

Article

Sex Expression and Seed Yield Stability in Thai Hemp (*Cannabis sativa* L.): Seasonal Effects on Dioecious Cultivars for Optimized Seed Production

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Abstract: This study investigates the environmental regulation of sex expression and seed yield stability in four Thai dioecious hemp (*Cannabis sativa* L.) cultivars (RPF1, RPF2, RPF3, and RPF4) under different seasonal conditions to optimize seed production. The experiment was conducted across two planting periods (in-season and off-season) to evaluate the effects of varying day lengths and temperatures on growth, reproductive development, and yield. The results showed that shorter day lengths and lower temperatures during the off-season led to an increased proportion of female plants across all cultivars, except RPF3, which exhibited a stable female-to-male ratio. RPF4 had the highest increase in female plants (16%), followed by RPF1 and RPF2 (10%). Seed yield was significantly influenced by seasonal changes, with RPF3 and RPF4 consistently outperforming the other cultivars. In the in-season, RPF3 and RPF4 produced the highest seed yields, reaching 83.4 g/plant and 81.6 g/plant, respectively. During the off-season, both cultivars experienced a decline in seed yield (by 24–26%), primarily due to a reduction in seed production in secondary inflorescences. However, RPF3 compensated for this loss with a 31% increase in seed production at main inflorescences, ensuring yield stability. RPF4 maintained its high yield potential by increasing the proportion of female plants, offsetting the decline in seed yield per plant. Additionally, cumulative growing degree days (CGDD) at harvest were comparable between seasons, with values of 2434 °Cd (in-season) and 2502 °Cd (off-season), indicating that temperature accumulation remained within an optimal range for seed maturation. The study highlights the importance of cultivar selection based on yield component stability and adaptability to seasonal variations. These findings provide valuable insights for improving hemp seed production strategies in Thailand's diverse agro-climatic conditions.

Keywords: hemp (*Cannabis sativa*); hemp seed yield; sex expression; off-season; yield components



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1. Introduction

Hemp (*Cannabis sativa* L. subsp. *sativa*) is a versatile plant with multiple applications. The fibers from its stalks are utilized in textile, paper, and biofuel production, while its inflorescences containing Tetrahydrocannabinol (THC), Cannabidiol (CBD), and terpenes are valuable in pharmaceuticals and cosmetics. Hemp seeds are recognized for their value

and are considered a superfood due to their health benefits. These seeds are packed with edestin, a globular storage protein that comprises about 65% of the total protein content, making hemp seeds a complete protein source [1,2]. This complete protein source is especially highly beneficial for vegetarians as it is easily digestible.

Additionally, hemp seeds have an oil content ranging from 16% to 38%, depending on the cultivar and growing conditions [3–5]. Hemp seed oil is rich in polyunsaturated fatty acids that are beneficial for health, particularly linoleic acid (55–64%) and alpha-linolenic acid (8–23%) [4–7]. The ratio of linoleic acid to alpha-linolenic acid in hemp seed oil is well-balanced and suitable for human health [8–10]. Several studies have explored the benefits of hemp seed oil. These include liver disease prevention [11,12], reduced brain inflammation, lowered cholesterol, and improved heart health [5,13,14]. In addition, hemp seeds contain several essential minerals, including potassium, magnesium, calcium, zinc, manganese, and iron [15–17], which play critical roles in various functions, including the immune system, and may contribute to reducing inflammation in the body. The high fiber content in hemp seeds also promotes better digestion and enhances the efficiency of the digestive system [18]. These diverse nutritional benefits have led to the increasing popularity of hemp seeds as an ingredient in health foods and dietary supplements.

In Thailand, hemp cultivation was legally authorized in 2022, presenting an opportunity to expand cultivation areas and diversify its applications. Traditionally, hemp has been grown primarily for fiber production, but there is increasing interest in cultivating hemp for seed production. This shift is driven by the growing demand for hemp seeds as a valuable raw material across various industries, leading to high returns, second only to producing essential compounds extracted from the inflorescences [19,20]. To achieve high-quality and high-yield hemp production that meets its intended purposes, it is necessary to consider the appropriate selection of cultivars, environmental conditions, and management practices. Hemp cultivars proposed for fiber production should be high in stem length, stem diameter, bast fiber content in the stem, and primary fiber yield. A strong potential for stem elongation during the vegetative growth phase promotes the development of long primary fibers that run vertically along the stem from the base to the tip. These primary fibers originate in the primary phloem, which separates from the procambium and accumulates cellulose, leading to thickened cell walls. This type of fiber is of high quality for textile fiber production [21–23]. In seed production cultivation, it is necessary to select cultivars with a high number of branches, as this increases the number of sites available for seed development on the branches [24]. Additionally, the flowering period and pollination timing should be synchronized to enhance the chances of fertilization [25,26]. Moreover, choosing cultivars with large seed size and high oil content is crucial [27].

Photoperiod sensitivity is a critical genetic trait influencing the optimal planting time for each hemp cultivar in seed production. The photoperiodic response allows the classification of hemp cultivars into the following groups: (1) Photoperiod-sensitive cultivars are highly responsive to changes in day length, typically flowering when daylight falls below a critical threshold (less than 14 h) [28–31]. (2) Photoperiod-insensitive or auto-flowering cultivars are suitable for cultivating regions with short growing seasons or multiple harvests within one season. Auto-flowering cultivars exhibit a shortened life cycle due to their ability to flower independently of photoperiod cues, contrasting with photosensitive cultivars. This trait is governed by a recessive gene disrupting phase transition and photoperiodic flowering pathways, allowing cultivation without labor-intensive light management, thus enhancing commercial viability [31]. (3) Hybrid cultivars result from crosses between photoperiod-sensitive and photoperiod-insensitive cultivars. Parental traits genetically influence photoperiodic responses in hybrid cultivars [32]. (4) Landrace cultivars: The

photoperiodic responses of these cultivars vary significantly depending on their origin and adaptive capacity [33,34].

