$ with the values of *a* and *b* presented in Table 2. The broken lines (barely visible) have a common T_b of 9 °C.

(d.f. = 66) of the variation in $1/t_{50\%}$ (broken lines in Fig. 2). Among the five long-day legume cover crops, the individual simple linear relationships combined to account for 97.7% (d.f. = 35) of the total variation in $1/t_{50\%}$ (solid lines in Fig. 3). Regression lines for five of the six long-day cover crops (excluding *V. dasycarpa*) with the best-fit common value of T_b = 1 °C, but with different slopes (Table 2), accounted for 97.2% (d.f. = 40) of the variation in $1/t_{50\%}$ (broken lines in Fig. 3). Thus, using a common estimate of T_b for $1/t_{50\%}$ for either short- or long-day cover

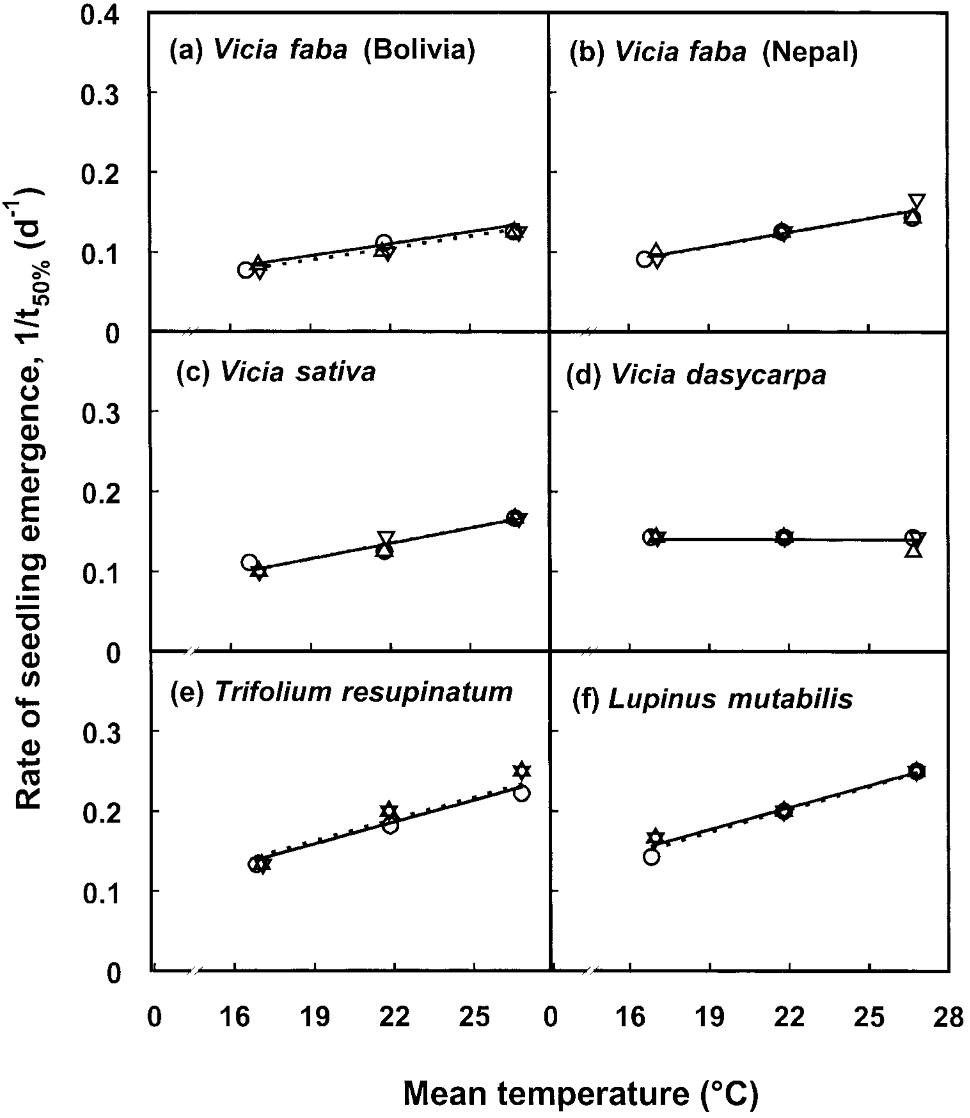

Fig. 3. Relationship between rate of progress from sowing to 50% seedling emergence ($1/t_{50\%}$) and mean air temperature for six long-day genotypes at photoperiods of 12.5 (○), 13.5 (△) and 14.5 h d^{-1} (▽). The solid lines fitted are $1/t_{50\%} = a + bT$ with the values of *a* and *b* presented in Table 2. The broken lines in a, b, c, e and f (barely visible) have a common T_b of 1 °C.

crops provided r^2 values and fitted relationships almost identical to those obtained with the individual relationships for each cover crop.

