




Article

Photoperiod Insensitivity in Pigeonpea Introgression Lines Derived from Wild *Cajanus* Species

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Abstract: Pigeonpea is a photoperiod-sensitive crop; therefore, the introgression of photoperiod insensitivity could increase its adaptability to new environments. We determined the effect of extended daylength (ED; 16 h light) on the phenotypical traits of extra-early, early, and mid-early maturing pigeonpea introgression lines (ILs) derived from wild *Cajanus* species belonging to secondary and tertiary gene pools. Plants were grown under natural daylength and extended daylength in a greenhouse. Comparisons of the time of floral bud initiation, days to flowering, plant height, number of branches, and number of leaf nodes on the main stem at flowering revealed photoperiod-insensitive lines. All traits varied widely among the ILs. Analyses of flowering traits revealed large genetic components with low genotype × treatment interactions and high broad-sense heritability. The photoperiod most strongly affected the number of primary branches, followed by plant height. The extended day advanced flowering by approximately four days in extra-early ILs, confirming that these ILs are quantitative, short-day plants. The photoperiod insensitivity index varied from 0.88 in ICPP 171541 (moderately photoperiod sensitive) to 0.99 in ICPP 171546 and ICPP 171561 (photoperiod insensitive). These photoperiod-insensitive extra-early flowering ILs can be used to enrich the genetic diversity of pigeonpea and to develop photoperiod-insensitive cultivars for cultivation in new environments.

Keywords: photoperiod; photoperiod insensitivity index; introgression lines (ILs); facultative; quantitative; wild *Cajanus* species; pigeonpea



Citation: Hussain, M.E.; Sharma, S.; Joel, A.J.; Kilian, B. Photoperiod Insensitivity in Pigeonpea Introgression Lines Derived from Wild *Cajanus* Species. *Agronomy* **2022**, *12*, 1370. <https://doi.org/10.3390/agronomy12061370>

Academic Editors: Yuan-Ming Zhang and Fengjie Sun

Received: 18 March 2022

Accepted: 28 May 2022

Published: 6 June 2022

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1. Introduction

Pigeonpea (*Cajanus cajan* (L.) Millspaugh), a protein-rich food legume crop with multiple benefits, is adapted to tropical and subtropical regions. Because of its multiple uses, viz., food, fodder, and soil improvement through nitrogen fixation, pigeonpea plays an important role in subsistence agriculture. Globally, it is grown across approximately 6.9 million hectares (ha) with an annual production of 5.9 million tonnes and an average yield of 852.4 kg/ha [1]. India, Myanmar, Malawi, Tanzania, Haiti, Kenya, the Dominican Republic, and Nepal are the primary pigeonpea-producing countries. In India, pigeonpea is cultivated mainly as a rain-fed crop across approximately 5.5 million ha, which accounts for approximately 80% of the global pigeonpea cultivation area. Despite substantial breeding efforts for pigeonpea improvement in India, its productivity has remained stagnant at approximately 0.8 t ha⁻¹. The low productivity is because of the lack of improved varieties suited to cultivation in varied agroclimatic conditions. Furthermore, because pigeonpea is cultivated in marginal lands with limited inputs, it is exposed to various biotic and

abiotic stresses. The narrow genetic base of pigeonpea cultivars, which is mainly due to the domestication history [2], makes this crop vulnerable to pests, diseases, and abiotic stresses.

Pigeonpea is inherently a short-day plant [3,4]. Pigeonpea cultivars with a range of maturation times, such as extra-early (<120 days), early (121–150 days), mid-early (151–165 days), medium (166–185 days), and long duration (>185 days), have been bred for different agroecological environments in India [5]. However, the cultivars classified into different maturity groups may show different responses in different locations because of their high sensitivity to photoperiod, temperature, and interactions. About two-thirds of the pigeonpea growing area in India is planted with medium-duration varieties such as Asha and Maruti, which mature around 160–200 days in southern and central India [6]. Although the recent development of medium-duration pigeonpea hybrids has led to increased yields [7], the current hybrids may not be suitable for all areas and/or cropping systems. Because of their long duration, these pigeonpea cultivars and/or hybrids cannot be rotated with other crops within the same year and are extremely sensitive to photoperiod variations affecting plant height, vegetative biomass, phenology, and grain yield [8]. When medium-maturing varieties are grown at higher latitudes, the vegetative phase coincides with a long photoperiod and warm temperatures, which affect photosynthate partitioning [9–12]. Under a long photoperiod, photosynthate partitioning to the grain decreases, and the redirection of photosynthates to organs results in excessive vegetative growth, thereby increasing dry matter production and leaf area [13]. Delayed flowering and maturity expose the plants to terminal drought in areas where the crop depends on residual soil moisture, and this can severely reduce grain yield. Due to these constraints, pigeonpea cultivation is restricted to areas beyond the latitudes of 30° S to 30° N, and its expansion is limited to higher latitudes and its use in alternative cropping systems [12]. There is an urgent need to develop photoperiod-insensitive pigeonpea cultivars that can be grown at a wider range of latitudes and altitudes and in different cropping systems.

Photoperiod insensitivity is associated with early flowering in many crops [14–16]. The development of early duration, photo-insensitive genotypes has played an important role in the adaptation of wheat and rice [17]. In chickpea, the development of early flowering, daylength-insensitive cultivars have led to the expansion of its cultivation in central and southern India. In pigeonpea, one of the major objectives of breeding programs is to develop new photoperiod-insensitive, short-duration cultivars, which can be grown in short cropping systems. This necessitates the use of new sources of variability for these important traits.

Wild *Cajanus* species are largely unexploited sources of genetic variation and can play an important role in enriching beneficial diversity in breeding pools as a source of novel alleles for pigeonpea improvement [18,19]. Wild *Cajanus* species such as *C. acutifolius* are highly resistant to pod borers, whereas *C. platycarpus* has several useful traits, such as extra-early flowering and maturity, photoperiod insensitivity, prolific flowering and pod setting, an annual growth habit, salinity tolerance, rapid seedling growth, and resistance to *Phytophthora* blight, cyst nematode, and *Helicoverpa* pod borer [20–24]. *C. volubilis* has been used for mapping determinacy in pigeonpea [25]. Prebreeding populations have been developed by using wild *Cajanus* species as donors and popular pigeonpea cultivars as recipients, thereby creating enormous variability for use in pigeonpea improvement programs [18,19].

