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Characterization of responses to temperature and photoperiod for time to flowering in a world lentil collection

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Summary. The times from sowing to first flowering (f) of 231 accessions of lentil (*Lens culinaris* Medik.), comprising germ plasm from eight countries and breeding lines from ICARDA in Syria, were recorded in four glasshouse environments; two photoperiods (16 and 13 h/day) combined with warmer (24°/13 °C) and cooler (18°/9 °C) day/night temperatures. The linear model $1/f = a + bT + cP$ (where T is mean diurnal temperature and P is photoperiod) provided an average fit over the 231 accessions of $r^2 = 0.852$. Since there is no interaction term in this linear model, the flowering responses of an accession to temperature and photoperiod are independent. The values of the constants b and c indicate relative responsiveness of rate of progress towards flowering ($1/f$) to temperature and photoperiod, respectively. Comparison among the 231 accessions showed a weak, but significant, negative correlation between the values of b and c ($r = -0.291$, $P < 0.01$). Since the proportion of the variance of b not attributed to its linear regression on c was > 0.91, we conclude that these phenological responses are under separate control and that there is considerable scope for selection of any combination of sensitivities to temperature and photoperiod in lentil. Just as a large proportion of the variation among accessions in mean time to first flowering was attributed to country of origin, so also was variability in the values of the constants a, b, and c. In particular, sensitivity to photoperiod (i.e., the value of constant c) was dependent upon latitude of origin. Breeding lines from ICARDA were equally variable in a, b, and c as were germ plasm accessions from elsewhere, while the mean values were similar to those of accessions from neighboring Jordan. A single accession of wild lentil (*L. culinaris* subsp. *orientalis*) from Turkey showed flowering responses to T and P similar to the mean value of accessions of cultivated lentil from that country. Results from diverse environments for the Argentinian cv Precoz show that the use of this linear model facilitates predictions of time to flowering in any environment (within wide limits) of known mean temperature and photoperiod. The model, then, minimizes the need for multisite evaluations of phenology, since predictions of pre-flowering duration in any environment, and characterization of flowering responses to photoperiod and temperature, can now be achieved by screening germ plasm in a few, carefully selected locations.

Key words: Lentil – Germ plasm – Flowering – Temperature – Photoperiod

Introduction

The major evolutionary force in the domesticated lentil (*Lens culinaris* Medik.) is known to have been selection pressure for an appropriate phenology (Erskine et al. 1989). Recognition of this fact underlies the emphasis in current national and international lentil crop improvement programs on improved adaptation through selection to match an appropriate phenology to diverse target environments. The now common, but pragmatic, approach taken to selection is to evaluate large germ plasm collections for phenological characters at a single or, at best, two locations (Erskine and Witcombe 1984), and then to grow a much smaller number of selected accessions in multilocation trials (e.g., ICARDA 1987).

An alternative approach to quantify genetic differences in phenology is advocated here, using a descriptive model of the flowering responses to environmental condi-

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tions which was developed from research on six diverse genotypes in controlled environments. In those investigations it was found that the flowering responses of lentil to wide ranges of temperature and photoperiod – the two major environmental factors that modulate times to flowering in this species (Summerfield et al. 1985 a) – were well described by the relation:

$$1/f = a + bT + cP, \quad (1)$$

where f is the time (days) from sowing to first flowering, T and P are the respective values of mean temperature and photoperiod during the same period, and a, b, and c are genotype-specific constants (Summerfield et al. 1985 b). The value of a is a partial estimate of the intrinsic earliness to flower of a genotype, while the values of b and c reflect relative responsiveness to temperature and photoperiod, respectively. The ranges of T (9.0°–21.5 °C) and P (10–16 h/day) used in that study span the major agro-ecological environments of lentil cultivation.