The expression of male and female sex in hemp is critical for seed production, influencing pollination and fertilization [35]. Hemp cultivars are categorized into two groups based on sexual characteristics: monoecious cultivars, with male and female flowers on the same plant, and dioecious cultivars, with separate male and female plants. Monoecious cultivars like Fedora, Felina, Ferimon, Futura, Uso-31, Zenit, and Monoica [25,36,37] and dioecious cultivars like Kompolti, Chamaeleon, CS, Fibranova, and Tiborszallasi [26,38,39] are preferred for seed production in temperate zones. The temperate zone's photoperiod and temperature differ significantly from Thailand's tropical zone, impacting planting seasons and cultivar selection. Thailand's hemp cultivation currently involves dioecious landraces from the highland regions of Chiang Mai and Vietnam [40–42]. The cultivars RPF 1, RPF 2, RPF 3, and RPF 4, selected in 2008 and officially recognized in 2011, are adapted to high altitudes, have low THC content, and produce high fiber yields, making them ideal for fiber production. These cultivars can be cultivated year-round for fiber with proper water management but are limited to one seed production cycle annually due to their short-day flowering response. Typically planted in August, these cultivars flower when day lengths shorten in October [43–46]. However, the period from October to February in Thailand, when day lengths are shorter than 12 h, presents an opportunity to increase the number of seed production cycles and expand cultivation to post-rice fields.

Increasing the cultivation cycles of hemp for seed production during the off-season, even with favorable day lengths for flowering, presents environmental challenges such as temperature, humidity, and light intensity, which can impact growth and development. Hemp's response in the off-season may differ from regular seasons, particularly in sex expression. While sex expression is primarily genetically determined, environmental factors can alter it, affecting the male-to-female plant ratio. Environmental stress has been shown to shift sex ratios, potentially decreasing seed yield, as female plants are essential for seed production. A higher proportion of female plants leads to greater seed yields. Cultivating RPF1, RPF2, RPF3, and RPF4 hemp cultivars, dioecious and photoperiod-sensitive short-day plants, during the off-season requires careful evaluation of growth potential and seed yield components. This study assesses these factors in the four Thai hemp cultivars across different planting periods. The results will be crucial for managing and selecting hemp cultivars to enhance the efficiency of hemp seed production throughout various growing seasons in Thailand.

2. Materials and Methods

2.1. Plant Material and Experimental Design

Thai dioecious hemp cultivars known as RPF1, RPF2, RPF3, and RPF4 were studied. These are photoperiod-sensitive, short-day cultivars certified for fiber production. The foundation seeds for the 2020/2021 growing season were provided by the public organization Highland Research and Development Institute (HRDI). The experimental design followed a Randomized Complete Block Design (RCBD), with each cultivar replicated in four blocks. Each block contained 10 plants of each cultivar, resulting in a total of 40 plants per cultivar across the experiment. Plants were arranged with a spacing of 1 × 1 m between plants and rows (Figure 1A). For each trial, seeds were sown in germination pots and, after 14 days, transplanted into 10-gallon grow bags containing a medium composed of 50% loam soil, 20% coconut husk, 10% bat guano mixed fertilizer, 10% chicken manure, 5% perlite, and 5% vermiculite. The soil mixture was sandy loam with the following average characteristics: 67.7% clay, 23.6% silt, 8.8% sand; pH 6.0; organic matter 6%; available P of 805.8 ppm (Bray II method); and extractable K of 1717.2 ppm (Atomic Absorption

Spectrometry). During the grain filling stage, individual plants were supported using bamboo poles, and each branch was secured with ropes to prevent breakage due to wind or heavy seed load.

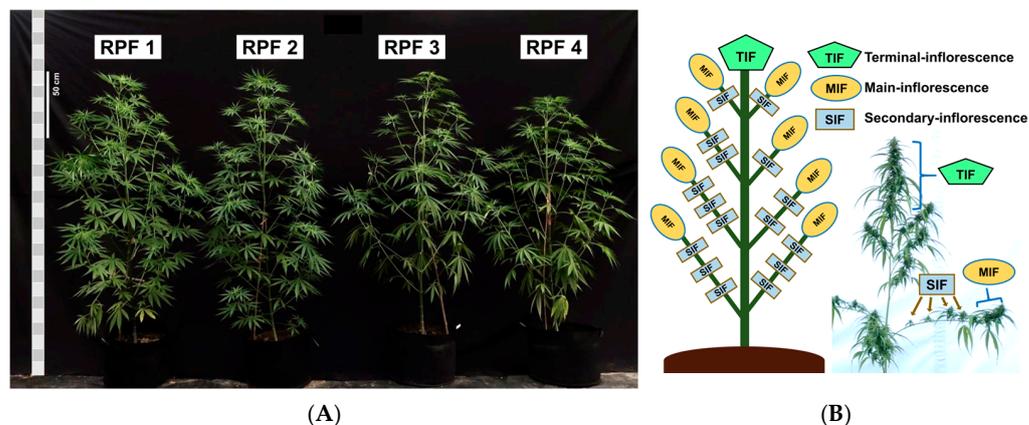


Figure 1. Morphology of four Thai dioecious hemp cultivars (A). Determination of inflorescence position (TIF = terminal inflorescence, MIF = main inflorescence, and SIF = secondary inflorescence) for collecting data on inflorescences and seeds (B).

2.2. Growth Conditions

The pot experiment was conducted outdoors at the Faculty of Agricultural Production, Maejo University (18°53'37.6" N 99°00'56.1" E; 320 MASL). Two planting periods were examined: in-season (September 2021 to January 2022) and off-season (December 2021 to April 2022). Weather conditions during each planting period were recorded, including maximum and minimum temperatures (measured 1.5 m above ground) and rainfall, using an outdoor weather station (Delta-T Devices, model WS-GP1) installed approximately 300 m from the experimental plots at the same altitude (320 MASL). Day-length data were obtained from the Thai Astronomical Society, <https://thaiastro.nectec.or.th/> (accessed on 1 September 2021). The cumulative growing degree days (CGDD) above a base temperature of 10 °C (T_b) [25] was determined using the following equation:

$$\text{CGDD} = \sum [(T_{\text{max}} + T_{\text{min}})/2 - T_b]$$

In this equation, T_{max} and T_{min} are represented as the daily maximum and minimum temperatures in degrees Celsius, respectively. CGDD represents accumulated thermal units that quantify plant developmental progress through various phenological stages rather than simply vegetative growth. This terminology is consistently used in hemp research literature [25,38] for analyzing developmental timing.