Rate of leaf appearance on the main stem (leaves d^{-1})

In general, the number of leaves produced by 28 days was greatest at 26.8 °C. However, *V. sativa*, *V. dasycarpa* and *L. mutabilis* produced the maximum number of leaves at 21.8 °C. At each temperature, the number of leaves on the main stem

Table 2. The fitted linear relationships between rate of progress from sowing to 50% seedling emergence ($1/t_{50\%}$) and mean air temperature for 12 legume cover crops. Standard errors are shown in parentheses. The coefficients *a* and *b*, and their corresponding standard errors, are all $\times 10^3$.

Assumed photoperiod response†	Species	*a*	*b*	T_b (°C)	θ (°Cd)	r^2 (*n*)	θ (°Cd) when a common T_b used‡
SDP	*Canavalia ensiformis*	−87.3 (18.9)	10.27 (0.853)	8.5 (1.2)	97	0.93 (12)	94
	Crotalaria juncea	−137.8 (15.3)	15.81 (0.698)	8.6 (0.6)	63	0.96 (12)	61
	Dolichos lablab	−116.8 (29.9)	12.50 (1.350)	9.3 (1.4)	80	0.89 (12)	82
	Mucuna pruriens	−75.6 (11.6)	8.33 (0.525)	9.1 (0.9)	120	0.96 (12)	121
	Pueraria phaseoloides	−82.8 (14.9)	9.60 (0.672)	8.7 (1.0)	104	0.95 (12)	102
	Stylosanthes hamata	−164.2 (17.1)	18.05 (0.681)	9.1 (0.6)	55	0.97 (12)	56
LDP	*Lupinus mutabilis*	−0.70 (1.32)	9.26 (0.959)	−0.1 (1.4)	108	0.96 (9)	104
	Trifolium resupinatum	−12.60 (34.40)	9.19 (1.550)	1.4 (1.5)	109	0.94 (9)	111
	Vicia dasycarpa	139.8 (1.98)	—§	—	—	—	—
	Vicia faba (Bolivia)	−0.53 (0.74)	4.68 (0.337)	−0.1 (1.6)	214	0.96 (9)	201
	Vicia faba (Nepal)	−3.40 (1.41)	5.81 (0.635)	0.6 (2.3)	172	0.91 (9)	169
	Vicia sativa	−6.10 (13.10)	6.41 (0.591)	0.9 (1.9)	156	0.94 (9)	156

†SDP is short-day plant and LDP is long-day plant; ‡best fit common T_b is 9 °C for short-day and 1 °C for long-day species; §no significant temperature response was found.

