

RELATIONSHIP OF FLOWER AND POD NUMBERS PER INFLORESCENCE WITH SEED YIELD IN LENTIL

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SUMMARY

This study, quantifying variation in flower and pod production in lentil (*Lens culinaris*), aimed to answer the question: Will selection for more pods per inflorescence increase seed yield? In Season 1 (1992–93) all open flowers were tracked to maturity in a field experiment with two lentil genotypes sown on two dates. Genotype Talia 2 had a higher rate of flower abortion than pod abortion, in contrast to genotype ILL 2581 which showed the reverse. Flower abortion accounted for 15% of flowers opened in early sowing and increased to 22% in the late sowing. Pod abortion was 19% (of flowers opened) in early sowing and 23% in the late sowing. These are the first quantitative estimates of flower and pod abortion in lentil. From the data, a rapid sampling method was developed to estimate the average number of pods per inflorescence at maturity. In Season 2 (1993–94) an experiment was conducted at two locations to estimate the average number of pods per inflorescence of 81 genotypes and to relate this to seed yield. Although the broad-sense heritability (h^2) of the number of pods per inflorescence was 0.68 and its phenotypic correlation with seed yield was $r = 0.71$, the highest-yielding genotypes were not those with the most pods per inflorescence. Selection for the number of pods per inflorescence cannot be recommended for increasing seed yield in lentil.

INTRODUCTION

Lentil (*Lens culinaris*) is an important food legume in West Asia, South Asia, North Africa, Ethiopia, and North and South America. Its seed has a high nutritive value for human consumption and the straw is an important animal feed (Bhatty, 1988). Since lentil is primarily a rainfed crop, yield stability is a major objective in any breeding programme. This could be achieved through a better understanding of the components contributing to final yield. However, these components vary from year to year and from location to location, even for the same lentil genotype (Muehlbauer *et al.*, 1985). Negative correlations are often found between morphological components of yield in crop plants. They probably arise primarily from developmentally-induced relationships. This happens when two developing structures of a plant body compete for a

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common, possibly limited nutrient supply due to high population or stress conditions. As a result component compensation might be expected as a regular feature of development (Adams, 1967). In lentil this negative association is well documented; for example, Muehlbauer (1974) and Hamdi *et al.* (1991) showed negative correlations between pods per plant and seeds per pod, and between pods per plant and 100-seed weights.

In addition to these yield components, genetic variation has been observed in the number of pods per inflorescence (Erskine and Solh, 1981). A range from 10 to 150 peduncles per plant was recorded in lentil (Malhotra *et al.*, 1974). Each peduncle normally bears 1–4 flowers, though in some conditions up to 7 flowers per inflorescence have been found. The variation in number of flowers or pods per inflorescence has been investigated by several researchers who obtained inconsistent results. For example, Muehlbauer (1974) studied 45 genotypes and found that single-podded inflorescences were most frequent followed by double-podded ones, and that triple- and four-podded inflorescences were rare. In contrast, Gill and Malhotra (1980) report double- and triple-flowered inflorescences as being very common in lentil.

There is variation in the number of flowers and pods produced per inflorescence within individual plants, among plants within a genotype, among genotypes, and as a result of environmental effects. This study was conducted to quantify such variations in flower and pod production, and then to answer the question: Will selection for many pods per inflorescence increase seed yield?

MATERIALS AND METHODS

The study was in two parts. In Season 1 (1992–93) the development and nodal position of all flowers in a field experiment on two lentil genotypes sown on two dates was investigated. From the data, a rapid sampling method was developed to estimate the average number of pods per inflorescence on many plots. In Season 2 (1993–94) an experiment was conducted at two locations to estimate the average number of pods per inflorescence of a wide range of genotypes using the sampling method and to relate this to seed yield.

