



## Photosynthetic Activity and Ecological Variety Testing of Flax under Contrasting Seeding Densities in a Strongly Continental Climate

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### ABSTRACT

This study evaluated the influence of different seeding rates on photosynthetic activity, growth, and productivity of flax varieties under Northern Kazakhstan's sharply continental climate. Field experiments were conducted in 2023–2024 using oil and long-fiber flax varieties at two seeding rates (10 and 23 million seeds/ha) in 2m<sup>2</sup> plots with three repetitions. Increasing the seeding rate significantly ( $P < 0.01$ ) enhanced plant height but reduced individual plant yield components. Productivity was significantly ( $P < 0.01$ ) higher at the lower seeding rate (10 million seeds/ha) for Talar ( $0.60 \pm 0.80$  t/ha), Lada ( $0.60 \pm 0.03$  t/ha), and UF1 ( $0.60 \pm 0.04$  t/ha) compared to the higher rate (e.g., Talar:  $0.52 \pm 0.1$  t/ha). The 1000-seed weight was significantly influenced ( $P < 0.01$ ) by variety, seeding rate, and interaction (e.g., Lada:  $7.0 \pm 0.7$  g at 10 million seeds/ha). Seed number per pod was significantly influenced by seeding rate ( $P < 0.01$ ), with Talar showing  $8.5 \pm 1.0$  seeds/pod at 10 million seeds/ha versus  $6.6 \pm 0.9$  at 23 million seeds/ha. Oil and protein content varied by genotype and density, but main effects and interaction with seeding rate were not statistically significant (ns). Talar recorded the highest oil content at 23 million seeds/ha ( $41.14 \pm 0.9\%$ ), while protein content increased with higher seeding rates (e.g., Talar:  $18.24 \pm 1.1\%$  at 10 to  $19.08 \pm 0.7\%$  at 23 million seeds/ha). Photosynthetic productivity and net photosynthetic productivity showed significant ( $P < 0.01$ ) varietal differences, but seeding rate effects were non-significant (ns). Lada had the highest PP ( $1554.0 \pm 2.3$  thousand m<sup>2</sup>/ha/day at 10 million seeds/ha), and Talar exhibited the highest NPP ( $4.23 \pm 0.0$  g/m<sup>2</sup>·day at 10 million seeds/ha). These findings provide recommendations for optimizing flax production.

**Keywords:** Flax varieties, Long-fiber flax, Yield, Productivity, Correlation analysis.

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### INTRODUCTION

Flax (*Linum usitatissimum* L.) is a historically significant and versatile crop cultivated worldwide for both its seeds and fibers (Savoskina et al., 2023; Hoque et al., 2024). Its seeds are a rich source of oil, particularly omega-3 fatty acids, lignans, proteins, minerals, and vitamins, making them highly valuable to the food, pharmaceutical and cosmetic industries (Pershakov et al., 2021a; Walkowiak et al., 2021; Yadav et al., 2022). The fibers, known for their strength and durability, are essential for textile production and various composite materials (Galinousky et al., 2020; Arslanoglu et al., 2022). Owing to this dual-purpose utility, flax holds considerable economic importance and is cultivated across diverse climatic zones. Flax is an unpretentious and highly adaptable crop that can grow

under a wide range of climatic conditions (Paliwal et al., 2023). For example, in China, flax is most often cultivated in the northern and northeastern regions, such as Heilongjiang and Inner Mongolia, where a moderate climate, short summers, sufficient moisture, and cool nights create optimal conditions for its growth. Belarus, one of Europe's traditional centers of flax cultivation, benefits from a moderate continental climate with mild winters and warm summers, providing the humidity needed during the growing season. In Kazakhstan, flax is mainly grown in northern regions such as Akmola, Kostanay, and North Kazakhstan, where the sharply continental climate with warm summers and cold winters, combined with sufficient summer moisture—especially after rainy springs—favors flax cultivation (Yalovik & Yalovik, 2023).