The calculation of the total growing period was divided into three distinct phases based on developmental progression, quantified using GDD: (1) the basic vegetative phase (BVP), defined as the period from germination to the first observation of sexual expression; (2) the sex expression phase (SE), encompassing the interval between the first and last observations of sexual expression within each sex and cultivar; and (3) the grain filling phase (GF), extending from the last observation of sexual expression to the date of harvest.

2.3. Sex Expression Determination

Data collection for sex expression was divided into two components: the first day of sex expression, measured in days after germination (DAG), and the female plant ratio (%). The first day of sex expression was assessed through daily monitoring conducted within each cultivar population, during which the age at which sexual expression was

first observed (DAG) for each plant was recorded. Female plants were identified by the emergence of stigmas and styles at the leaf axils, while male plants were identified by the appearance of pollen sacs (anthers) at the leaf bracts [25]. The female plant ratio (%) was calculated to evaluate the proportion of female plants relative to potential yield per unit area for each cultivar, using the following formula: (number of female hemp plants \times 100)/total number of hemp plants.

2.4. Yield and Yield Component Determination

Hemp seeds were harvested when approximately 70% of the seeds were ripe, exhibiting an average moisture content of 15% to 24% (wet basis). All cultivars were harvested simultaneously. Growth variables, including plant height (cm) and the number of branches, were recorded. Yield components were then assessed as illustrated in Figure 1B. Measurements included the length of the terminal inflorescence (TIF), the number of seeds in the terminal inflorescence (SNTIF), the number of main inflorescences at the end of each branch (MIF), and the number of seeds in the main inflorescence (SNMIF). The number of secondary inflorescences (SIF) and the number of seeds in the secondary inflorescence (SNSIF) located along lateral branches were also measured. The seed yield per plant was weighed, and 100 well-developed seeds were randomly selected and weighed in triplicate per plant to determine the 100-seed weight using a four-decimal-place balance. To calculate yield per unit area, the seed yield per plant was multiplied by the number of female plants per hectare. The number of female plants per hectare was estimated based on the percentage of female plants within each cultivar.

2.5. Statistical Analysis

Statistical analysis was performed using R software (version 4.3.2). Data for all traits were subjected to analysis of variance (ANOVA), and means were separated using Fisher's least significant difference (LSD) test at $p \leq 0.05$.

3. Results

3.1. Growth Conditions

Day lengths in Thailand decrease below 12 h from October to February, providing an opportunity for an extended cultivation period termed the 'off-season'. As illustrated in Figure 2, the in-season experiment began with a day length of 12 h and 25 min, which decreased to below 12 h 39 days after planting and reached a minimum of 11 h by the end of the season. This period coincided with the start of the off-season planting, during which day length gradually increased, reaching 12 h after 104 days and extending to 12 h and 52 min by the end of the off-season. During the in-season, with planting beginning in the third week of August, the average maximum and minimum temperatures during the BVP and SE were 33.2 °C and 23.6 °C, respectively. For the GF to harvest, temperatures averaged 30.8 °C and 20.4 °C, respectively. For the off-season, starting in the first week of December, the average maximum and minimum temperatures during BVP and SE were 30.6 °C and 17.2 °C, respectively, while during GF and harvest, they were 36.1 °C and 22.1 °C (Figure 2).

In the in-season planting period, day length initially measured at 12 h and 35 min (long day) on the planting date and gradually decreased over time (Figure 2). The first appearance of male and female sex organs occurred as day length decreased (11.58–11.40 h) 41 days after planting, with sex expression in the entire population completed within 6–10 days (Figure 3A,B). During the off-season, increasing day length resulted in a gradually decreasing dark period from 11.06 to 12.30 h between planting and harvest. Despite the initial exposure to a dark period shorter than the critical day length, no flowering occurred

until 51 days after planting. Moreover, first day of sex expression showed high variability, taking 30–40 days for complete sex expression across the population (Figure 3C,D).

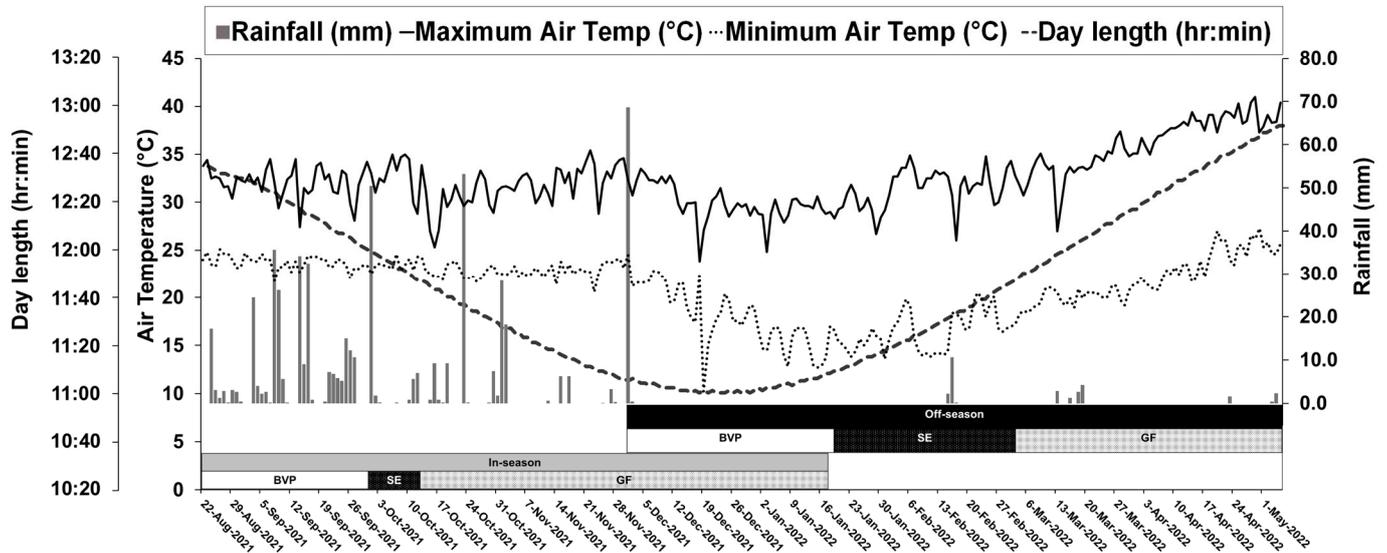


Figure 2. Weather conditions and phenology in the experiments, daily maximum temperature, minimum temperature, rainfall, and day length during the growing seasons (BVP = basic vegetative phase, SE = sex expression phase, GF = grain filling phase).