Season 1

The lentil genotypes Talia 2 and ILL 2581, contrasting in numbers of flowers per inflorescence, were sown at two sowing dates, 28 November 1992 and 15 February 1993, in a factorial arrangement in randomized complete blocks with three replicates at the Agricultural Research and Education Center (AREC), lat 33°55'N, long 36°0'E, 900 m asl, in the Beka'a Valley, Lebanon. The soil was Vertic Xerochrept (Soil Survey Staff, 1975). Seeding was at the rate of 300 seeds m⁻² and plots were composed of five rows, each 2 m in length and 25 cm apart. Fifty kg P₂O₅ ha⁻¹ was applied as triple superphosphate prior to sowing, and 25 kg N ha⁻¹ was given as ammonium

nitrate on 26 February 1993 for the first sowing date and on 25 March 1993 for the second date. The seed was not inoculated, but upon inspection plants were found to be well nodulated in this and the subsequent season. A light supplemental irrigation (about 30 mm) was given on 27 April 1993 for both sowing dates. The pyrethroid insecticide, Deltamethrin 2.5% was applied on 26 February 1993 for the first sowing date and on 30 April 1993 for both sowing dates to control the infestation of *Sitona* weevil. Plots were hand-weeded as necessary.

Before flowering, a sample of five plants was selected randomly in each plot from the middle three rows. On these plants the number and nodal position of all open flowers was recorded daily. The subsequent development of each flower was tracked to maturity. Thus the numbers of open flowers, aborted flowers, aborted pods, pods and seed yield were recorded on a plant basis and sectorially on main stems, and on primary, secondary and tertiary branches.

Season 2

The variability in pod numbers per inflorescence among 81 genotypes of lentil was studied at two locations: International Center for Agricultural Research in Dry Areas (ICARDA), lat 35°55'N, long 36°55'E, 300 m asl, Tel Hadya, Syria, and AREC in the 1993–94 season. The experiment was sown on 19 December 1993 at ICARDA and on 12 January 1994 at AREC. The 81 genotypes represented a sample from the gene pool of lentil genotypes adapted to West Asia and were arranged in a quadruple (9 × 9) lattice design. Plots were 5 rows, 3.5 m in length and 30 cm apart, sown at 230 seeds m⁻². Phosphorus was applied as in Season 1. Seeds were dressed with fungicides Tridemorph M + Benomyl (1:1). Herbicide cyanazine was applied pre-emergence at a rate of 1 L ha⁻¹ to control broad-leaved weeds. At AREC, Deltamethrin was applied to control *Sitona* weevil on 3 March 1994.

Five plants were selected randomly in each plot. At physiological maturity the two basal primary branches were cut and collected in separate paper bags; the remainder of each plant was harvested into another bag. The number of pods per inflorescence was recorded at each node on the two basal branches. The harvest of the remaining plot was at 90% pod maturity. The net harvested area was 1.8 m² per plot.

Characters studied on a plot basis included the time to flower and physiological maturity, plant height, 100-seed weight and seed yield. Traits investigated on a whole-plant basis were the numbers of full and empty pods. On the two basal primary branches the traits studied were the numbers of seeds per pod and full pods per inflorescence.

A combined analysis of variance was carried out over locations for each character. The components of variance were calculated and used to estimate broad-sense heritability for each trait (Erskine and Goodrich, 1988). Phenotypic correlations were calculated among characters.

RESULTS AND DISCUSSION

Season 1

When first flowers opened on plants in sowing date 1 the maximum temperature was 25°C (Fig. 1). It then dropped to 15°C and rose steadily to 24°C by the end of flowering. In contrast, during flowering of plants with sowing date 2 the maximum temperature rose steadily from 15 to 30°C. Comparing flowering between the sowing dates showed that the warmer flowering period with sowing date 2 decreased the total number of flowers produced and reduced the duration of flowering from 36 d with sowing date 1 to 25 d with sowing date 2. Flower production peaked after 16 d with sowing date 1 and after 12 d with sowing date 2.

Overall, the percentage contributions to final yield were 22.2% from the main stem, 60.1% from primaries, 14.3% from secondaries and 3.5% from tertiaries (Fig. 2). Seed yield was markedly reduced by late sowing (Fig. 2). The yield reduction was proportionally greater on primary branches than on the main stem or secondary branches. Tertiary branches bore pods only with the early sowing date.