The unambiguous limits to the validity of the predictive model [Eq. (1)] have been described elsewhere (Roberts and Summerfield 1987; Ellis et al. 1990). Briefly, the temperature limits are a base (T_b) and an optimum value (T_o), whereas the photoperiodic limits are the critical (P_c) and ceiling (P_{ce}) day lengths. When $T \leqslant T_b$, then $1/f = 0$ (i.e., $f = \infty$); and when $T = T_o$, $1/f$ is maximal (i.e., f is a minimum value). When $P \geqslant P_c$ then $1/f$ is maximal (i.e., f is minimal), and when $P \leqslant P_{ce}$ then $1/f$ is minimal.

Preliminary field tests of the utility of Eq. (1) for lentil have been undertaken (Summerfield et al. 1985 b; Gray and Delgado 1990). Those trials predicted flowering times with reassuring precision when the field environments were within the limits between T_b and T_o and between P_c and P_{ce}. However, as expected, if $T < T_b$ then model predictions were unreliable unless calculations of mean temperature had taken that fact into account.

This paper reports the utility of Eq. (1) to characterize the flowering responses to temperature and photoperiod of a diverse range of lentil germ plasm grown in four photothermal environments in a glasshouse, and examines possible correlations between the parameters defining the responses and between these and the geographical origins of the germ plasm.

Materials and methods

Plant material

A total of 231 lentil accessions were grown in glasshouses at the Plant Environment Laboratory (PEL) at Reading during 1987 in each of four photothermal environments. The accessions comprised randomly selected germ plasm from the following major lentil-producing countries: Afghanistan (25 accessions), Egypt (26), Ethiopia (26), India (27), Jordan (28), Pakistan (25), Turkey (26), and the Soviet Union (25) – all from the ICARDA World Lentil Collection – together with elite lines (22) from the ICARDA breeding program and a single accession of wild material, *Lens culinaris* subsp. *orientalis* (ILWL 7), from Turkey.

Photothermal regimes

The four growing environments comprised longer (16 h) and shorter (13 h) days, each combined with warmer (24°/13 °C) and cooler (18°/9 °C) day/night temperatures. The plants were grown on mobile trolleys, which were drawn into and out of night compartments automatically at the appropriate times. Day-night temperature changes coincided with photoperiod, so the design mean diurnal temperatures were 15.0° and 20.5 °C in the 16 h/day regimes compared with 13.9° and 19.0 °C in the 13 h/day combinations. Night temperatures were maintained within ±0.5 °C of the target values throughout the investigation. Day temperatures, typically, were within ±1 °C of the values required, although on a few days the upper temperature limit was exceeded by up to 2 °C. Calculations of mean pre-flowering temperatures took account of all deviations, the actual mean diurnal temperatures provided being 13.9° and 18.9 °C in the 13 h/day regimes and 15.0° and 20.3 °C in the 16 h/day regimes. Within each growing environment (main plots) the individual accessions were randomized in single pots with three replications.

Plant culture and husbandry

Full details of plant husbandry and culture techniques appropriate for pot-grown lentil plants in controlled environments have been given elsewhere (Summerfield and Muehlbauer 1982). Briefly, individual plants were grown in 12.5 cm (0.35 l capacity) square plastic pots containing a rooting medium of vermiculite (grade size DM), sand (coarse and washed), gravel (0.6 cm crushed), and loamless peat compost mixed in proportions of 4:2:4:1 V/V, respectively. All components of the rooting medium, other than the vermiculite, had been steam-sterilized at 96 °C and 3 kg cm^{-2} for 10–20 min before use.

All plants were inoculated with a broadly infective and symbiotically effective strain of *Rhizobium leguminosarum* (ICARDA strain LE 19) and were irrigated automatically with a defined nutrient solution, complete except for containing only 20 mg l^{-1} N (20 ppm). At this concentration of inorganic nitrogen, the plants were expected to rely heavily on symbiotic dinitrogen fixation.

Records were taken for individual plants in all environments of the time (days) from sowing until the appearance of the first open flower (corolla color visible).