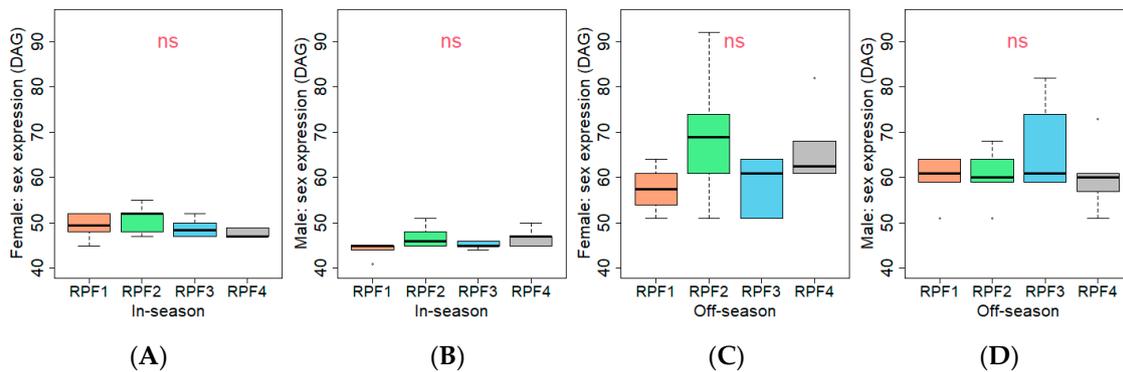


Figure 3. First day of sex expression (DAG) of female and male plants in the in-season (A,B) and off-season (C,D); ns = non-significant differences.

During the off-season, hemp plants did not initiate flowering despite exposure to short-day conditions. During the BVP, the CGDD for all hemp cultivars in the off-season ranged from 636 to 833 °Cd, compared to 734 to 834 °Cd in the in-season (Figure 4). The CGDD for BVP was similar for both male and female hemp plants and corresponded with the first day of sex expression in both sexes (Figure 3). The CGDD at harvest for female hemp plants was 2434 °Cd during the in-season and 2502 °Cd during the off-season (Figure 4). The similarity of these values shows that thermal accumulation requirements remained consistent between seasons despite the different calendar durations, indicating that CGDD measurements accurately track developmental progression across varying environmental conditions.

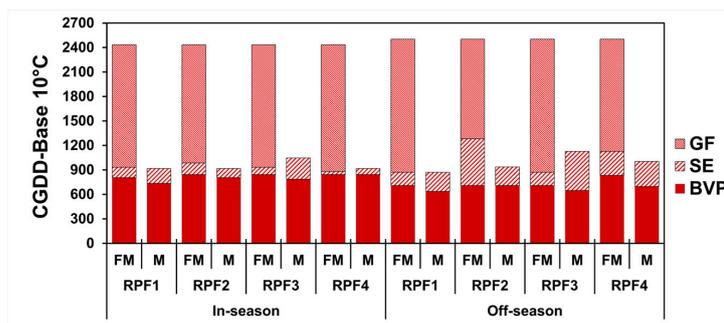


Figure 4. Cumulative growing degree days (Base Temp 10 °C) of FM (female plants) and M (male plants) in four Thai dioecious hemp cultivars with growth stages: BVP, SE, and GF. In-season and off-season seeds were harvested at 148 and 156 DAG, respectively.

3.2. Hemp Development

All four hemp cultivars are dioecious plants characterized by distinct male and female individuals. During the in-season period, the first appearance of female flowers occurred 45–55 days after planting, with no significant differences observed among the hemp cultivars (Figure 3A). The first appearance of male flowers occurred 41–51 days after germination, with all cultivars showing similar timing (Figure 3B). The timing of male and female flower appearance was during a short period of 10 days. In contrast, during the off-season, while short daylengths were present from planting (Figure 2), day length did not induce immediate flowering in hemp. Instead, vegetative growth continued until 51 days after planting, when male and female flowers began appearing (Figure 3C,D). All four hemp cultivars exhibited similar timing for the first appearance of sex. Still, within the population of 40 plants per cultivar, the period for the first appearance of female flowers varied from 51 to 92 days, while for male flowers, it varied from 51 to 82 days. This indicates a higher variability in sex expression during the off-season than in-season. Nevertheless, all hemp plants in the off-season expressed sex under day lengths of no more than 12 h. In addition, it was found that the first appearance of sex in hemp populations planted during the off-season was delayed by approximately 6–10 days compared to the in-season.

During the in-season period, the four hemp cultivars exhibited a lower proportion of female plants than male plants, except for RPF3, which had a nearly equal ratio of female to male plants (Figure 5). During the off-season, all hemp cultivars showed an increase in the proportion of female plants compared to the in-season, except for RPF3, which showed no change in sex ratio. Specifically, during the off-season, RPF4 experienced an increase of approximately 16% in the proportion of female plants, while RPF2 and RPF1 each showed an increase of 10% in the proportion of female plants.

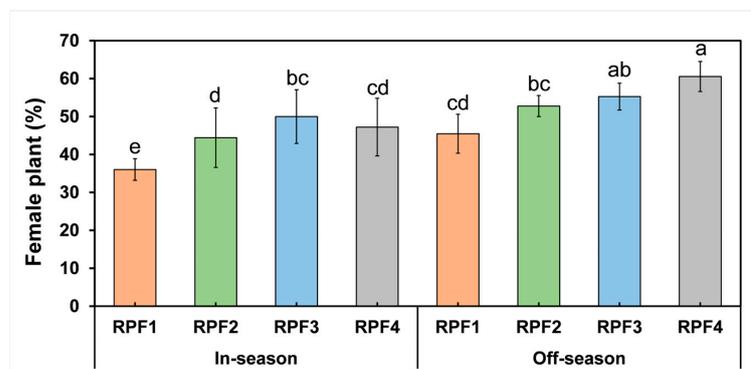


Figure 5. Female plant ratio (%) of four dioecious hemp cultivars in two seasons. Means followed by the same letter are not significantly different (LSD at $p < 0.001$). Error bars are standard deviations.