There was a genotype \times sowing date interaction for both flower and pod abortion, and for pods retained on plants (Fig. 3). Genotype Talia 2 consistently had a higher rate of flower abortion than pod abortion, while ILL 2581 showed the reverse. Overall, flower abortion was 15% (of flowers opened) with early sowing and 22% with late sowing. Pod abortion was 19% (of flowers opened) with early sowing and 23% with late sowing. The temperature stress associated with late sowing increased both flower and pod abortion. This was in agreement with Summerfield *et al.* (1989) who showed the pronounced effect of temperature on

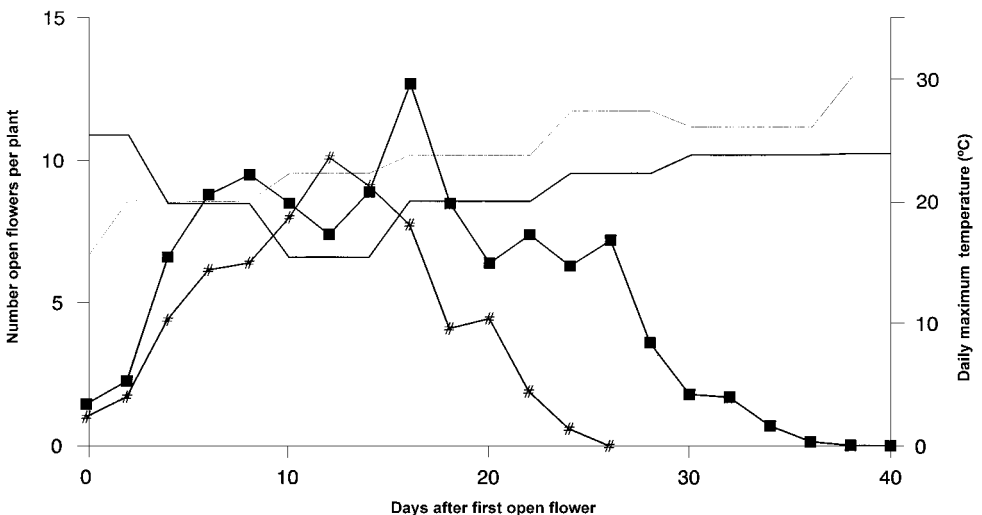


Fig. 1. Pattern of flower production in lentils shown as the average number of open flowers per plant each day after first open flower for sowing dates 1 (—■— 28 November 1992, D1) and 2 (---#--- 15 February 1993, D2) and averaged over genotypes together with average maximum temperature (—■— D1, ---#--- D2).

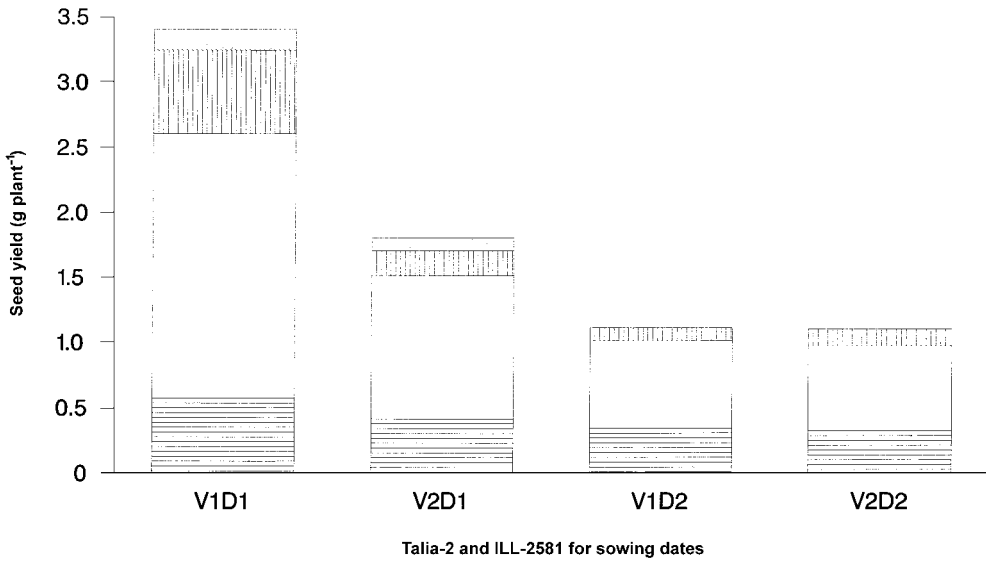


Fig. 2. Seed yield per plant (g) of lentil cultivars Talia 2 (V1) and ILL 2581 (V2) at sowing dates 1 (28 November 1992, D1) and 2 (15 February 1993, D2) on the main stem (▨), primary branches (□), secondary branches (▤) and tertiary branches (▧). S.e. mean yield per plant = 0.11.