There is no specific and standardized method to evaluate photoperiod sensitivity in pigeonpea. The previous studies in pigeonpea and other crops such as soybean have reported days to flowering as the most important and the basic trait determining photoperiod sensitivity [26,27]. In the present study, advanced generation introgression lines (ILs) derived from *C. platycarpus*, *C. volubilis*, *C. acutifolius*, and *C. cajanifolius* with extra-early, early, and mid-early maturity were used to study the effect of an extended photoperiod on flowering and preflowering phenological traits, and to identify photoperiod-insensitive ILs for use in pigeonpea improvement programs.

2. Materials and Methods

2.1. Plant Materials

The advanced generation ILs with extra-early, early, and mid-early maturity were grouped into two sets, Set I and Set II, on the basis of their growth habit. Set I consisted of 16 extra-early maturing ILs with a determinate (DT) flowering pattern along with two checks, viz., ICPL 11255 and ICPL 85010. These 16 DT ILs were in the F₁₀ generation derived from an interspecific cross between the popular pigeonpea cultivar ICPL 85010 and the *C. volubilis* accession ICP 15774 [28]. ICPL 11255 and ICPL 85010 are super-early and extra-early maturing varieties, respectively, both with a DT flowering pattern. Set II consisted of 15 early and mid-early maturing ILs with an indeterminate (IDT) flowering pattern along with three checks, viz., ICPL 20325, ICPL 88039, and ICPL 87119. Of these 15 IDT ILs, eight ILs in the BC₄F₁₂ generation were selected from the prebreeding population derived from the interspecific cross between the cross-incompatible wild *Cajanus* species *C. platycarpus* ICPW 68 and the pigeonpea cultivar ICPL 85010. This prebreeding population was developed using embryo rescue [28,29]. Three ILs, viz., ICPP 171266, ICPP 171303, and ICPP 171328, in the BC₂F₈ generation, were selected from the prebreeding population derived from the interspecific cross between the pigeonpea cultivar ICPL 87119 and the *C. acutifolius* accession ICPW 12. One IL, ICPP 171188, in the BC₁F₁₄ generation, was selected from the prebreeding population derived from the interspecific cross between the pigeonpea cultivar ICPL 85010 and the *C. acutifolius* accession ICPW 04. The remaining three ILs (ICPP 171406, ICPP 171498, and ICPP 171537), all in the BC₂F₈ generation, were selected from the prebreeding population derived from the interspecific cross between the pigeonpea cultivar ICPL 87119 and the *C. cajanifolius* accession ICPW 29 [18]. ICPL 20325 and ICPL 88039 are super-early and early maturing pigeonpea varieties, respectively, whereas ICPL 87119, also known as Asha, is a medium-duration leading variety in India, and all three varieties have an IDT flowering pattern. These ILs were selected based on their desirable agronomic performance, such as high seed yield and 100-seed weight, in extra-early, early, and mid-early maturity duration groups (Supplementary Table S1).

2.2. Methodology

The study was conducted at the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT), Patancheru, India, in a greenhouse controlled at 25 ± 2 °C in the 2019 and 2020 rainy seasons (planted in July) as per the method used by Upadhyaya et al. [26]. In both years, Set I, comprising 16 DT ILs and two checks, and Set II, comprising 15 IDT ILs and three checks, were evaluated under a 16 h light/8 h dark photoperiod (extended daylength; ED), and under natural daylength (ND, control). Seeds were treated with fungicide (2 g/L carbendazim) and sown in 10-inch diameter pots containing a mixture of black soil, sand, farmyard manure, and vermicompost at a 2:2:2:1 ratio. Three seeds were sown in each pot, and seedlings were thinned to one per pot at 10 days after germination. Three plants per genotype were maintained in each treatment. In total, 108 pots were allocated randomly to each treatment in a completely randomized design with three replications in separate chambers in the greenhouse, with one plant as one replication. For the extended daylength, the natural daylength was extended to 16 h using 60 W incandescent bulbs controlled by an automatic timer control operating from 1800 h to 2200 h with 50 µmolm⁻²s⁻² at plant canopy. The treatment was applied at 1 month after germination when the seedlings were fully established. For the natural daylength, seedlings were maintained under natural daylength (approximately 11 h) in the greenhouse. The light intensity ranged from 300 to 600 µmolm⁻²s⁻² during the daytime in both extended daylength and natural daylength. The photon flux density was measured with an integrating quantum/radiometer/photometer (LI-188B, LI-COR Inc., Lincoln, NE, USA).

2.3. Data Collection and Statistical Analyses

In both years, data were recorded for traits related to photoperiod sensitivity, including the initiation of the first floral bud (end of the juvenile phase, EJP), days to flowering (DF),

plant height at first floral initiation (PH), number of leaf nodes on the main stem at flowering (NN), and number of branches at first visual bud (NPB). These attributes were measured in all replications under extended daylength and natural daylength for extra-early DT ILs in Set I. Because the IDT lines did not flower under extended daylength, data were not recorded for the IDT lines in Set II except for plant height. Plant height in IDT lines under extended daylength were recorded on the day of first floral initiation under natural daylength. Analysis of variance (ANOVA) was conducted using a completely randomized design with three replications and two photoperiod treatments. The replicationwise values were used for statistical analysis. For pooled analysis, ANOVA was conducted using a completely randomized design for various factors, and their interactions were identified using GenStat 15 (VSN International, Hemel Hempstead, United Kingdom). The sum of squares due to treatments and treatment \times genotype interactions were calculated. The significance of differences among genotypes, between extended daylength and natural daylength, and among interaction means was tested using Tukey's test at the 5% level of significance. Broad-sense heritability (H^2), expressed as a percentage, was calculated based on the ratio of genotypic variance to phenotypic variance [30]. The H^2 was categorized as low (0–30%), moderate (30–60%), and high (>60%).

2.4. Measurements of Photoperiod Sensitivity

We calculated the photoperiod insensitivity index (PII) for each line from the days to flowering using the following function [26]:

$$\text{PII} = 1 - [(B - A)/A] \quad (1)$$

where B is the number of days to flowering under extended daylength and A is the number of days to flowering under natural daylength. Based on this value, the accessions were classified as photoperiod insensitive (PII of 0.91 to 1.0), moderately insensitive (PII of 0.71 to 0.90), and sensitive (PII of <0.70).