Data analyses

A preliminary analysis of variance was undertaken of times from sowing to first flowering (f). Equation (1) was then applied to the data for individual accessions using multiple linear regression techniques (e.g., Weisberg 1980) once values of f had been transformed to $1/f$ (i.e., the rate of progress towards flowering). Finally, one-way analyses of variance based on country of origin of accessions were undertaken for time to first flower (f) and the values of the three constants of Eq. (1), i.e., the intercept a [the reciprocal of which is a partial estimate of the intrinsic earliness of an accession, intrinsic earliness actually being $1/(a + bT_o + cP_c)$, which gives the minimum value of f for the accession] and the response constants b (temperature) and c (photoperiod), respectively.

Results

Times from sowing to flowering (f) differed greatly among the 231 accessions and also varied across photothermal regimes. Not surprisingly, longer days and

Table 1. Range (in parentheses) and mean time from sowing to first flowering (days)[a] of 231 accessions of lentil grown in four photothermal regimes in a glasshouse

Temperature (day/night)	Photoperiod (h/day)		Mean (SE)
	13	16	
Cool (18°/9°C)	67.5 (48.3–108.0)	47.0 (39.7–64.3)	57.2 (0.4)
Warm (24°/13°C)	59.3 (36.3–102.5)	37.7 (30.0–58.5)	48.2 (0.6)
Mean (SE)	63.3 (0.5)	42.4 (0.3)	

[a] The ranges given are mean values for the earliest and latest accession to come into flower in each of the four environments

warmer temperatures hastened flowering (Table 1), the extreme treatment combinations providing a more than threefold difference in f: 30 days (SE 0.0) for ILL 2537 (India) in warm and long days compared with 108 days (SE 3.0) for ILL 1756 (Afghanistan) in cool and short days. Analysis of variance of the response of time of flowering (f) to temperature, photoperiod, and genotype – the traditional approach (Summerfield et al. 1985a) – not only showed significant effects of each main factor but also of the first and second order interactions ($P<0.05$). However, application of Eq. (1) showed that it was possible to describe the observations without recourse to interaction terms once they were transformed to rates of progress towards flowering. The average coefficient of determination (r^2) over 231 accessions for Eq. (1) was 0.852.

The application of Eq. (1) to cultivated lentil has been demonstrated previously (Summerfield et al. 1985b), but it is now clear that it can also be applied successfully to the wild lentil accession ILWL 7 (Fig. 1). Clearly, once the observations are transformed to rates of progress towards flowering, the temperature and photoperiodic responses are without interaction and are thus independent.

There were large differences among the 231 accessions in their respective values of the constants a, b, and c of Eq. (1). The considerable variability among accessions in response to both temperature and photoperiod is illustrated in Fig. 2. Five accessions – three from the USSR (ILL 504, 597, and 4876), one from Egypt (ILL 799), and one from Jordan (ILL 5225) – provided negative estimates of the response to temperature (Fig. 2). This aspect of the results is considered later. Analysis of the estimates of b and c for the 231 accessions showed a weak negative correlation ($r=-0.291$, $P<0.01$). Nevertheless, the considerable proportion of the variance, which remains unexplained, suggests that the temperature and photoperiod responses, already shown to be physiologically independent (e.g., Fig. 1), are also unlikely to be genetically linked. Appropriate crosses are required to confirm this hypothesis.