3.3. Hemp Seed Yield Productivity

RPF3 and RPF4 had a seed yield more than double that of RPF1 and RPF2 (Table 1). However, when considering the weight of 100 seeds, RPF4 had the highest 100-seed weight, followed by RPF3, RPF2, and RPF1, respectively. The cultivar RPF3 exhibited more variability in seed yield per plant compared to the other cultivars. In comparing the two growing seasons, RPF3 and RPF4 cultivated in-season showed yields per plant that were 24–26% higher than during the off-season. However, RPF1 and RPF2 showed no significant difference in yield per plant between the growing seasons. For RPF3 grown in the off-season, the 100-seed weight was lower than during the in-season, while RPF1 had a higher 100-seed weight when grown in the off-season.

Table 1. Comparison of seed yield and 100-seed weight of four hemp cultivars (RPF1, RPF2, RPF3, and RPF4) grown during in-season and off-season cultivation.

Season	Cultivar	Seed Yield (g/Plant)	100-Seed Weight (g)
In-season	RPF1	28.6 ± 4.6 cd	3.13 ± 0.04 e
	RPF2	37.6 ± 9.1 c	3.43 ± 0.06 bcd
	RPF3	83.4 ± 15.8 a	3.52 ± 0.07 ab
	RPF4	81.6 ± 10.9 a	3.67 ± 0.11 a
Off-season	RPF1	22.6 ± 5.4 d	3.43 ± 0.05 bcd
	RPF2	40.0 ± 6.1 c	3.32 ± 0.17 cd
	RPF3	61.7 ± 9.7 b	3.31 ± 0.16 d
	RPF4	61.9 ± 11.9 b	3.48 ± 0.27 bc
F-test		***	***
C.V. (%)		18.90	4.02

Note: Values are expressed as mean ± standard deviation. Letters (a, b, c, d, e) indicate significant differences among cultivars in both seasons. *** denotes a *p*-value < 0.001.

3.4. Yield Component Performance

This study evaluated plant height, branch number, and various yield components. The results from the in-season period showed that all hemp cultivars had similar plant heights and branch numbers (Figure 6A,D). However, RPF3 and RPF4 had significantly higher seed numbers per plant compared to other cultivars (Figure 6A). This indicates that plant height and branch number are not direct indicators of seed quantity per plant. However, when considering the high seed yield per plant in RPF3 and RPF4 along with other yield components, it becomes evident that these two cultivars had a higher number of seeds in the secondary inflorescences (Figure 6H), main inflorescences (Figure 6F), and terminal inflorescences (Figure 6G), respectively. During the off-season, RPF3 and RPF4 continued to have higher seed numbers per plant compared to RPF1 and RPF2 (Figure 6A), with consistently high seed numbers in secondary inflorescences (Figure 6H), main inflorescences (Figure 6F), and terminal inflorescences (Figure 6G), similar in the in-season planting. The number of secondary inflorescences was comparable across all cultivars (Figure 6H), but RPF3 exhibited twice the number of seeds in secondary inflorescences compared to other cultivars (Figure 6I). Although secondary inflorescences are yield components positioned on the branches, this study found no correlation between the number of secondary inflorescences per plant and the number of branches per plant in both in-season and off-season plantings (Figure 6H,D and Figure 7H,D).