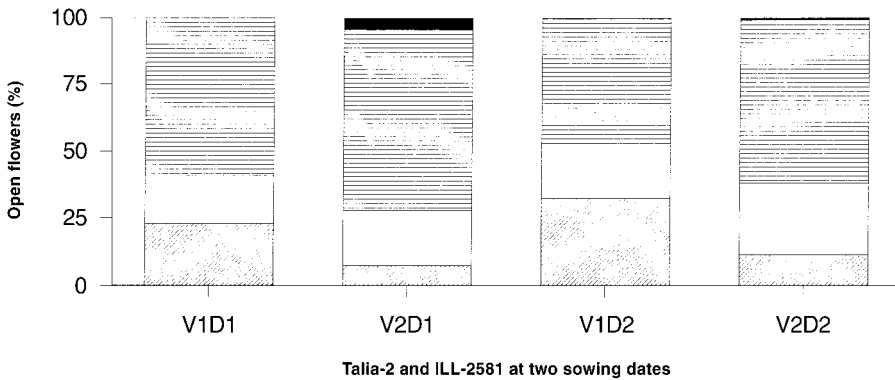


Fig. 3. Distribution (%) of total open flowers among aborted flowers (▧), aborted pods (□) and mature pods (▨) on lentil genotypes Talia 2 (V1) and ILL 2581 (V2) at sowing dates 1 (D1) and 2 (D2). Unaccounted flowers (■) are also indicated. S.e. aborted flowers = 4.3, s.e. aborted pods = 2.7, s.e. pods = 2.6.

potential production of pods and reduced capability of plants to fill them. In summary, the percentage of pods retained from open flowers was 65% with early sowing date, but only 53% with late sowing. These are the first quantitative reports of flower and pod abortion in lentil.

Development of a rapid sampling method

Owing to the impracticality of counting the flowers and pods per inflorescence at all inflorescences on a large number of plots, a rapid sampling technique for use

at maturity was developed based on the data obtained in Season 1. As primary branches contributed more to final seed yield than the main stem, secondary branches or tertiaries (Fig. 2), primary branches were targeted for sampling. The contribution of individual primary branches (first basal, second and so on) to yield was investigated. The two basal primary branches collectively contributed 33% of overall seed yield per plant. Sampling for the number of pods per inflorescence was therefore focused on the two basal primary branches in Season 2.

Season 2

The genotype \times location ($G \times L$) mean square was significantly greater than the mean square for pooled error in all characters (Table 1). The genotype mean square was significantly greater than the $G \times L$ mean square, except for plant height. Broad-sense heritability (h^2) values ranged from 0.11 to 0.87 (Table 2). Seed yield and plant height had low heritability. Components of yield such as numbers of full and empty pods per plant, seeds per pod, pods per inflorescence and 100-seed weight had high heritability estimates.

The average seed yield was 2067 kg ha⁻¹ at ICARDA, but only 832 kg ha⁻¹ at AREC. At ICARDA the genotypic means ranged from 771 to 2658 kg ha⁻¹, compared with a range of 423 to 1103 kg ha⁻¹ at AREC. The average number of pods per inflorescence was 1.3 at ICARDA and 1.0 at AREC.

In Season 2 sampling for the number of pods per inflorescence was done only at maturity and 'empty' pods comprised both small, flattened pods and fully-developed but empty pods. Overall, 49% of pods were empty with 54% empty at ICARDA and 47% empty at AREC. This is a strikingly high rate of pod abortion. The only other estimate of pod abortion in lentil available for comparison is that from Season 1, when plants were given a light irrigation during pod-filling. In Season 2, plants at both locations were stressed during pod formation and pod-filling. Although the average maximum temperature during pod-setting was moderate (23°C), there was a hot spell at both locations (reaching 31°C at AREC). Additionally, there was little rain during April, the reproductive growth period. The high percentage of empty pods was due to the combined effects of high temperature and moisture stress.

Among phenotypic correlation coefficients, the number of pods per inflorescence was positively correlated with seed yield ($r = 0.71$, $p = 0.001$) and also the number of pods per plant ($r = 0.73$, $p = 0.001$). The relationship between the number of pods per inflorescence and seed yield is shown in Fig. 4 for AREC and ICARDA. The number of pods per inflorescence was negatively correlated with seeds per pod, empty pods per plant and average seed weight.