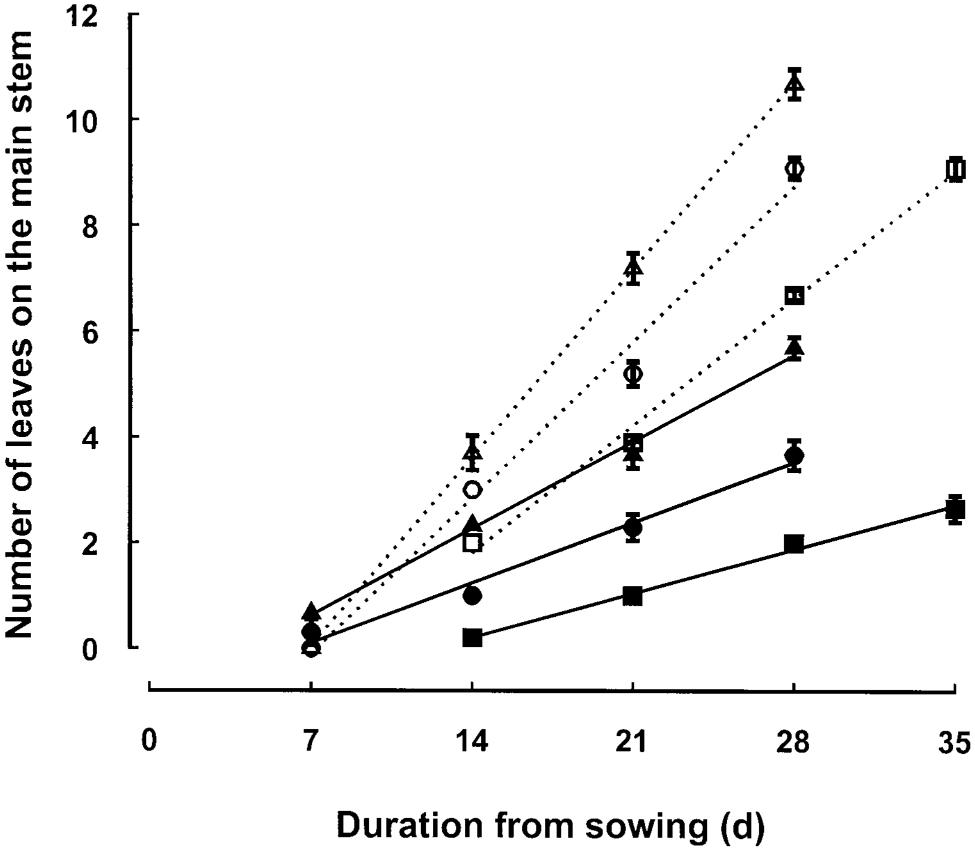

Fig. 4. Relationship between the number of leaves on the main stem and duration from sowing for *Canavalia ensiformis* (solid symbols, solid lines) and *Vicia faba* (Bolivia) (open symbols, broken lines) at 16.8 (□, ■), 21.8 (○, ●) and 26.8 °C (△, ▲). Each symbol is the mean of four observations for *C. ensiformis* and three observations for *V. faba*. The vertical bars denote standard errors.

increased linearly with days after sowing in all species as exemplified by *C. ensiformis* and *V. faba* (Bolivia) (Fig. 4).

In all six short-day species, leaves d^{-1} was a linear function of mean air temperature (Fig. 5). Linear relationships over the whole range of temperatures were also found in *V. faba* (Bolivia and Nepal) and in *T. resupinatum* (Fig. 6a, b, e). However, leaves d^{-1} in *V. sativa*, *V. dasycarpa* and *L. mutabilis* were similar at 21.8 and 26.8 °C (Fig. 6c, d, f). The effects of photoperiod response group, legume genotype, and their interactions on these relationships between leaves d^{-1} and temperature were significant, but the effect of photoperiod was not. The estimated linear relations for all species are given in Table 3 together with the calculated T_b and θ.

Fitting six individual linear relations within the six short-day species combined to account for 98.5% (d.f. = 60) of the total variation in leaves d^{-1} (solid lines in Fig. 5). Nonetheless, regression lines fitted for the six short-day species with the