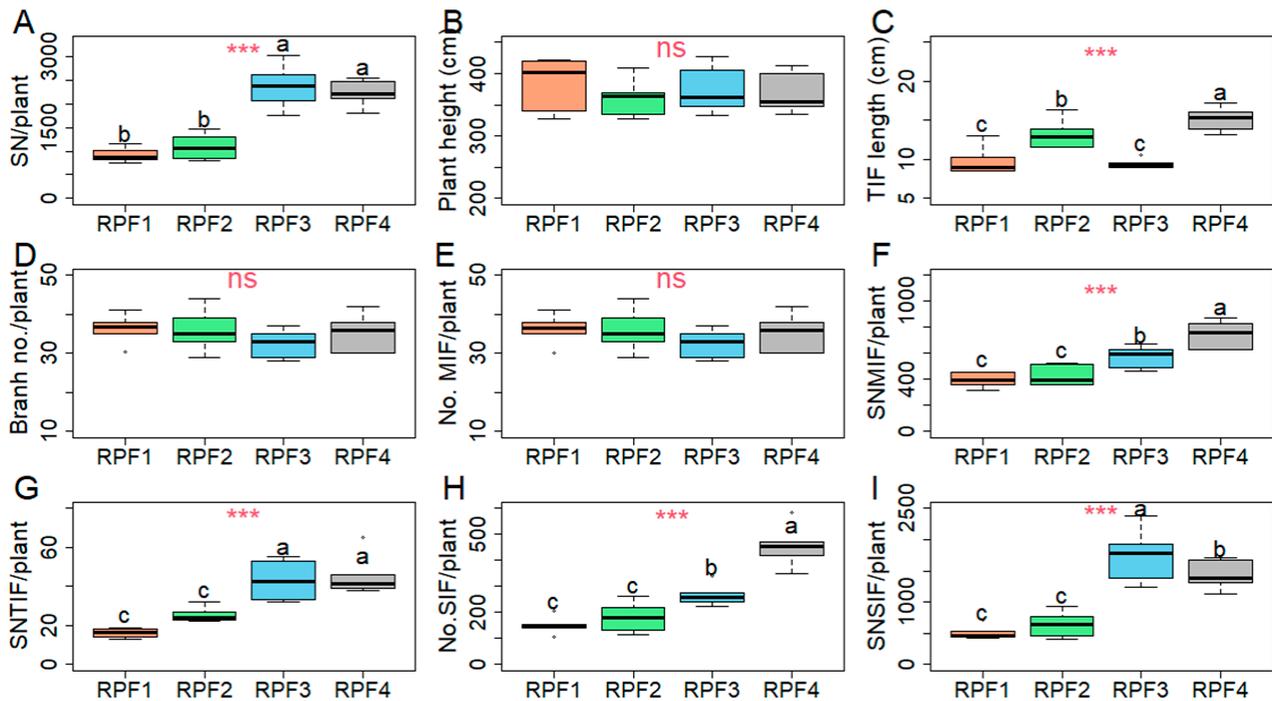


Figure 6. Comparative analysis of key morphological and reproductive traits among four hemp cultivars, RPF1, RPF2, RPF3, and RPF4, planted in-season (August 2021–January 2022): (A) seed number per plant, (B) plant height, reflecting (C) terminal inflorescence length, (D) branch number per plant, (E) number of primary inflorescences per plant, (F) seed number in primary inflorescence (SNMIF), (G) seed number in terminal inflorescence (SNTIF), (H) number of primary inflorescences per plant, and (I) seed number in secondary inflorescence (SNSIF). Box plots display the median, interquartile range, and data spread, with outliers represented as dots. Letters (a, b, c) indicate significant differences among cultivars, with *** denoting a p -value < 0.001 and “ns” signifying non-significant differences.

RPF3 and RPF4 yields are high in both planting seasons, with seed distribution varying across different positions on the plant in each season. During the in-season, RPF3 and RPF4 exhibited a high proportion of seeds in the secondary inflorescence positions (SNSIF), accounting for 64–73% of the seed number compared to other positions on the same plant. The seed yield per plant for RPF3 was similar in both planting seasons, but during the in-season, more seeds were concentrated in the secondary inflorescences. However, in the off-season, the seed numbers in secondary inflorescences decreased by 35%, with more significant variability in seed numbers at this position than in other cultivars (Figure 7I). Despite this, RPF3 in the off-season showed a 31% increase in seed number at the terminal branch inflorescences, compensating for the overall high yield comparable to the in-season (Figure 7F). RPF4, while also being a high-yielding cultivar like RPF3, exhibited a decrease in seed yield per plant during the off-season compared to the in-season (Table 1). Considering seed positions, it was found that the seed numbers in secondary inflorescences decreased by 44%. In contrast, the seed numbers at the terminal branch and primary inflorescences remained relatively high and consistent with the in-season planting.

Seed yield per plant in hemp results from the combined effects of seed number and seed weight, both of which are influenced by physiological processes. The factors affecting these processes and the potential and response of each hemp vary, leading to differences in seed number and weight across planting periods (Table 1). Seed number is a trait influenced by growth and development, with critical yield components including plant height, branch number, secondary inflorescence number, and flowering duration. During the in-season

planting period, hemp experienced an average temperature of 27.9 °C and day lengths of 12 to 12.5 h for 40 days during the BVP, resulting in high photosynthetic rates that promoted more excellent stem elongation and branching compared to hemp grown during the off-season.

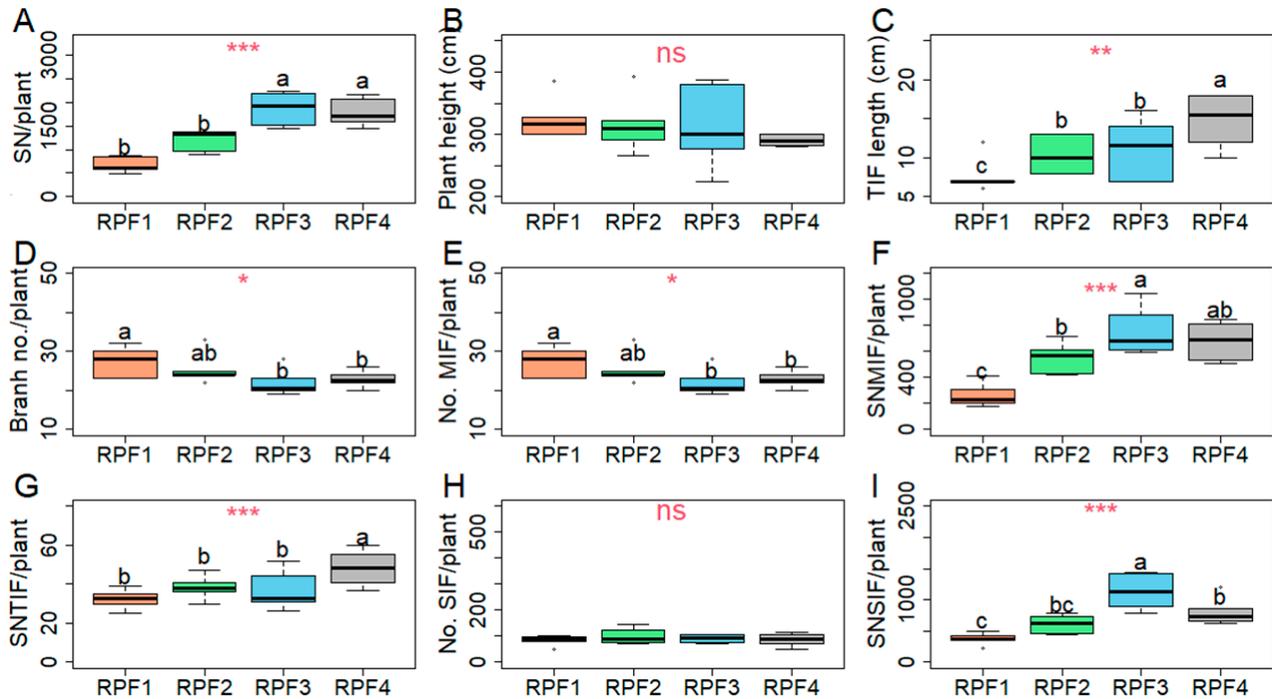


Figure 7. Comparative analysis of key morphological and reproductive traits among four hemp cultivars, RPF1, RPF2, RPF3, and RPF4, planted off-season (December 2021–April 2022): (A) seed number per plant, (B) plant height, reflecting (C) terminal inflorescence length, (D) branch number per plant, (E) number of primary inflorescences per plant, (F) seed number in primary inflorescence (SNMIF), (G) seed number in terminal inflorescence (SNTIF), (H) number of primary inflorescences per plant, and (I) seed number in secondary inflorescence (SNSIF). Box plots display the median, interquartile range, and data spread, with outliers represented as dots. Letters (a, b, c) indicate significant differences among cultivars, with *, **, and *** denoting a p -value < 0.05, 0.01, and 0.001, respectively. “ns” signifies non-significant differences.