3. Results

3.1. Analysis of Variance

We conducted ANOVA only for the extra-early DT lines. None of the early and mid-early IDT ILs flowered under extended daylength, indicative of their high photoperiod sensitivity. Because these IDT lines did not flower under extended daylength, they were not included in further analyses.

In extra-early DT lines, yearwise (Supplementary Tables S2 and S3) and pooled analyses (Table 1) revealed significant differences among genotypes and significant treatment \times genotype interactions ($p < 0.001$) for all traits. These analyses indicated that the photoperiod significantly affected the end of the juvenile phase ($p < 0.001$), days to flowering ($p < 0.001$), number of leaf nodes on the main stem at flowering ($p < 0.001$), number of branches at first visual bud ($p < 0.001$), and plant height at first floral initiation ($p < 0.001$). Further partitioning of the sum of squares showed that the photoperiod treatment explained 16% of the variation in the end of the juvenile phase and days to flowering, 14% of the variation in the number of leaf nodes on the main stem at flowering, 44% of the variation in the number of branches at first visual bud, and 32% of the variation in plant height at first floral initiation. Genotype explained 38% of the variation in days to flowering, 40% of the variation in the end of the juvenile phase, 9% of the variation in the number of leaf nodes on the main stem at flowering, 12% of the variation in the number of branches at first visual bud, and 19% of the variation in plant height at first floral initiation. The genotype \times treatment interaction accounted for only 4% of the variation in the end of the juvenile phase and days to flowering, 3% of the variation in the number of leaf nodes on the main stem at flowering, 9% of the variation in the number of branches at first visual bud, and 6% of the variation in plant height at first floral initiation.

Table 1. Pooled analysis of variance for photoperiod-sensitivity-related traits of pigeonpea under normal daylength (ND) and extended daylength (ED) conditions at ICRISAT, Patancheru, India.

Sources of Variation	Df *	EJP	Fpr	DF	Fpr	NN	Fpr	NPB	Fpr	PH	Fpr
Replications	2	2.2		4.7		1.56		0.33		7.42	
Genotypes (G)	17	121.68	<0.001	131.39	<0.001	10.14	<0.001	2.70	<0.001	160.89	<0.001
Treatment (E)	1	828.37	<0.001	933.33	<0.001	268.89	<0.001	170.66	<0.001	4657.45	<0.001
Year (Y)	1	277.89	<0.001	425.04	<0.001	1044.56	<0.001	29.62	<0.001	198.37	<0.001
G × E	17	11.67	<0.001	13.73	<0.001	3.45	0.006	2.62	<0.001	49.18	<0.001
G × Year	17	57.13	<0.001	82.70	<0.001	6.92	<0.001	0.58	0.482	140.82	<0.001
E × Y	1	6.33	0.206	1.04	0.592	27.44	<0.001	0.90	0.218	45.38	0.069
G × E × Y	1	9.9	0.002	3.35	0.541	4.40	<0.001	0.72	0.257	58.11	<0.001
Residual	142	3.92		3.6		1.54		0.59		13.50	
Total	215										

Notes: * Df, degrees of freedom; EJP, end of juvenile phase, i.e., initiation of first floral bud; DF, days to flowering; NN, number of leaf nodes on main stem at flowering; NPB, number of branches at first visual bud; PH, plant height at first floral initiation; Fpr, *F* probability.

3.2. Response of Extra-Early DT ILs to Photoperiod

All extra-early DT ILs flowered under both natural daylength and extended daylength, and the following observations were made for different traits:

3.2.1. End of Juvenile Phase

The average was 57 days (range, 48 to 62 days) under natural daylength, and 61 days (range, 55 to 68 days) under extended daylength (Table 2). The end of the juvenile phase differed significantly among ILs under both extended daylength and natural daylength. In most of the ILs, floral bud initiation was delayed under extended daylength, except for ICPP 171561 that showed the floral bud initiation on the same day (57 days) under both extended daylength and natural daylength. Both ICPP 171542 and ICPP 171564 showed no significant difference in the end of the juvenile phase between extended daylength and natural daylength (Table 2). The maximum delay in the end of the juvenile phase under extended daylength was approximately 6 days, which was recorded for six ILs, ICPP 171581, 171580, 171553, 171539, 171541, and 171559. For the checks ICPL 85010 and ICPL 11255, the first visible bud appeared in 60 days and 48 days, respectively, under natural daylength, and in 63 days and 55 days, respectively, under extended daylength. These results show that even in the super-early check ICPL 11255, the end of the juvenile phase was delayed under extended daylength (~63 days) compared with natural daylength (60 days).

3.2.2. Days to Flowering

In the extra-early flowering lines, the days to flowering was 70 days (range, 60–75 days) under natural daylength and 74 days (range, 66–80 days) under extended daylength (Table 2). In most of the ILs, flowering was significantly delayed under extended daylength, except for ICPP 171546 and ICPP 171561, which showed no significant difference in days to flowering between extended daylength and natural daylength. The days to flowering was delayed by a maximum of 7 days in three ILs: ICPP 171556, 171559, and 171541. In the checks, flowering was delayed by 6 days in ICPL 11255 (60 days under natural daylength and 66 days under extended daylength) but only 2 days in ICPL 85010 (74 days under natural daylength and 76 days under extended daylength).

3.2.3. Node Number

Sensitivity to daylength is also reflected by the number of leaves formed on the main stem before flower induction. For all the ILs, the number of leaf nodes on the main stem at flowering was higher under extended daylength than under natural daylength (Table 2), indicative of sensitivity to daylength even in ILs that did not show differences in days to flowering between extended daylength and natural daylength. The average number of leaf nodes on the main stem at flowering was 15 (range, 14–18) under natural daylength and 18 (range, 16–20) under extended daylength (Table 2). The largest difference

in the number of leaf nodes on the main stem at flowering between extended daylength and natural daylength was in ICPP 171559. Three ILs, ICPP 171579, ICPP 171578, and ICPP 171539, showed no significant difference in the number of leaf nodes on the main stem at flowering between extended daylength and natural daylength (Table 2). In the checks ICPL 85010 and ICPL 11255, the number of leaf nodes on the main stem at flowering was 15 and 14, respectively, under natural daylength, and 18 and 15, respectively, under extended daylength.

Table 2. Pooled mean comparison showing the effect of a photoperiod on photoperiod-sensitive traits in extra-early flowering pigeonpea introgression lines at ICRISAT, Patancheru, India.