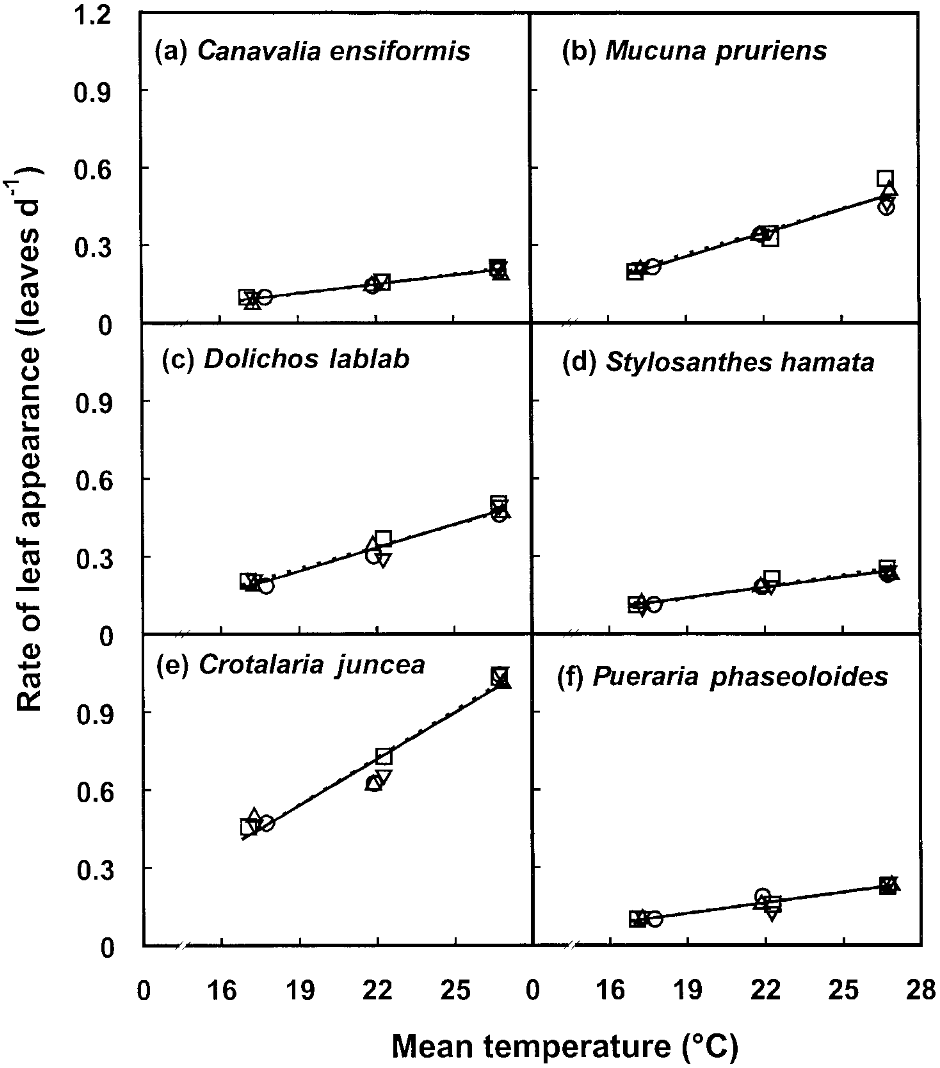

Fig. 5. Relationship between the rate of leaf appearance (leaves d^{-1}) and mean air temperature for six short-day species grown at photoperiods of 11.5 (□), 12.5 (○), 13.5 (△) and 14.5 h d^{-1} (▽). The solid lines fitted are leaves d^{-1} = $a + b$T with the values of a and b presented in Table 3. The broken lines (barely visible) have a common T_b of 10 °C.

best-fit common T_b of 10 °C, but with different slopes (Table 3), accounted for 98.3% (d.f. = 66) of the variation in leaves d^{-1} (broken lines in Fig. 5). When data at the supra-optimal temperature (26.8 °C) were excluded for *V. sativa*, *V. dasycarpa* and *L. mutabilis*, comparison of regression lines between the six long-day cover crops revealed that *V. dasycarpa* was significantly different from the other five; that is, T_b for leaves d^{-1} in *V. dasycarpa* was considerably higher than for the other long-day plants. The five individual linear relationships for the five long-day