Consequently, the BVP during the off-season was 10 days longer than during the in-season (Figure 2). Despite the extended BVP, the height and branch number growth were 13–21% (Figures 6B and 7B) and 25–35% (Figures 6D and 7D) lower than in-season. The reduced branch number led to fewer main inflorescences. However, all cultivars except RPF 1 showed an increase in seed number per main inflorescence by 41–95%, resulting in a higher proportion of seeds produced from main inflorescences (Figure 8). Additionally, RPF 3 produced more seeds in secondary inflorescences than all other cultivars in both planting periods (Figures 6I and 7I). This highlights that all cultivars exhibited a higher proportion of seed production in secondary inflorescences compared to other positions in both seasons.

In this study, the 100-seed weight of hemp showed no correlation with the number of seeds per plant. For instance, cultivars with a higher seed count per plant had a greater 100-seed weight than those with fewer seeds across both planting periods (Table 1). This may be due to the inherent potential of each cultivar. During the in-season, RPF 4 exhibited the highest 100-seed weight, followed by RPF3, RPF2, and RPF1. Conversely, in the off-season, all cultivars showed high variability in 100-seed weight, except for RPF1. However, the average 100-seed weight across all cultivars was not statistically different (Table 1). The

gradual increase in temperatures from the flowering stage (29/15 °C; day/night) to harvest (40/25 °C) during the off-season led to a 3–6% reduction in seed weight for RPF2, RPF3, and RPF4.

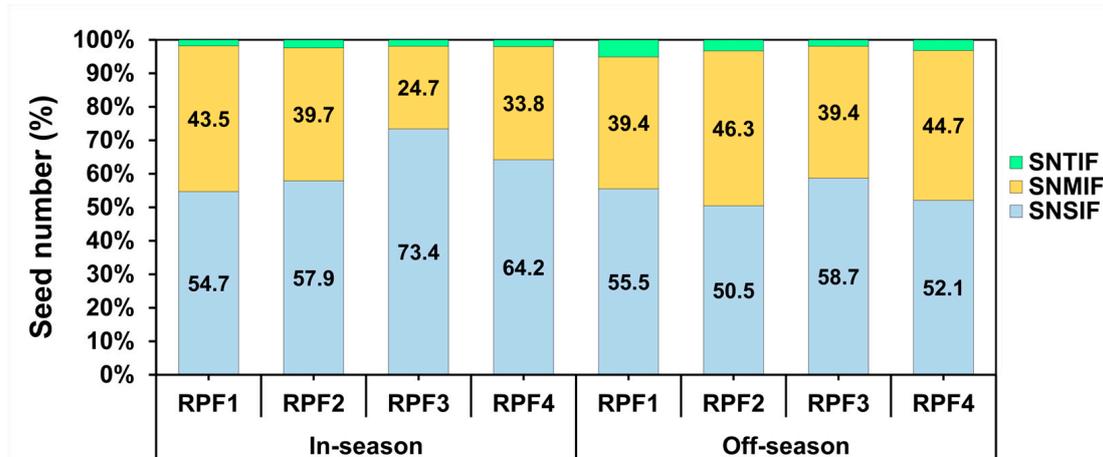


Figure 8. Seed number distribution (%) in the different inflorescence positions of four Thai dioecious hemp cultivars (SNTIF = seed number in terminal inflorescences, SNMIF = seed number in main inflorescences, SNSIF = seed number in secondary inflorescences).

Based on the study of sex ratio and yield per plant, when extrapolated to yield per unit area calculated here based on a planting density of 1 × 1 m, resulting in 10,000 plants per hectare, the yield per area is shown in Figure 9. RPF3 and RPF4 hemp cultivars produced similar seed yields per area, significantly higher than those of RPF1 and RPF2 across both planting periods. Considering yield stability across the in-season and off-season, RPF3 reduced seed yield per area by 18%, while RPF4 maintained consistent seed yields across both planting periods. The key factor contributing to the stability of RPF4’s yield was the 26% increase in the proportion of female plants, which compensated for the 26% reduction in yield per plant during the off-season.

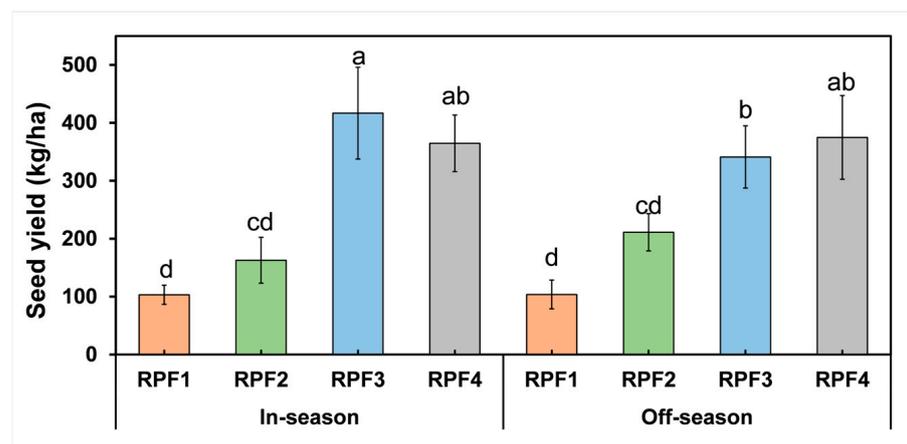


Figure 9. Seed yield per hectare is calculated by combining seed yield per plant, plant population, and female plant ratio in each cultivar under different growing seasons. Data are means, error bars are standard deviations, and the same letters are not significantly different (LSD at the $p < 0.001$).