Among classical yield components, there were also negative correlations. For example, the number of seeds per pod was negatively correlated with pods per plant, empty pods per plant and average seed weight. Additionally, the number of pods per plant was negatively correlated with average seed weight. This was because it is impossible to have two traits of a compensatory nature improved

Table 1. Mean squares for combined analysis of variance and averages (overall, location means and maximum and minimum genotype means within locations) for some agronomic traits of 81 lines of lentil grown at AREC and ICARDA in 1993–94.

| Source | d.f. | Days to flower | Days to maturity | Plant height (cm) | Seeds per pod | Pods per inflorescence | Pods per plant | Empty pods per plant | 100-seed weight (g) | Seed yield (kg ha ⁻¹) |
|------------------------|------|----------------|------------------|-------------------|---------------|------------------------|----------------|----------------------|---------------------|-----------------------------------|
| Location | 1 | 1257 | 650 | 17 199 | 0.6 | 18 | 12 529 | 1680 | 2.03 | 250 855 421 |
| Replicates in location | 6 | 6.3 | 19.9 | 12.5 | 0.13 | 0.93 | 75.3 | 522.2 | 0.62 | 959 838 |
| Genotypes | 80 | 61 | 55.8 | 23.8 | 0.13 | 0.14 | 75.1 | 218.4 | 5.72 | 281 360 |
| Significance† | — | *** | *** | NS | *** | *** | *** | *** | *** | * |
| G × L | 80 | 8.9 | 24.9 | 21.1 | 0.02 | 0.07 | 36.2 | 43.1 | 0.74 | 201 309 |
| Significance‡ | — | *** | *** | *** | ** | ** | *** | ** | *** | *** |
| Error | 480 | 1.4 | 4.4 | 5.7 | 0.01 | 0.04 | 21.1 | 27.2 | 0.18 | 117 712 |
| CV% | — | 1.3 | 1.6 | 7.8 | 20.0 | 17 | 23.9 | 28.7 | 10.2 | 23.6 |
| Overall mean | — | 93 | 129.6 | 30.9 | 0.59 | 1.2 | 19.2 | 18.2 | 4.1 | 1454 |
| ICARDA | | | | | | | | | | |
| mean | — | 92 | 129 | 36 | 0.62 | 1.3 | 19.8 | 23.6 | 4.1 | 2067 |
| minimum | — | 83 | 120 | 19 | 0.36 | 1.1 | 13.0 | 7.7 | 1.7 | 771 |
| maximum | — | 99 | 137 | 43 | 1.2 | 1.8 | 33.0 | 38.7 | 6.8 | 2658 |
| AREC | | | | | | | | | | |
| mean | — | 95 | 131 | 26 | 0.57 | 0.98 | 16.6 | 14.8 | 4.2 | 832 |
| minimum | — | 91 | 123 | 24 | 0.3 | 0.61 | 8.9 | 6.6 | 1.9 | 423 |
| maximum | — | 99 | 134 | 29 | 1.0 | 1.3 | 23.4 | 30.0 | 6.6 | 1103 |

† Significant level of probability for genotypes; ‡ probability for G × L interaction, *, **, *** and NS = significant at $p = 0.05, 0.01$ and 0.001 and non-significant respectively.

Pods per inflorescence in lentil

Table 2. Phenotypic correlation coefficients and broad-sense heritability values (h^2) among time to flowering, physiological maturity, plant height, components of yield and seed yield of 81 lentil lines over locations in 1993–94 at AREC and ICARDA.

| Character | (2) | (3) | (4) | (5) | (6) | (7) | (8) | (9) | h^2 |
|--|---------|---------|----------|----------|----------|----------|----------|----------|-------|
| Time to flower (1) | 0.56*** | −0.38** | −0.22** | −0.38*** | −0.33*** | 0.07 | 0.18* | −0.41*** | 0.85 |
| Time to maturity (2) | | −0.22** | −0.46*** | −0.50*** | −0.42*** | 0.21** | 0.56*** | −0.36*** | 0.56 |
| Plant height (3) | | | 0.14 | 0.67*** | 0.68*** | 0.28*** | −0.04 | 0.89*** | 0.11 |
| Seeds per pod (4) | | | | −0.60*** | −0.34*** | −0.62*** | −0.52*** | 0.16* | 0.81 |
| Pods per inflorescence (5) | | | | | 0.73*** | −0.23** | −0.31*** | 0.71*** | 0.68 |
| Pods per plant (6) | | | | | | 0.34*** | −0.38*** | 0.72*** | 0.71 |
| Empty pods per plant (7) | | | | | | | 0.17* | 0.25** | 0.75 |
| 100-seed weight (8) | | | | | | | | 0.01 | 0.87 |
| Seed yield (kg ha^{-1}) (9) | | | | | | | | | 0.48 |

*, **, *** = significant at $p = 0.05, 0.01$ and 0.001 respectively.