ID No.	Genotypes	Treatment	EJP *	DF	NN	NPB	PH
ID 01	ICPL 11255	ED	55 ± 1.03 ^{a#}	66 ± 0.70 ^a	15 ± 1.05 ^a	6 ± 0.23 ^a	67.83 ± 2.63 ^a
		ND	48 ± 1.09 ^b	60 ± 0.85 ^b	14 ± 0.85 ^a	5 ± 0.64 ^a	59 ± 2.68 ^b
ID 02	ICPL 85010	ED	63 ± 1.66 ^a	76 ± 1.03 ^a	18 ± 1.08 ^a	7 ± 0.47 ^a	76.67 ± 3.06 ^a
		ND	60 ± 1.03 ^b	74 ± 0.87 ^b	15 ± 0.85 ^b	6 ± 0.64 ^a	62.5 ± 1.89 ^b
ID 03	ICPP 171539	ED	63 ± 1.65 ^a	75 ± 2.16 ^a	19 ± 1.03 ^a	7 ± 0.85 ^a	78.17 ± 4.14 ^a
		ND	58 ± 1.47 ^b	69 ± 2.27 ^b	18 ± 1.09 ^a	5 ± 0.94 ^b	66.67 ± 1.70 ^b
ID 04	ICPP 171540	ED	59 ± 2.32 ^a	70 ± 2.28 ^a	18 ± 1.05 ^a	8 ± 0.23 ^a	78.17 ± 4.59 ^a
		ND	55 ± 2.49 ^b	67 ± 2.69 ^b	16 ± 0.64 ^b	5 ± 0.87 ^b	71.17 ± 3.34 ^b
ID 05	ICPP 171541	ED	59 ± 1.35 ^a	75 ± 1.09 ^a	16 ± 1.24 ^a	7 ± 0.64 ^a	76.67 ± 2.33 ^a
		ND	54 ± 1.47 ^b	67 ± 1.09 ^b	14 ± 0.47 ^b	6 ± 0.87 ^a	73.5 ± 3.34 ^b
ID 06	ICPP 171542	ED	60 ± 1.93 ^a	73 ± 2.95 ^a	18 ± 0.62 ^a	7 ± 0.64 ^a	75 ± 2.29 ^a
		ND	59 ± 1.66 ^a	71 ± 1.24 ^b	15 ± 1.22 ^b	4 ± 0.47 ^b	72.83 ± 2.25 ^b
ID 07	ICPP 171546	ED	57 ± 1.43 ^a	69 ± 1.43 ^a	18 ± 1.05 ^a	8 ± 0.64 ^a	75.83 ± 3.45 ^a
		ND	55 ± 1.66 ^b	68 ± 1.22 ^a	15 ± 0.94 ^b	5 ± 0.23 ^b	62.67 ± 3.84 ^b
ID 08	ICPP 171553	ED	62 ± 1.09 ^a	75 ± 1.44 ^a	18 ± 1.24 ^a	7 ± 0.64 ^a	69 ± 1.49 ^a
		ND	56 ± 0.70 ^b	70 ± 1.44 ^b	16 ± 0.81 ^b	5 ± 0.23 ^b	63 ± 2.97 ^b
ID 09	ICPP 171556	ED	61 ± 2.49 ^a	75 ± 1.03 ^a	19 ± 1.22 ^a	7 ± 0.47 ^a	80.17 ± 2.67 ^a
		ND	56 ± 1.03 ^b	68 ± 1.32 ^b	15 ± 0.64 ^b	6 ± 0.85 ^a	74 ± 2.2 ^b
ID 10	ICPP 171559	ED	64 ± 0.87 ^a	76 ± 1.44 ^a	20 ± 0.85 ^a	7 ± 0.47 ^a	80 ± 2.86 ^a
		ND	58 ± 1.33 ^b	69 ± 1.93 ^b	15 ± 0.81 ^b	5 ± 0.64 ^b	70.67 ± 4.13 ^b
ID 11	ICPP 171561	ED	57 ± 1.69 ^a	69 ± 1.08 ^a	20 ± 0.81 ^a	7 ± 0.47 ^a	80 ± 2.05 ^a
		ND	57 ± 1.31 ^a	68 ± 1.03 ^a	16 ± 0.47 ^b	6 ± 0.23 ^a	64.33 ± 3.33 ^b
ID 12	ICPP 171564	ED	59 ± 1.66 ^a	72 ± 1.22 ^a	19 ± 0.81 ^a	8 ± 0.47 ^a	75.17 ± 2.27 ^a
		ND	58 ± 1.44 ^a	68 ± 1.44 ^a	15 ± 0.64 ^b	7 ± 0.23 ^a	63 ± 2.57 ^b
ID 13	ICPP 171566	ED	62 ± 2.18 ^a	74 ± 1.63 ^a	18 ± 0.84 ^a	8 ± 0.47 ^a	75.33 ± 3.69 ^a
		ND	57 ± 0.64 ^b	70 ± 1.22 ^b	16 ± 0.81 ^b	6 ± 0.47 ^b	62.33 ± 2.25 ^b
ID 14	ICPP 171568	ED	62 ± 2.49 ^a	75 ± 1.87 ^a	18 ± 0.85 ^a	7 ± 0.47 ^a	73.5 ± 2.90 ^a
		ND	58 ± 0.70 ^b	70 ± 1.11 ^b	16 ± 1.09 ^b	6 ± 0.70 ^a	64.17 ± 2.31 ^b
ID 15	ICPP 171578	ED	64 ± 1.54 ^a	75 ± 1.26 ^a	16 ± 1.09 ^a	7 ± 0.64 ^a	72.5 ± 2.28 ^a
		ND	61 ± 0.64 ^b	72 ± 0.70 ^b	15 ± 0.81 ^a	6 ± 0.47 ^a	61.67 ± 1.17 ^b
ID 16	ICPP 171579	ED	64 ± 1.09 ^a	76 ± 0.81 ^a	18 ± 0.81 ^a	7 ± 0.81 ^a	72.83 ± 2.25 ^a
		ND	61 ± 1.03 ^b	74 ± 1.24 ^b	17 ± 1.41 ^a	6 ± 0.70 ^a	70.5 ± 0.40 ^b
ID 17	ICPP 171580	ED	67 ± 1.09 ^a	79 ± 0.85 ^a	17 ± 1.05 ^a	7 ± 0.64 ^a	73.17 ± 3.72 ^a
		ND	61 ± 0.81 ^b	72 ± 0.87 ^b	15 ± 1.11 ^b	5 ± 0.70 ^b	61.67 ± 1.66 ^b
ID 18	ICPP 171581	ED	68 ± 1.03 ^a	80 ± 1.49 ^a	17 ± 1.09 ^a	7 ± 0.47 ^a	74.5 ± 2.33 ^a
		ND	62 ± 1.99 ^b	75 ± 1.65 ^b	15 ± 0.64 ^b	5 ± 0.64 ^b	63.67 ± 2.66 ^b
	Mean	ED	61 ± 1.59 ^a	74 ± 1.43 ^a	18 ± 0.99 ^a	7 ± 0.54 ^a	75.25 ± 2.83 ^a
		ND	57 ± 1.25 ^b	70 ± 1.34 ^b	15 ± 0.85 ^b	5 ± 0.58 ^b	65.96 ± 2.54 ^b
	SE(d)	ED	1.81	1.62	1.08	0.55	3.10
		ND	1.36	1.46	0.93	0.66	2.89
	LSD ($p \leq 0.05$)	ED	3.62	3.2	2.16	1.10	6.19
		ND	2.72	2.92	1.86	1.31	5.77