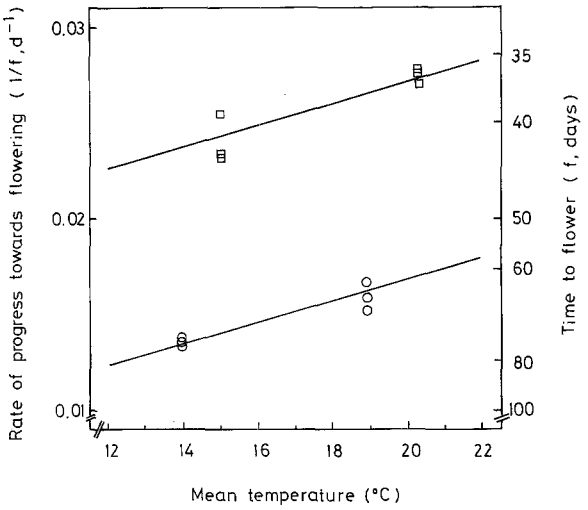

Fig. 1. Relations between rate of progress towards first flowering ($1/f$) and temperature for plants of the wild lentil accession ILWL 7 (*L. culinaris* subsp. *orientalis*) from Turkey in photoperiods of 13 (○) or 16 h/day (□). The regressions show the model provided by Eq. (1), where $a=-0.0387$ (SE 0.0009), $b=0.000548$ (SE 0.000095), and $c=0.00343$ (SE 0.00017) ($r^2=0.984$). The right-hand ordinate axis shows the nonlinear scale for time to first flower (f)

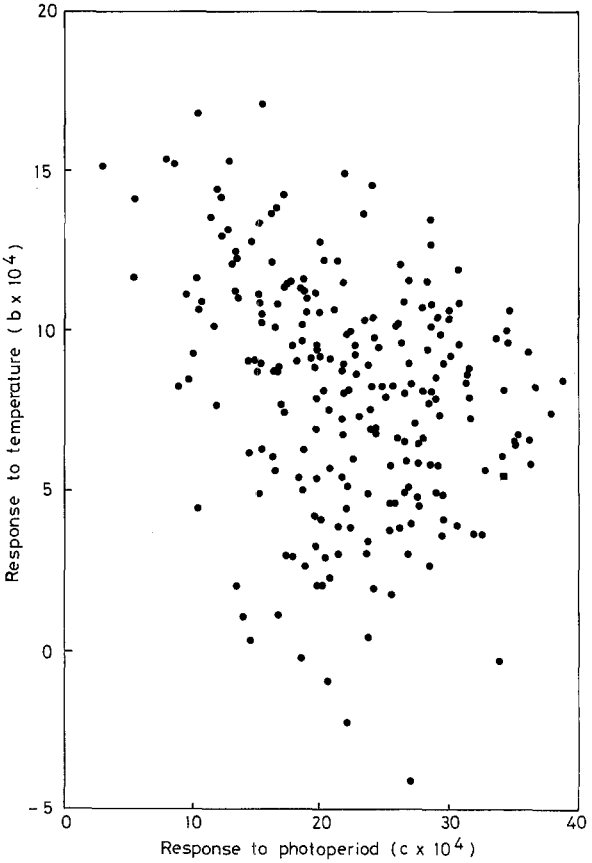

Fig. 2. Sensitivity of rate of progress towards flowering to temperature (b) and photoperiod (c) of 230 cultivated lentil accessions (●) and one wild lentil accession from Turkey (■)

Table 2. Mean times (days) from sowing to first flowering (f) across four photothermal regimes, and values of the intercept constant a from Eq. (1) ($\times 10^3$), with SE values in parentheses, for lentil accessions from different countries and from ICARDA, Syria

Country of origin	No. of accessions	Mean value of f (days)	Mean value of a ($\times 10^3$)
Afghanistan	25	64.6 (0.99)	−27.9 (1.6)
USSR	25	62.5 (0.99)	−19.9 (3.4)
Turkey	26	59.7 (0.97)	−35.7 (1.7)
Pakistan	25	54.4 (0.99)	−32.4 (2.8)
Jordan	28	50.4 (0.94)	−27.3 (1.5)
ICARDA	22	50.3 (1.06)	−24.9 (2.7)
Egypt	26	48.4 (0.97)	−19.7 (2.4)
Ethiopia	26	45.1 (0.97)	−15.7 (1.1)
India	27	41.8 (0.95)	−18.5 (0.7)