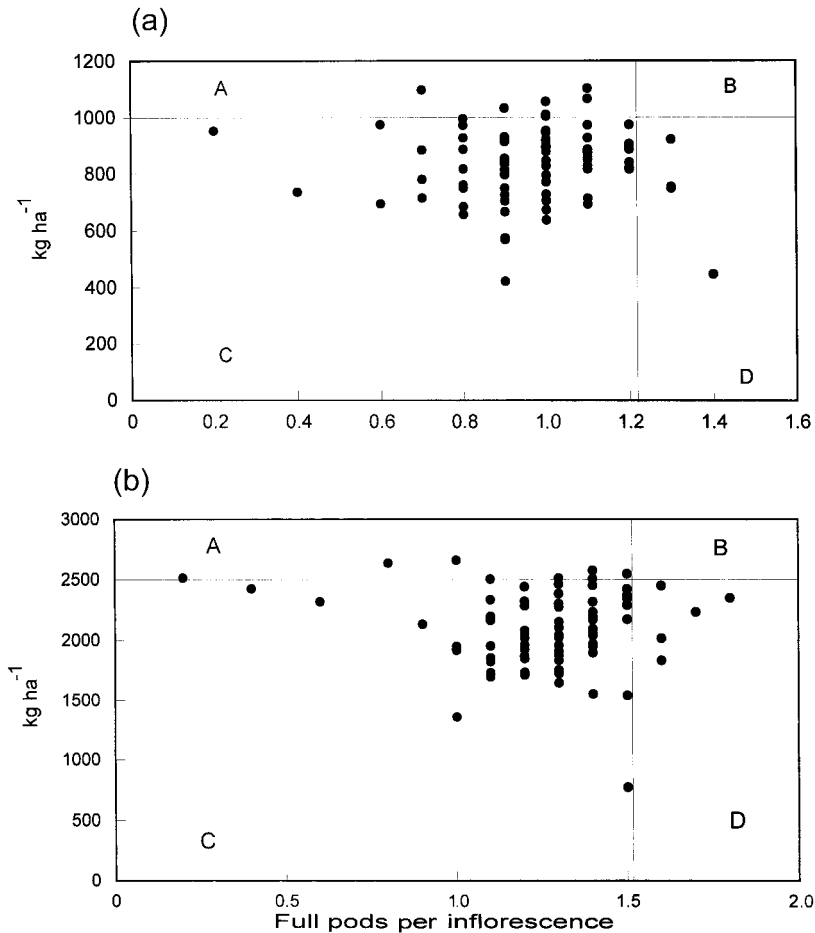


Fig. 4. Scatter plots for number of pods per inflorescence and seed yield for 81 genotypes of lentil grown at (a) AREC and (b) ICARDA in 1993–94. The top 10% for both traits are marked by lines which divide the scatter plots into four quadrats (A–D).

simultaneously, particularly when plants are stressed. These results illustrate the concept of yield-component compensation postulated by Adams (1967).

To answer the question: Will selection for a high number of pods per inflorescence increase seed yield?, the distribution of seed yield and the numbers of pods per inflorescence over genotypes requires examination (Fig. 4). The top 10% for both traits are marked by lines which divide the scatter plots into four quadrats (A–D). Despite the correlation between the traits, genotypes with the highest number of pods per inflorescence were not the highest yielding.

The clear implication for breeding is that selection for the number of pods per inflorescence did not identify those genotypes with the highest yield. Where lentil is grown in a Mediterranean climate, the conditions in Season 2 of low rainfall in April were typical, but accompanying temperatures above 30 °C were unusually high. The question might well be asked: To what extent do the peculiar

temperature conditions in Season 2 affect the relationship between pod number per inflorescence and yield and hence the conclusion of the trials? Selection systems, whether directly for yield or indirect selection via other traits, must be robust to be useful in plant breeding and the utility of environmentally-dependent selection strategies is limited. Consequently, selection for a high number of pods per inflorescence cannot be recommended to increase seed yield in lentil.

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