Notes: * EJP, end of juvenile phase, i.e., initiation of first floral bud; DF, days to flowering; NN, number of leaf nodes on main stem at flowering; NPB, number of branches at first visual bud; PH, plant height at first floral initiation; ND, normal daylength; ED, extended daylength; Fpr, F probability. # Values followed by different letters within a column for each treatment are significantly different (Tukey's test, $p < 0.05$).

3.2.4. Number of Primary Branches

The photoperiod affected the number of branches at first visual bud in ILs, with an average of 5 (range, 4–7) under natural daylength and 7 (range, 6–8) under extended daylength. All the ILs had a higher number of branches at first visual bud under extended daylength than under natural daylength. The largest differences in the number of branches at first visual bud between extended daylength and natural daylength were in ICPP 171540, ICPP 171546, and ICPP 171542. The number of branches at first visual bud did not differ significantly between extended daylength and natural daylength in both the checks, ICPL 11255 and ICPL 85010, and in seven ILs, ICPP 171541, 171556, 171561, 171564, 171568, 171578, and 171579 (Table 2).

3.2.5. Plant Height

The average plant height at first floral initiation was 66 cm (range, 59–74 cm) under natural daylength and 75 cm (range, 68–80 cm) under extended daylength (Table 2). All the lines showed a significant increase in plant height at first floral initiation under extended daylength compared with natural daylength. The photoperiod strongly affected plant height at first floral initiation in ICPL 171561, with the plant height at first floral initiation in extended daylength being more than 24% higher than that in natural daylength. The smallest differences in plant height at first floral initiation between extended daylength and natural daylength were in ICPP 171542 and ICPP 171579. The plant height at first floral initiation of the checks ICPL 11255 and ICPL 85010 was 15% and 23% higher, respectively, under extended daylength than under natural daylength (Table 2).

3.2.6. Heritability

The H^2 was high for the end of the juvenile phase and days to flowering under extended daylength (70.2% and 61.2%, respectively) and moderate under natural daylength (51.5% and 52.8%, respectively), and was moderate for the number of leaf nodes on the main stem at flowering under both natural daylength and extended daylength (36.3% under natural daylength and 43.3% under extended daylength). The H^2 of plant height at first floral initiation was moderate under natural daylength (33.5%) but low (25%) under extended daylength.

3.2.7. Trait Associations

We conducted correlation analyses to detect relationships between traits in the extra-early ILs under natural daylength and extended daylength. The strongest positive correlations were between the end of the juvenile phase and days to flowering under natural daylength ($r = 0.95^{**}$) and extended daylength ($r = 0.95^{**}$) treatments. There were no significant correlations between flowering-related traits and other vegetative traits under both treatments. Among the vegetative traits, the number of leaf nodes on the main stem at flowering and plant height at first floral initiation ($r = 0.76^{**}$) showed a significantly positive correlation under extended daylength (Supplementary Figure S1).

3.2.8. Photoperiod Insensitivity Index

The PII, which was calculated from the pooled values for mean days to flowering, ranged from 0.88 to 0.99 (Table 3). All the extra-early determinate ILs had PII values greater than 0.9, except for ICPP 171541 (PII 0.88).

As shown in Table 3, two ILs, ICPP 171546 and ICPP 171561, had PII values higher than that of the check ICPL 85010 (0.97). Twelve ILs (ICPP 171539, ICPP 171540, ICPP 171542, ICPP 171546, ICPP 171553, ICPP 171561, ICPP 171564, ICPP 171566, ICPP 171568, ICPP 171578, ICPP 171579, and ICPP 171581) had PII values higher than that of the super-early check, ICPL 11255 (0.90).

Table 3. Days to flowering under different photoperiods and photoperiod insensitivity indexes of extra-early maturing pigeonpea introgression lines at ICRISAT, Patancheru, India.

Genotypes	ED *	ND	PII	Score	Flowering Pattern
ICPL 11255	66	60	0.90	Insensitive	Determinate
ICPL 85010	76	74	0.97	Insensitive	Determinate
ICPP 171539	75	69	0.91	Insensitive	Determinate
ICPP 171540	70	67	0.96	Insensitive	Determinate
ICPP 171541	75	67	0.88	Moderately sensitive	Determinate
ICPP 171542	73	71	0.97	Insensitive	Determinate
ICPP 171546	69	68	0.99	Insensitive	Determinate
ICPP 171553	75	70	0.93	Insensitive	Determinate
ICPP 171556	75	68	0.90	Insensitive	Determinate
ICPP 171559	76	69	0.90	Insensitive	Determinate
ICPP 171561	69	68	0.99	Insensitive	Determinate
ICPP 171564	72	68	0.94	Insensitive	Determinate
ICPP 171566	74	70	0.94	Insensitive	Determinate
ICPP 171568	75	70	0.93	Insensitive	Determinate
ICPP 171578	75	72	0.96	Insensitive	Determinate
ICPP 171579	76	74	0.97	Insensitive	Determinate
ICPP 171580	79	72	0.90	Insensitive	Determinate
ICPP 171581	80	75	0.93	Insensitive	Determinate

Notes: * ED, extended daylength; ND, natural daylength; PII, photoperiod insensitivity index.