One-way analyses of variance on the basis of country of origin revealed highly significant differences among country means for each of the mean values of time to flower ($P<0.005$), intercept (a) ($P<0.005$), response to temperature (b) ($P<0.005$), and response to photoperiod (c) ($P<0.005$). On average, accessions from India were the earliest to flower, whereas those from Afghanistan and the USSR were the latest, but estimates of a showed a different pattern with respect to country of origin (Table 2). Indeed, there was no significant correlation ($r=-0.547$, $P>0.05$) between these values of f and a. This simply confirms that the value a is only a partial estimate of intrinsic earliness and that estimates of P_c, T_o, b, and c are all required to describe intrinsic earliness per se.

The mean responses to temperature (b) and photoperiod (c) of accessions from various countries and from ICARDA are shown in Fig. 3. It is clear that the Indian germ plasm is the most responsive to temperature and the USSR accessions the least responsive. For responsiveness to photoperiod, the extremes are represented by germ plasm from Ethiopia and India (least sensitivity) and Turkey (acute sensitivity). In terms of mean time to flower and values for each of the constants a, b, and c of Eq. (1), the 22 ICARDA breeding lines occupy a central position in comparison with the germ plasm from the eight diverse countries tested here, and in almost all these respects are similar to the accessions from neighboring Jordan (Table 2, Fig. 3). Inspection of the SE values in Table 2 and Fig. 3 reveals that the variations in these attributes among the ICARDA breeding lines are similar to those detected within the most variable countries. The accessions from Turkey, neighboring Syria (ICARDA) to the north, showed a similar sensitivity to temperature, but were rather more sensitive to photoperiod and took on average about 20% longer to flower (Table 2, Fig. 3). Finally, Fig. 2 and comparisons of Fig. 1 with Table 2

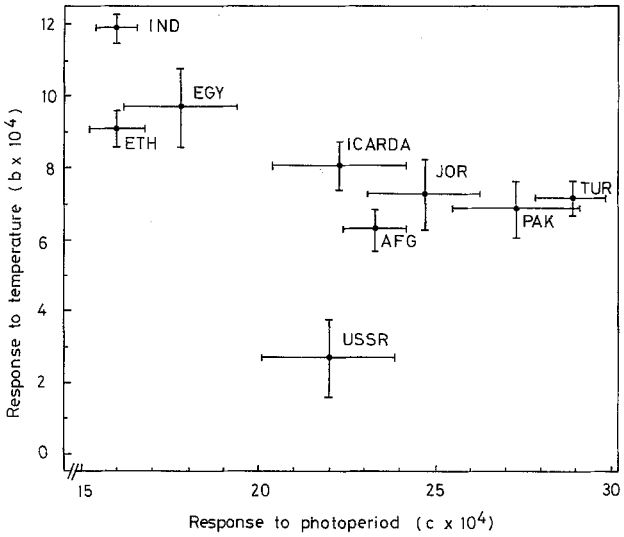

Fig. 3. Mean sensitivity of rate of progress towards flowering to temperature (b) and photoperiod (c) of accessions from eight lentil-producing countries and from ICARDA, Syria. The *vertical* and *horizontal bars* indicate means ±SE

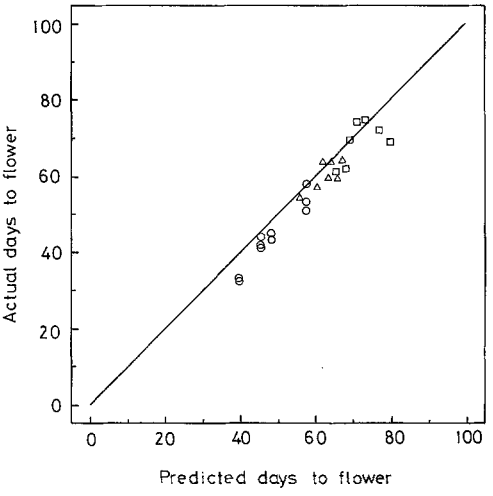

Fig. 4. Comparisons for plants of cv Precoz between the observed times from sowing to first flowering (d) in the four glass house environments in this study (o) and to 50% flowering (d, mean of many plants) in serial field sowings in Argentina during 1985 (□) and 1986 (△), as reported by Gray and Delgado (1990), with those predicted for first flowering by the use of Eq. (1) and the values provided for the constants a, b, and c by Summerfield et al. 1985b. The *solid diagonal line* indicates the position of perfect agreement ($y=x$)