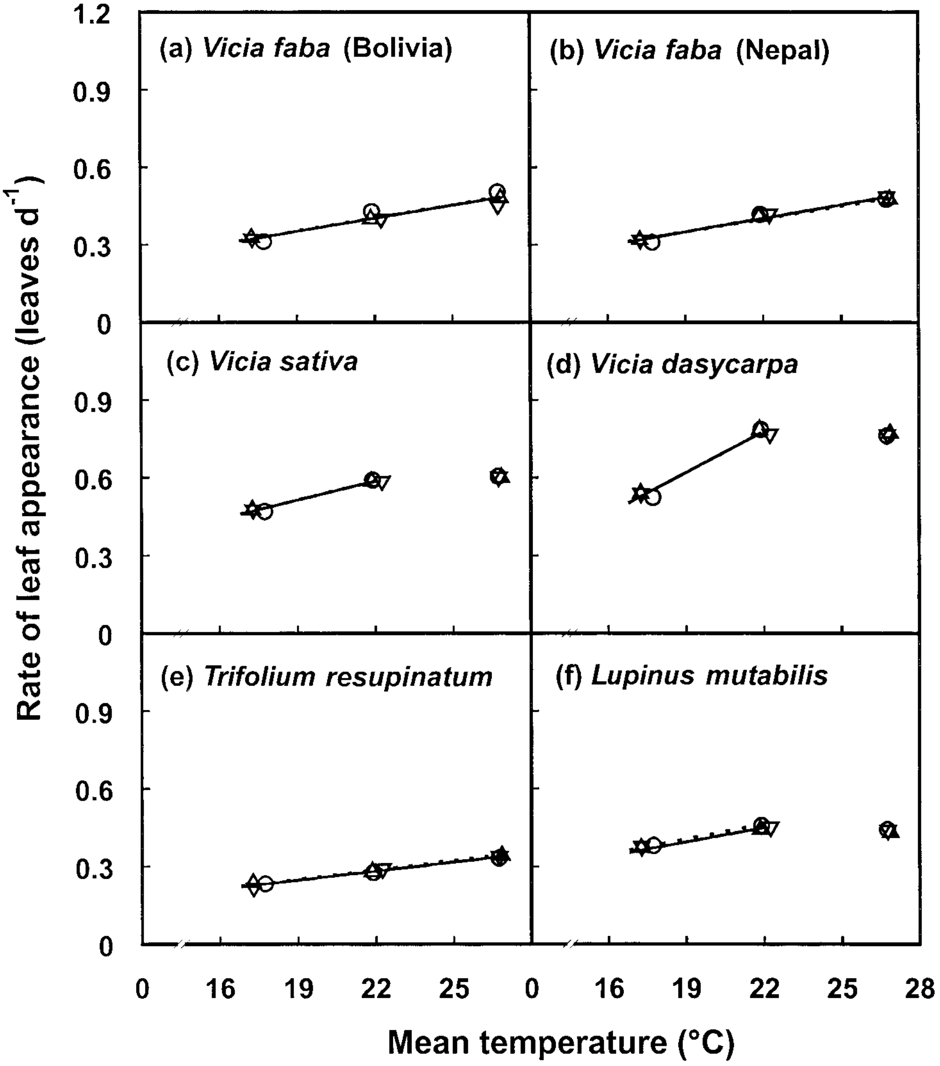

Fig. 6. Relationship between the rate of leaf appearance (leaves d^{-1}) and mean air temperature for six long-day genotypes grown at photoperiods of 12.5 (○), 13.5 (△) and 14.5 h d^{-1} (▽). The solid lines fitted are leaves $d^{-1} = a + bT$ with the values of a and b presented in Table 3. The broken lines in a, b, c, e and f (barely visible) have a common T_b of −2 °C.

cover crops (excluding *V. dasycarpa*) combined to account for 98.5% (d.f. = 29) of the total variation in leaves d^{-1} (solid lines in Fig. 6). Nevertheless, these five relationships when fitted with the best-fit common T_b of −2 °C, but with different slopes (Table 3), accounted for 98.2% (d.f. = 34) of the variation in leaves d^{-1} (broken lines in Fig. 6). Thus, using a common estimate of T_b for leaves d^{-1} for either short- or long-day (except *V. dasycarpa*) cover crops also provided r^2 values and fitted relationships almost identical to those obtained with the individual relationships for each cover crop.

Table 3. The fitted linear relationships between the rate of leaf appearance on the main stem (leaves d^{-1}) and the mean air temperatures for 12 legume cover crops. Standard errors are shown in parentheses. The coefficients *a* and *b*, and their corresponding standard errors are all $\times 10^3$.