3.3. Responses of Early and Mid-Early IDT ILs to Photoperiod

3.3.1. Days to Flowering

Under natural daylength, the average days to flowering in IDT ILs was 101 days (range, 86–127 days) and in the checks it was 96 days (76–128 days). Only one check, ICPL 20325, flowered under extended daylength (days to flowering, 77 days). None of the ILs flowered under extended daylength, indicative of their high photoperiod sensitivity (Table 4).

Table 4. Days to flowering and plant height under different photoperiod treatments and photoperiod insensitivity indexes of the early and mid-early maturing pigeonpea introgression lines at ICRISAT, Patancheru, India.

Genotypes	Days to Flowering		Plant Height		Photoperiod Insensitivity		Flowering Pattern
	ND *	ED	ND	ED	PII	Score	
ICPL 20325	76	77	96.70	128.33	0.98	Insensitive	Indeterminate
ICPL 88039	83	No flowering	108.30	116.66	0.00	Sensitive	Indeterminate
ICPL 87119	128	No flowering	156.70	173.33	0.00	Sensitive	Indeterminate
ICPP 171031	113	No flowering	103.33	123.33	0.00	Sensitive	Indeterminate
ICPP 171040	92	No flowering	106.67	145.00	0.00	Sensitive	Indeterminate
ICPP 171073	102	No flowering	96.67	115.00	0.00	Sensitive	Indeterminate
ICPP 171111	90	No flowering	131.67	155.00	0.00	Sensitive	Indeterminate
ICPP 171112	87	No flowering	108.33	143.33	0.00	Sensitive	Indeterminate
ICPP 171113	96	No flowering	115.00	163.33	0.00	Sensitive	Indeterminate
ICPP 171117	91	No flowering	123.33	125.00	0.00	Sensitive	Indeterminate
ICPP 171137	86	No flowering	140.00	165.00	0.00	Sensitive	Indeterminate
ICPP 171188	89	No flowering	160.00	163.33	0.00	Sensitive	Indeterminate
ICPP 171328	87	No flowering	138.33	145.00	0.00	Sensitive	Indeterminate
ICPP 171266	121	No flowering	115.00	168.33	0.00	Sensitive	Indeterminate
ICPP 171303	127	No flowering	151.67	165.00	0.00	Sensitive	Indeterminate
ICPP 171537	120	No flowering	149.00	148.33	0.00	Sensitive	Indeterminate
ICPP 171498	118	No flowering	126.67	145.00	0.00	Sensitive	Indeterminate
ICPP 171406	97	No flowering	111.67	150.00	0.00	Sensitive	Indeterminate

* ND, Natural daylength; ED, Extended daylength; PII, Photoperiod insensitivity index.

3.3.2. Plant Height

Plant height in IDT ILs under extended daylength was measured to study the growth rate compared to the normal daylength. As mentioned earlier, the plant height in IDT ILs under extended daylength was measured on the day when the first floral initiation occurred in the normal daylength. The average plant height at first floral initiation in the IDT ILs was 125.2 cm (range, 96.7–125.2 cm) under natural daylength and 148 cm (range, 115–168.1 cm) under extended daylength. The plant height in the IDT ILs was approximately 18% higher under extended daylength than under natural daylength. The largest increase in plant height under extended daylength was in ICPP 171266 (46.4% higher under extended daylength than under natural daylength); and the smallest increases in plant height under extended daylength were in ICPP 171117 and ICPP 171188 (1.4% and 2% higher, respectively, under extended daylength than under natural daylength). Surprisingly, the plant height of one IL, ICPP 171537, was lower under extended daylength than under natural daylength. The average plant height at the first floral initiation of the checks was 120.6 cm (range, 96.7–156.7 cm) under natural daylength and 139.4 cm (range, 116.7–173.3 cm) under extended daylength. The plant height of ICPL 88039 was increased by 7.7% and that of ICPL 20325 was increased by 33% under extended daylength compared with natural daylength (Table 4).

4. Discussion

4.1. Photoperiod-Sensitivity-Related Traits Are Extensively Diverse and Heritable but Also Adaptable to Specific Environments

Photoperiod sensitivity in pigeonpea is one of the factors restricting its adaptation to wider agroecologies worldwide. The development of photoperiod-insensitive pigeonpea genotypes will play a crucial role in extending its cropping area and allow it to be cultivated in double or multiple cropping systems. Wild *Cajanus* species harbor many valuable genes and provide enormous genetic variation for use in pigeonpea improvement programs. In this study, extra-early, early, and mid-early maturing ILs derived from *C. platycarpus*, *C. volubilis*, *C. acutifolius*, and *C. cajanifolius* were evaluated under natural daylength and extended daylength to understand the effects of photoperiod on phenological traits. In previous studies, flowering and plant height at the first floral initiation were used as indicators of the photoperiod response because these traits are most strongly affected by the photoperiod [31–35]. To further elucidate the genetic characteristics of photoperiod sensitivity, we investigated five photoperiod-sensitivity-related traits in pigeonpea. All of the traits showed wide variability in the extra-early DT ILs under natural daylength and extended daylength conditions, indicative of a wide variation in photoperiod sensitivity among these ILs. Further, the genotypes showed differences in their responses to the photoperiod, as indicated by significant genotype \times treatment interactions. The results showed that some ILs were more sensitive than others to photoperiod. It seems likely that the phenotypic variation associated with the genotype \times treatment interactions may be controlled by genotypic plasticity, wherein certain genes are expressed under specific conditions. Nonetheless, for all traits, the proportion of variation attributed to the genotype \times treatment interaction component was much smaller than the proportions of variation attributed to the genotype and treatment components. Similar results highlighting small genotype \times treatment interactions have been reported for flowering-related traits in faba bean [36] and lentil [37]. Sasaki and coworkers also reported significant genotype \times treatment interactions for flowering time in *Arabidopsis* [38]. Therefore, the genotype \times treatment interaction effects for these traits do not strongly affect the ranking of ILs across treatments or selection decisions.

Heritability information reveals how much of the phenotypic variation in a population is attributable to individual genetic differences. In this study, the H^2 for flowering-related traits (end of the juvenile phase and days to flowering) was high under extended daylength but moderate under natural daylength. This differential response suggests that the ILs used in this study have different sets of alleles, and that different loci are expressed under

different treatments. Higher H^2 (70–90%) under abiotic stress conditions has also been reported for other crops [39,40]. In contrast, the number of leaf nodes on the main stem at flowering and plant height at the first floral initiation showed low H^2 under both extended daylength and natural daylength, indicating that selection for these traits will not be effective. This may be due to the higher influence of the environment for the expression of phenotypic variation. Lower H^2 was also observed for similar traits in common bean [41].