and Fig. 3 illustrate that the wild lentil accession ILWL 7 from Turkey showed very similar durations and photothermal responses to the mean value of accessions of cultivated lentil from that country.

In addition to the 231 accessions described thus far, the six genotypes included in our earlier study were also grown in the four glasshouse environments. The results for five of the genotypes are discussed later, but here

(Fig. 4) the times from sowing to flowering determined in this study for the Argentinian cv Precoz are compared with the predictions obtained by applying Eq. (1) and the estimates of a, b, and c already provided for this cultivar (Summerfield et al. 1985 b). Data from Gray and Delgado (1990) for cv Precoz in serial field sowings in Argentinia in 1985 and 1986 are also compared with this model in Fig. 4. Clearly, the earlier model for Precoz derived from growth cabinet studies provides an extremely good estimate of the results from both glasshouse and field environments, these results being only 2 days shorter than predicted, on average.

Discussion

The model used in this study [Eq. (1)] to describe different genetic responses in phenology to changes in mean temperature and photoperiod was based on a set of just six genotypes of lentil grown under a wide range of conditions under artificial light in controlled-environment growth cabinets (Summerfield et al. 1985 b). The adequacy of the model for a much wider range of germ plasm accessions grown under a restricted set of four photothermal environments in a glasshouse under natural light may be assessed by the mean coefficient of determination of the 231 accessions, i.e., $r^2 = 0.852$. Clearly, the model describes these extensive data ($n = 2688$) well. This is despite the fact that it is now known that lentil plants are not equally sensitive to environmental conditions throughout the duration of vegetative growth – the sensitive (inductive) phase is sandwiched between photoperiod-insensitive pre- and post-inductive phases (Roberts et al. 1986). By assuming that the entire pre-flowering period is sensitive to photoperiod, then, the responses fitted here are, strictly speaking, only approximations.

Mean values of time to flowering merely illustrate the variation within the germ plasm in phenology. The model, on the other hand, has uncovered and quantified the breadth of diversity within the germ plasm in phenological responses to both temperature and photoperiod separately. Additionally, it is now clear for the first time, from the wide spread of sensitivity in rate of progress towards flowering to temperature and photoperiod (Fig. 2), that the responses to these two factors are physiologically and probably genetically independent (despite showing a weak correlation). Hence, the phenological flowering response to temperature appears to be under separate genetic control and not closely linked to that for the response to photoperiod.

The value of the model is its predictive power, as exemplified by Fig. 4. Herein lies the utility of the approach to quantifying genetic variation in phenology. The time to flower of any of the tested accessions can be predicted for any environment of known photoperiod and temperature profile within the limits of photoperiod between P_c and P_{ce} and for temperatures between T_b and T_o. The wide range of environmental conditions used by Summerfield et al. (1985 b), in which Eq. (1) was first applied to the crop, covered typical average values of photoperiod and temperature experienced by lentil crops during the vegetative stage in the principal production regions in Ethiopia, India, Turkey, Syria, the USA, and Canada. However, despite the excellent predictability of the model for cv Precoz in both field and glasshouse studies (Fig. 4), comparisons between times to flower for the other five common accessions in this investigation and the models provided by Summerfield et al. (1985 b) were disappointing – plants in the latest experiment flowered much earlier than predicted. While it is disconcerting that earlier predictions overestimated the times to first flowering in these accessions, we do not believe the fault lies with the model per se. The maximum day temperature imposed previously (28 °C), we now suspect, may well have been supra-optimal, and although the seed stocks used in the two experiments had identical accession numbers, they were of different origin.