4. Discussion

Hemp cultivation for fiber production focuses on utilizing the stems during the vegetative stage, where changes in photoperiod do not impact fiber yield, allowing for multiple planting cycles within a year. In contrast, seed production cultivation requires an

appropriate basic vegetative phase followed by flowering and seed setting. As observed in our results, hemp must undergo an essential vegetative phase (BVP) before flowering, with temperature playing a critical role in determining the duration of the BVP. This demands consideration of the photoperiodic response of the hemp cultivar to determine optimal planting times for growth and yield. Regarding photoperiod-sensitive hemp cultivars, flowering depends on the critical day length specific to each variety and the day length during the planting period [29]. Phytochrome-mediated responses to day/night light cycles regulate flowering in hemp as a short-day plant, with longer nights promoting the physiological changes necessary for flowering induction [28,46–49]. However, in a study [25] on monoecious plants at 50° N latitude, a Tbase of 10.2 °C was used to calculate GDD during both the vegetative and flowering stages. It has also been reported that monoecious and dioecious hemp cultivars do not differ significantly in GDD requirements during the BVP [38], nor is there a significant difference between male and female plants [25]. Nevertheless, there is variability among cultivars, with GDD values during the BVP ranging from 306 to 636 °Cd [50,51]. Additionally, the accumulated GDD until seed harvest for monoecious and dioecious hemp cultivars is similar, ranging from 2415 to 3339 °Cd [52]. The CGDD at seed harvest in this study falls within this range.

Cultivating dioecious hemp for seed production requires the presence of both male and female plants in the growing area. However, a higher proportion of male plants than female plants can result in lower seed yields, as only female plants produce seeds. Both genetic and environmental factors influence sex expression in hemp. Sex determination follows the XY chromosomal system, but expression can be modified by genes on both sex chromosomes and autosomes [53]. Environmental factors interact with genetic components through hormonal regulation [54,55]. Specifically, photoperiod and temperature influence sex expression, with short days and lower temperatures generally favoring female flower development, while long days and higher temperatures tend to promote male flower formation [56,57]. The study results indicate that the cultivar RPF3 exhibited a consistent ratio of female to male plants across both planting seasons. This lack of variability suggests that genetic factors predominantly influence sex expression in RPF3. In contrast, the sex ratios of RPF1, RPF2, and RPF4 varied between seasons, with a higher proportion of female plants observed during the off-season. This increase in female plants may be attributed to the lower temperatures and shorter photoperiods experienced during the BVP, which likely contributed to the increased proportion of female plants (Figure 2). This finding aligns with [53] the report that lower temperatures can increase the number of female hemp plants. Lower temperatures may reduce GA levels in the plants, which is consistent with [58] the finding that reduced GA levels can enhance the development of female flowers in monoecious hemp.

Additionally, lower temperatures can lead to the accumulation of IAA and ABA, resulting in a higher IAA/ABA ratio and promoting the formation of female flowers [57]. Moreover, short day lengths have been shown to favor the development of female plants over male plants [59,60]. Short photoperiods also increase ethylene levels in plants [61], which can inhibit male gene expression and promote genes that direct tissue development toward female flowers [62,63]. Therefore, this study's increased proportion of female plants may result from low temperatures and short day lengths, influencing plant physiology and hormonal levels related to sex expression.

The higher seed number in each position may be due to an increased number of flowers per inflorescence, which enhances seed set opportunities [46,64,65]. This finding aligns with studies on various crops, where high temperatures negatively impact translocation, seed development, and seed growth, ultimately reducing seed weight. For instance, ref. [66] high night temperatures reduced nitrogen and nonstructural carbohydrate transport, adversely

affecting rice seed weight and quality. High daytime temperatures can also impair phloem transport by causing callose formation, which blocks sieve plates and reduces seed weight, as observed in cotton [67]. Heat stress at 33/28 °C significantly decreased lentil seed growth by 30–44%, shortening the seed-filling period by 6–8 days and reducing seed weight by 20–39% compared to 28/23 °C [68]. The timing of high temperatures also matters; exposure to 34/20 °C during early seed filling (7–21 days post-flowering) accelerated dehydration, leading to lower seed weight, while later exposure enhanced desiccation tolerance and preserved seed viability [69,70]. In temperate zones, average temperatures above 23 °C during grain filling reduced seed fat accumulation, decreasing seed size and weight [71]. However, RPF1 exhibited an 8% increase in seed weight when grown in the off-season (Table 1), consistent with the interspecific trade-off relationship between seed number and seed weight. The decrease in seed number per plant led to an increase in seed weight, reflecting resource allocation during seed set, where average seed weight decreases as seed number increases, varying by plant species [72]. It should be noted that this study was conducted with a planting spacing of 1 × 1 m to minimize plant competition, which differs from commercial production systems where optimal yields are typically achieved under conditions of moderate plant density. The patterns of sex expression and the distribution of yield components observed in this study may respond differently under higher planting densities commonly employed in field conditions. Specifically, the compensatory yield mechanisms observed in cultivars RPF3 and RPF4 may be modified when plants compete more intensely for resources. Although our spacing approach allowed us to assess each cultivar's maximum individual potential without the influence of competition, commercial production would necessitate optimizing planting density to maximize yield per unit area. Further research focusing on these cultivars across a range of planting densities would serve to complement the current findings and refine recommendations for commercial hemp seed production in Thailand.

5. Conclusions

Selecting cultivars with a high proportion of female plants is crucial to optimize seed yield per area in dioecious hemp. Extending hemp seed production cycles by planting during the off-season in Thailand is influenced by low temperatures and short day lengths during the BVP, which promotes an increase in female plant expression but adversely affects physiological processes and stem growth. This results in decreased seed production at different positions on the plant, with variations across different cultivars. In this study, RPF3 showed a significant increase in seed number in the main inflorescences during the off-season, effectively maintaining overall yield despite reducing seed number in secondary inflorescences. Similarly, RPF4 sustained high seed yield by increasing the proportion of female plants during the off-season, compensating for decreased seed yield per plant. These shifts in yield component distribution between seasons suggest the need to adapt or develop management practices to optimize seed yield during the off-season. The research findings underscore the importance of utilizing this information in selecting hemp cultivars for seed production (hemp seed ideal type). This research highlights the importance of looking at yield and considering different yield components. The results can help improve or select hemp seed cultivars by focusing on their ability to balance seed production, compensating for lower yield in one area by increasing it in another. This ability is crucial for ensuring stable hemp seed production across seasons.

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