Assumed photoperiod response†	Species	*a*	*b*	T_b (°C)	θ (°Cd)	r^2 (*n*)	θ (°Cd) when a common T_b used‡
SDP	*Canavalia ensiformis*	−108.9 (21.7)	11.74 (0.968)	9.3 (1.1)	85	0.92 (12)	81
	Crotalaria juncea	−592.0 (95.6)	59.54 (4.270)	9.9 (1.0)	17	0.95 (12)	17
	Dolichos lablab	−327.6 (43.2)	30.03 (1.930)	10.9 (0.9)	33	0.95 (12)	36
	Mucuna pruriens	−326.2 (49.4)	30.59 (2.210)	10.7 (1.0)	33	0.95 (12)	34
	Pueraria phaseoloides	−136.6 (13.6)	13.62 (1.180)	10.0 (1.1)	73	0.92 (12)	74
	Stylosanthes hamata	−115.6 (22.7)	13.42 (1.010)	8.6 (1.2)	75	0.94 (12)	68
LDP	*Lupinus mutabilis*§	47.9 (23.9)	18.25 (1.310)	−2.6 (2.2)	48	0.96 (6)	53
	Trifolium resupinatum	27.1 (12.6)	11.60 (1.564)	−2.3 (2.5)	86	0.98 (9)	85
	Vicia dasycarpa§	−390.2 (80.0)	53.12 (4.030)	7.3 (1.2)	30	0.97 (6)	—¶
	Vicia faba (Bolivia)	32.1 (37.7)	16.82 (1.680)	−1.9 (2.4)	60	0.93 (9)	60
	Vicia faba (Nepal)	19.2 (23.9)	17.42 (1.070)	−1.1 (1.4)	57	0.97 (9)	60
	Vicia sativa§	47.5 (31.4)	24.51 (1.580)	−1.9 (1.5)	41	0.98 (6)	41

†SDP is short-day plant and LDP is long-day plant; ‡best fit common T_b is 10 °C for short-day and −2 °C for long-day species; §only data at sub-optimal temperatures were included; ¶*Vicia dasycarpa* was significantly different from other long-day species and was not included in the best-fit common T_b analysis.

Table 4. Area of the third leaf on the main stem of 12 legume cover crops grown at a mean temperature of 26.8 °C and at a photoperiod of 14.5 h d^{-1}.

Short-day plants		Long-day plants	
Species	Leaf area (cm^2)	Species	Leaf area (cm^2)
Canavalia ensiformis	378.1	*Lupinus mutabilis*	10.9
Crotalaria juncea	18.9	*Trifolium resupinatum*	6.1
Dolichos lablab	216.6	*Vicia dasycarpa*	8.2
Mucuna pruriens	223.7	*Vicia faba* (Bolivia)	39.7
Pueraria phaseoloides	45.2	*Vicia faba* (Nepal)	46.4
Stylosanthes hamata	3.1	*Vicia sativa*	10.6

L.s.d. at $p = 0.05$ between species is 17.0.

Leaf area of the third leaf on the main stem

The area of the third leaf varied more than 100-fold among the legume species (Table 4). Of the six short-day legume species, *C. ensiformis* produced the largest third leaf followed by *M. pruriens* and *D. lablab*, while *S. hamata* produced the smallest. Variation in leaf area among the long-day legume species was less; *V. faba* produced the largest third leaf.

DISCUSSION

Selecting the most appropriate legume cover crop for a particular farming system is made difficult because no one legume species is likely to fulfil all the requirements of an 'ideal' cover crop (Bourke, 1975). Moreover, the most appropriate cover crop species will vary depending on the characteristics of the target environment. Quantitative models which describe the growth and development of different cover crops will aid the selection of genotypes that are adapted to the target environment. Such models, which predict the vegetative and reproductive durations of cover crops, now exist (Keatinge *et al.*, 1998). This paper has quantified two more processes important to the establishment of ground cover (seedling emergence rate and leaf appearance rate) for diverse cover crops in different photothermal environments.

The effects of temperature on the rates of seedling emergence and leaf appearance are in accordance with the thermal time approach (Monteith, 1977). In many other crops linear relationships between these rates and sub-optimal temperatures have been reported (Angus *et al.*, 1981; Wheeler and Ellis, 1992 for the rate of seedling emergence and Ellis *et al.*, 1993; Craufurd *et al.*, 1997 for the rate of leaf appearance). The absence of photoperiodic effects on the rate of leaf appearance in all species examined here was also observed in cowpea (*Vigna unguiculata*) (Craufurd *et al.*, 1997) and is assumed implicitly in crop simulation models given that leaf production can be successfully modelled by a thermal time approach (Hoogenboom *et al.*, 1991).