The analysis of variance on the basis of country of origin of mean time to flower confirms the large differences in flowering time between lentil germ plasm adapted to different agro-ecological conditions (Erskine et al. 1989). Furthermore, it is now clear that there are also substantial differences between the average responses in rate of progress towards flowering to temperature of germ plasm accessions from different countries. The same is true of responses to photoperiod. With phenological adaptation to the ecological environment as a major factor in the domestication and dissemination of the species, it is likely that selection for local adaptation has acted separately on the putatively independent genetic systems that control progress towards flowering under different ecological conditions.

Most crops with short-day photoperiodic responses originated in the tropics, whereas all crops with long-day responses originated in latitudes greater than 30° (Roberts and Summerfield 1987; Summerfield and Roberts 1987). Until now, the relative sensitivity of long-day responses has not been clear. However, in the case of lentil, Fig. 5 shows that photoperiod sensitivity is dependent on latitude of origin. Note that although the broken line in Fig. 5 infers continuous variation in photoperiod sensitivity with latitude of origin, these results could equally well provide evidence of two discrete categories of germ plasm: the first from Mediterranean and temperate latitudes, including those within which the crop was domesticated; and a second closer to the equator, to which this LDP crop was subsequently disseminated. It is suggested that at least part of the reason for the dependence of photoperiod sensitivity on latitude of origin is that near the equator, where day lengths are always relatively

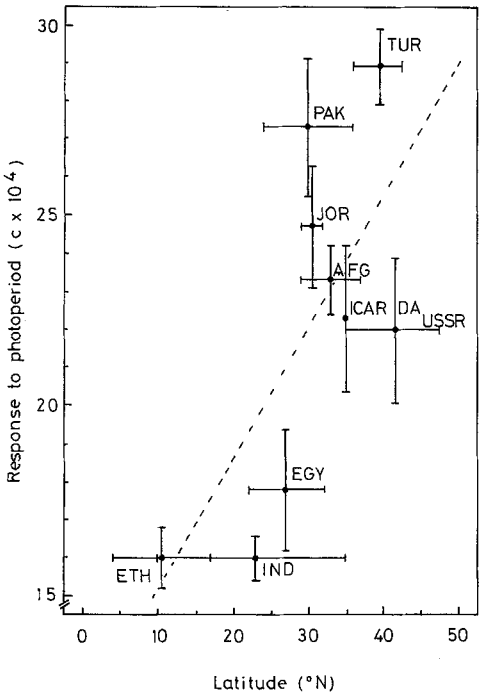

Fig. 5. Relation between mean response of rate of progress towards flowering to photoperiod (c) and latitude of provenance for accessions from eight lentil-producing countries and from ICARDA, Syria. *Vertical bars* for the value of c indicate means $\pm$SE. *Horizontal bars* indicate latitude extremes of individual countries, with the symbol • shown midway between those extremes (for the USSR the northern limit was chosen arbitrarily as 47°30'N, the assumption being that most lentils are grown south of this latitude). The *broken line* shows the linear regression for the assumption that c is dependent on latitude of provenance ($r^2 = 0.487$)

short, a marked long-day response would result in excessive delay in flowering, whereas in higher latitudes it is important that flowering is delayed until later in the spring or early summer in order to fully exploit the growing season.

Whether or not this ecological explanation is correct, the correlation of latitude of provenance with relative photoperiod sensitivity in lentil (Fig. 5) could have important implications for plant breeding. It may also be rewarding to evaluate the relation between relative temperature sensitivity (b) and temperature expectations during the growing season: from Fig. 3 one might speculate that the hotter the growing season, the greater the temperature sensitivity of the adapted genotypes.