We detected a significant positive correlation between two flowering traits, the end of the juvenile phase, and days to flowering, under both extended daylength and natural daylength, and between the number of leaf nodes on the main stem at flowering and plant height at the first floral initiation only under extended daylength. No correlations were detected between the vegetative traits such as number of leaf nodes on the main stem at flowering, the number of branches at first visual bud, and plant height at the first floral initiation and the flowering traits such as end of the juvenile phase and days to flowering under extended daylength and natural daylength. These results indicate that the flowering time, which is dictated mainly by the timing of the transition from vegetative to reproductive growth, is determined by photoperiod. The transition to flowering involves the existence of a florigen—a mobile signal that travels from the leaf to the Shoot Apical Meristem (SAM) through the phloem [42,43]. In our study, the extra-early DT ILs showed a slight delay in flowering under extended daylength; however, the slightly longer time from sowing to flowering in these ILs will not cause problems for practical farming. The enhanced flowering is due to the quantitative response of each genotype to the photoperiod. Previous studies showed that the flowering time of pigeonpea is delayed under a long photoperiod [9,44]. The photoperiod had a stronger effect on the early and mid-early maturing IDT ILs, as they did not flower under extended daylength. Although these ILs failed to flower under extended daylength, they continued to grow vegetatively. Pigeonpea is a short-day plant, and the length of the vegetative growth period depends on the shift from long-day to short-day conditions. The vegetative growth period is characterized by biomass production, whereas resources are redirected to flower development during the reproductive growth period [13]. In this study, plant height was increased to a greater extent in IDT ILs than in DT lines under extended daylength. For the determinate ILs, SAM switches from vegetative growth to reproductive growth soon after photoperiod induced floral transition and stem growth stops [45]. In contrast, the transition of SAM to floral meristem is suppressed in indeterminate ILs while vegetative growth of SAM continues [46]. Similar findings were reported previously for pigeonpea [9,47] and common bean [48]. Indeed, both flowering (photoperiod-insensitive) and nonflowering (photoperiod-sensitive) ILs were observed under the extended daylength treatment in the present study.

4.2. Implications of the Flowering Trait Diversity in the Development of New Pigeonpea Cultivars with Photoperiod Insensitivity

The PII in extra-early DT ILs ranged from 0.88 to 0.99. Based on pooled mean values, 13 promising photoperiod-insensitive ILs ($PII > 0.9$) were identified: ICPP 171540, ICPP 171542, ICPP 171546, ICPP 171553, ICPP 171556, ICPP 171561, ICPP 171564, ICPP 171566, ICPP 171568, ICPP 171578, ICPP 171579, ICPP 171580, and ICPP 171581. Of these, two, ILs ICPP 171542 and ICPP 171579, had PII values (0.97) equal to that of the check ICPL 85010 (0.97). However, ICPP 171542 flowered earlier than ICPL 85010 under both ND and extended daylength. Remarkably, we identified two ILs, ICPP 171546 and ICPP 171561, with PII values of 0.99, indicative of very high photoperiod insensitivity (Figure 1). Further, these ILs flowered earlier than the check ICPL 85010. Flowering is a highly complex polygenic trait. Indeed, approximately 300 genes are estimated to be involved in flowering in *Arabidopsis* [49,50]. A robust genetic mechanism might work to control the performance of the flowering trait so that it is less sensitive to treatment differences. Although both ICPP 171546 and ICPP 171561 were photoperiod insensitive, their plant height at the first floral initiation was increased under extended daylength, indicating that they showed rapid stem growth without a prolonged vegetative phase. This suggests that some genes may control

the activity of stem elongation in a manner that is independent of flowering time. These lines can be used for developing mapping populations to identify QTLs associated with photoperiod insensitivity in pigeonpea.