Quantifying the effects of temperature on the rates of seedling emergence and leaf appearance could be simplified because (with the notable exception of *V. dasycarpa*) within each photoperiod response group there was a common T_b. The estimates of T_b for seedling emergence rate were 9 °C for the short-day species, and 1 °C for long-day species (except *V. dasycarpa*). For the rate of leaf appearance these values were 10 °C for short-day species and −2 °C for long-day species (except *V. dasycarpa*). Thus, future modelling of seedling emergence and leaf appearance of legume cover crops in target environments could start by adopting these respective common values of T_b. Keatinge *et al.* (1998) reported a range of T_b values from 8.5 to 9.5 °C for the rate of progress from sowing towards flowering for the six short-day species investigated here. Values for seedling emergence similar to those determined here (0.6 °C for cv. Alfred) were also reported for *V. faba* by Dumur *et al.* (1990), but −4.0 °C for cv. Sutton and Aquaduce were reported by Ellis *et al.* (1987) and 9.6 °C for *D. lablab* by Angus *et al.* (1981). Within the range of temperatures imposed here the absence of a significant temperature effect on the rate of seedling emergence for *V. dasycarpa* was also detected for the rate of progress towards flowering and from flowering towards maturity (Keatinge *et al.*, 1998), and clearly distinguishes *V. dasycarpa* from the other cover crops investigated.

Rapid development of ground cover may aid conservation of soil water and protect the soil from erosion (Derpsch *et al.*, 1986; Frye *et al.*, 1988). Using a minimum data set of daily records of minimum and maximum temperatures, these simple thermal time models can now be employed to identify whether or not a given legume species is potentially adapted to a particular cropping environment in terms of rapid establishment of ground cover. Table 5 shows the calculated duration from sowing to seedling emergence at selected constant temperatures

Table 5. The calculated duration (d) from sowing to seedling emergence at 11, 13, 15 and 17 °C for 11 legume cover crops.

Assumed photoperiod response†	Species	11 °C	13 °C	15 °C	17 °C
SDP	*Canavalia ensiformis*	38.9	21.6	15.0	11.4
	Crotalaria juncea	27.7	14.8	10.1	7.6
	Dolichos lablab	48.3	21.9	14.1	10.4
	Mucuna pruriens	62.6	30.6	20.2	15.2
	Pueraria phaseoloides	43.8	23.8	16.3	12.4
	Stylosanthes hamata	29.1	14.2	9.4	7.0
LDP	*Lupinus mutabilis*	10.0	8.0	7.2	6.5
	Trifolium resupinatum	11.4	9.4	8.0	6.9
	Vicia faba (Bolivia)	19.6	16.6	14.3	12.7
	Vicia faba (Nepal)	16.5	13.9	11.9	10.6
	Vicia sativa	15.5	13.0	11.1	9.7

†SDP is short-day plant and LDP is long-day plant.

from 11 to 17 °C for the 11 cover crops. Such calculations assume that the quality of the seed is similar to that used in these investigations (Khah *et al.*, 1986). The practical consequence of Table 5 is that the long-day legume species would be more suitable for temperate conditions as found at the more extreme latitudes or at higher elevations in the tropics and subtropics in order to achieve more rapid seedling emergence and earlier soil cover. The relatively cool supra-optimal temperatures for leaves d^{-1} in *V. sativa*, *V. dasycarpa* and *L. mutabilis* confirm that these species would not be the most suitable for lowland tropical environments, but may have considerable potential in the tropical highlands (> 1000 m).

The considerable interspecific variation in rates of seedling emergence and leaf appearance, and individual leaf sizes, permits the multi-purpose use of these legume cover crops to be assessed for different environments. For example, legume species with relatively large leaves and rapid leaf production (that is, a small θ requirement per leaf produced) would be more suitable for suppressing weeds and producing a large biomass in a short season. *Mucuna pruriens* and *D. lablab* grown in tropical environments may belong to this division of legume species. The widespread use of *M. pruriens* for control of *Imperata cylindrica* by farmers in Benin (Versteeg *et al.*, 1998) exemplifies this conclusion. However, the highly competitive nature of such cover crop species can also be hazardous in inter- or relay-cropping situations. The simple leaf appearance models described in this paper might also be used for the prediction of 'safe' delayed sowing times for leguminous cover crops grown in relay with cereals such as maize or millet.

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