Germ plasm from India, e.g., is both more sensitive to temperature and less sensitive to photoperiod than genetic material from West Asia, where the crop was domesticated. Although approximately 40% of the world lentil area is to be found in India, genetic diversity within Indian germ plasm is very narrow and exclusively within the *pilosae* type (Barulina 1930; Erskine and Hawtin 1983). Additional evidence of the paucity of variation within Indian germ plasm may be seen from the small standard errors for India of f and a (Table 1) and b and c (Fig. 3). Phenological problems associated with the introduction of Mediterranean germ plasm into the Indian subcontinent led to the suggestion of the existence of a "day length bottle-neck", restricting the flow of germ plasm into India (Erskine and Hawtin 1983). Current data show this to be an oversimplification, because selection during the spread of the crop into India has been directed toward increased sensitivity to temperature and reduced sensitivity to photoperiod. The Indian example documents the results of selection for local adaptation based on phenological response to the environment, re-emphasizing the role of selection on phenology in the evolutionary history of lentil.

Some caution is required when considering estimates of the value of b. Where these are small, or apparently even negative, there is the possibility that the estimate is incorrect, since the day temperatures in warmer regimes may have been in the supra-optimal range for some genotypes, as mentioned earlier. For example, close examination of the data for the five accessions for whcih the value of b was negative (albeit not significantly different to a value of zero) (Fig. 2) indicates that, in these cases, $T_o < 24\,°C$ since the plants flowered consistently sooner in the cooler than the warmest regimes. The strong possibility exists, then, that many accessions from the USSR, e.g., may have $T_o < 24\,°C$ and so a greater sensitivity to suboptimal temperatures than shown in Fig. 3.

This investigation included a single Turkish accession of wild lentil (*L. culinaris* subsp. *orientalis*). Interestingly, its flowering parameters, a, b, and c were broadly similar to the average values of a, b, and c from cultivated Turkish germ plasm (Figs. 1 and 3). This finding raises more questions than it answers, and a survey of the flowering responses of a larger sample of wild lentils collected from different areas would be of considerable interest, and is planned.

The variability among ICARDA-selected lines (at Tel-Hadya in Syria) was not significantly greater than that recorded among accessions from any other country, while the mean values of a, b, and c were similar to those for the 28 accessions from neighboring Jordan. Although the comparison could not be made critically with the experimental design used, this sounds a warning for applying selection pressure only at ICARDA in the Levant. For although there is access to a wide range of moisture regimes, there is only a restricted set of photothermal regimes. Diversification in the breeding program at ICARDA towards selection under different photothermal regimes typical of the various agro-ecological conditions of major production areas is now underway.

Although more attention to genetic variation in optimum temperatures is required, it is clear that characterization of phenology in the lentil germ plasm can be

achieved by the approach outlined here. We therefore suggest that the rather narrow definition of characterization as, e.g., "recording those characters which are highly heritable, can be easily seen by the eye, and are expressed in all environments" (IBPGR 1985) could usefully be widened, since it is now possible to screen easily for physiological characteristics that cannot be seen by the eye but, nevertheless, are highly heritable and expressed in all environments. The coefficients derived from studies such as our own, although derived from observations by eye, cannot in themselves be "easily seen by eye". Such a widening of the definition of characterization would also satisfy the aim of those such as Frankel (1989), who would wish to consider, e.g., isozyme data under this heading. In fact this point of view may have already been accepted. The IBPGR (1989) has recently defined characterization data as "characters that are highly heritable and expressed in all environments", whereas evaluation data refer to "environmentally influenced characters". Clearly, the time to flowering in a given environment is evaluation data, but we believe that the parameters *a*, *b*, and *c* represent characterization data because their values are not altered by environment, but they collectively quantitatively predict the response to environment.

Whether characterization is possible by direct observation or is calculated indirectly following observation, or as a result of some laboratory test, seems less important from the practical point-of-view than whether it can be done simply and economically on a large number of accessions. If this is accepted, then characterization of the flowering response of lentil (and other species) to photoperiod and temperature now appears feasible and potentially valuable.

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