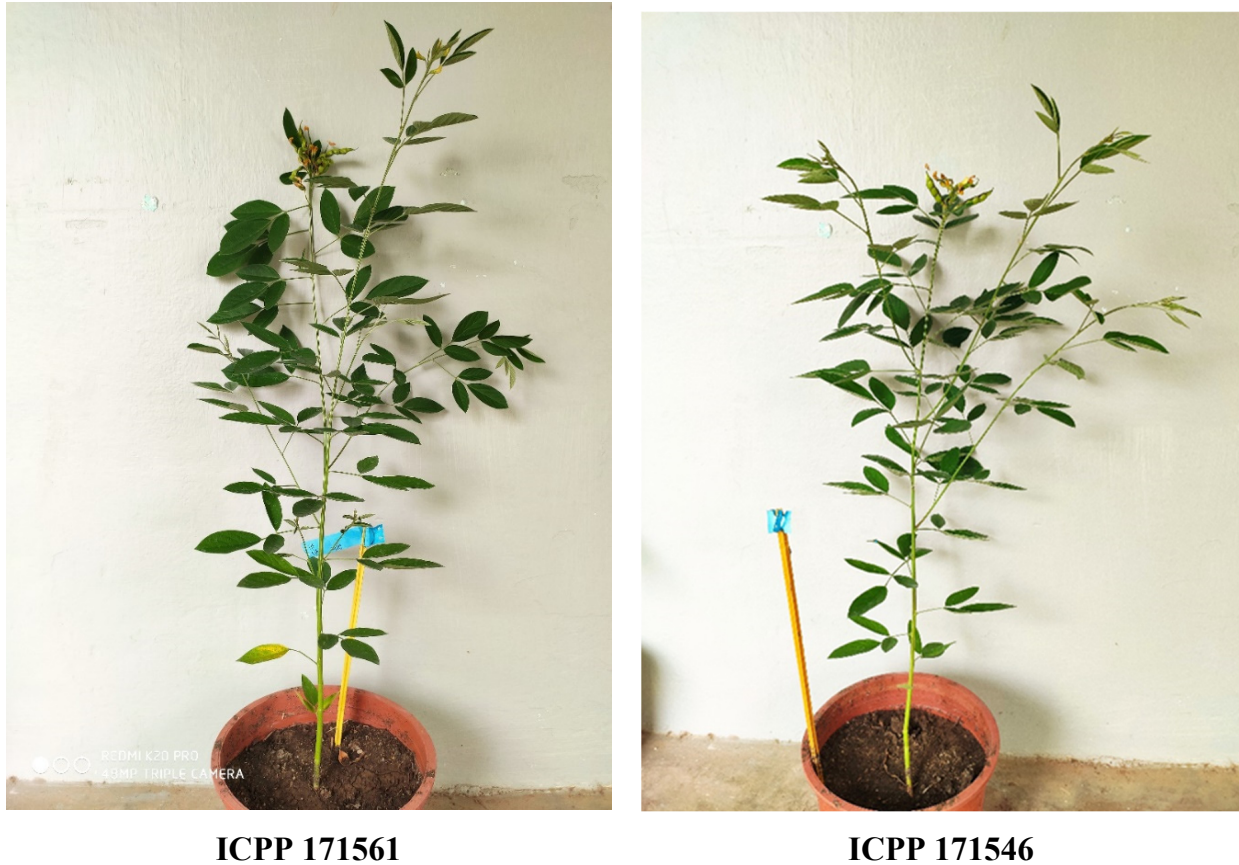


Figure 1. Photoperiod insensitive ILs.

Compared with long-duration pigeonpea cultivars, short-duration cultivars take less time to flower and mature and have a slightly higher harvest index [51]. They are also less sensitive to photoperiod than are long- and medium-duration cultivars [52,53]. Therefore, short-duration cultivars have the potential to increase cropping options and enhance the productivity of pigeonpea. These extra-early maturing, photoperiod-insensitive DT ILs are candidates for cultivation in rice fallows, where they can use residual moisture. There are vast rice fallows (about 10 million ha) in districts of eastern India, such as Jharkhand, Bihar, Chhattisgarh, Odisha, and West Bengal, which offer opportunities to expand the pigeonpea cultivation area. Similarly, it could be grown at a higher population density as a monocrop and fit into rotations with wheat in the Indo-Gangetic plain [54]. Farmers need early maturing, photoperiod-insensitive pigeonpea cultivars to fit into wheat cropping systems. The photoperiod-insensitive extra-early ILs identified in the present study could reasonably fit into a pigeonpea–wheat cropping system.

The development of short-duration photoperiod-insensitive lines is urgently needed to improve the genetic gains of pigeonpea. Breeders can use these promising photoperiod-insensitive prebreeding ILs to develop varieties directly in particular niches after multilocation evaluations at a variety of latitudes and longitudes. These ILs can also be used as parents in pigeonpea breeding programs as sources of earliness and photoperiod insensitivity. Other advantages of using these ILs in genetic studies include their rapid generation turnover, allowing for faster introgression of the traits of interest. Photoperiod insensitivity traits were well distributed across these ILs, indicating that they can be combined with other traits to maximize pigeonpea yield. The use of these ILs in breeding programs will

facilitate the development of new high-yielding, photoperiod-insensitive cultivars that can be grown in new niche areas.

5. Conclusions

The result of the study recommends positive prospects for the development of new cultivars with photoperiod insensitivity. In particular, ILs reveal a large genetic variation for photoperiod sensitivity in the ILs' population evaluated under natural daylength and extended daylength. This study showed that extra-early DT ILs are facultative, short-day plants, and flowering will occur in natural daylength and extended daylength, but floral initiation was slightly delayed. The flowering time traits in extra-early DT ILs showed large heritable variation under extended daylength that can be used in breeding programs. In addition, all traits showed statistically significant genotype, treatments, and genotypes \times treatment component, in different percentages depending upon the traits. These results suggest that the phenotypic variation for photoperiod-sensitivity-related traits has a fraction of the heritable variation sensitive to the treatment controlled by genetic mechanisms. Furthermore, the relationships between traits show that breeding for one trait may result in possible trade-offs in another. The correlation results in extra-early determinate ILs showed that the end of the juvenile phase and days to flowering are associated under the extended daylength and natural daylength and can be taken as selection criteria for developing photoperiod-insensitive genotypes. The correlation coefficients between the number of leaf nodes on the main stem at flowering, number of branches at first visual bud, and plant height at first floral initiation traits with the flowering time-related traits were much smaller. This result indicates that flowering time was dictated mainly by the timing transition from vegetative to reproductive development, determined by photoperiod. Two ILs, namely, ICPP 171546 and ICPP 171561, showed PII 0.99, revealing a high photoperiod-insensitivity level. The robust genetic mechanism might control the expression of these traits so that they are less sensitive to treatment differences. These ILs showed rapid stem growth without prolonging the vegetative phase. This further illustrates that some genes may control the activity of stem elongation independent of flowering time. Finally, the large genetic variation found in the ILs can be exploited for future photoperiod-insensitivity breeding programs in pigeonpea. The identified photoperiod-insensitive lines can be used in a breeding program or can be released directly as a variety.

Supplementary Materials: The following supporting information can be downloaded at: <https://www.mdpi.com/article/10.3390/agronomy12061370/s1>, Figure S1: Correlation between traits under normal daylength and extended daylength; Table S1: List of determinate and indeterminate ILs used in the study; Table S2: Analysis of variance for photoperiod sensitivity-related traits in pigeonpea under normal day length (ND) and extended day length (ED) conditions during 2019 rainy season at ICRISAT, Patancheru, India; Table S3: Analysis of variance for photoperiod sensitivity-related traits in pigeonpea under normal day length (ND) and extended day length (ED) conditions during 2020 rainy season at ICRISAT, Patancheru, India.

Author Contributions: S.S. planned the study and provided prebreeding material; M.E.H. conducted the experiments, recorded and analyzed the data, and prepared the first draft; S.S., B.K. and A.J.J. provided inputs and finalized the draft; All authors have read and agreed to the published version of the manuscript.

Funding: This work was undertaken as part of the initiative "Adapting Agriculture to Climate Change: Collecting, Protecting and Preparing Crop Wild Relatives" which is supported by the Government of Norway (QZA-14/0005) and managed by the Global Crop Diversity Trust (GS18010) (<http://www.cwrdiversity.org/> (accessed on 17 March 2022)). This research was also supported by the CGIAR Research Program on Grain Legumes and Dryland Cereals (GLDC).

Institutional Review Board Statement: Not applicable.

Informed Consent Statement: Not applicable.

Data Availability Statement: All datasets generated for this study are included in the article.

Acknowledgments: We thank Jennifer Smith for editing the English text of a draft of this manuscript.

Conflicts of Interest: The authors declare no conflict of interest.

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