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Globally, flax is cultivated in more than 50 countries (Stavropoulos et al., 2023), with the leading producers being Canada, India, Russia, Kazakhstan, and China (Stavropoulos et al., 2023; Raut et al., 2025). The total global area under flaxseed exceeds 3.5 million hectares, while the annual gross seed harvest reaches 2.2–2.7 million t. In 2017, Russia was the world's largest producer of linseed (610,118 t), followed by Canada (507,606 t), China (362,034 t), India (184,000 t), and the USA (97,590 t) (Walkowiak et al., 2021). In recent years, demand for flaxseed has grown steadily, driving expansion of cultivated areas, including in Kazakhstan, where diversification strategies and the inclusion of oilseeds and industrial crops in rotations have expanded total oilseed acreage to 3 million hectares, with more than 1.5 million hectares sown with oil flax (Pershakov et al., 2021b; Bureau of National Statistics, 2023). Oil flax is a highly valuable industrial crop and a key source of high-quality oil, used extensively in multiple sectors (Turin et al., 2021; Minevich, 2022). Flax also has important industrial uses beyond oil and fiber: it is employed in the production of fabrics, explosives, rocket and torpedo fuel, and specialized protective clothing for astronauts, divers and military personnel (Luchkina et al., 2020; Mazurova, 2023; Tsitskiev et al., 2023).

In Russia, 36.2 thousand hectares were sown with flax in 2022, while the area under oil flax exceeded 5 million hectares. Studies conducted in various regions have shown that agrometeorological conditions significantly influence seed yield and other economically important traits (Kolotov, 2019; Rozhmina et al., 2020b; Kolotov, 2021). For instance, the highest seed yield (2.88 t/ha) was obtained under favorable moisture conditions (HTC = 1.28), while dry conditions (HTC = 0.96) reduced yields by 1.27 t/ha. In humid conditions (HTC = 2.10), yields reached 2.12 t/ha. Oil content was less sensitive to weather variability compared to other traits. Recent global research (2020–2025) has greatly expanded knowledge about flax productivity, resilience, and optimal cultivation strategies. Advances include improved nutrient management, such as optimizing phosphorus application for growth and soil health (He et al., 2024), and the use of pre-sowing seed treatments, like magnetic gradient fields, to enhance plant development and yield (Yudaev et al., 2025). Genetic studies are increasingly focused on identifying high-performing linseed genotypes (Kaur et al., 2024) and unraveling mechanisms of stress tolerance through integrative omics approaches (Yadav et al., 2022; Paliwal et al., 2023; Li et al., 2024). Transcriptomic tools, such as RNA-Seq, have enabled the identification of genes associated with seed size (Jiang et al., 2022) and salt tolerance (Li et al., 2024). Breeding programs aim to improve seed yield, oil content and quality, plant height, and earliness, recognizing the complex genotype × environment dependence of these traits (Zare et al., 2021).

One of the key agronomic factors influencing flax productivity is the seeding rate, which directly affects plant density and yield formation. Extensive literature shows that the relationship between plant density and yield follows the density–yield theory, which describes a curvilinear relationship: at very low densities, individual

plants produce more branches and capsules, but total yield per area remains low; as density increases, total yield increases until it reaches an optimum; beyond this, excessive density intensifies competition for resources and leads to decreased plant performance (Patil et al., 2020; Arslanoglu et al., 2022; Koriem et al., 2023). High plant populations often reduce chlorophyll content and stem thickness while increasing lodging risk. For fiber flax, high plant density is commonly recommended to ensure fiber quality, while reduced densities promote a more open canopy and higher productivity per plant (Ethridge et al., 2022). The response of flax to density is also strongly influenced by genotype-by-density interactions, since different varieties have distinct architecture, photosynthetic potential, and stress tolerance (Arslanoglu et al., 2022). Interactions with nutrient inputs, for example, potassium affecting lignin synthesis and lodging resistance (Wu et al., 2023)—and with environmental factors such as annual climatic variation (Xie et al., 2023) further demonstrate the complexity of these relationships. Significant variability has also been recorded between yellow- and brown-seeded genotypes under water stress, affecting seed yield and its components (Zare et al., 2021, 2023). Thus, optimal density is genotype-specific and depends on local growing conditions.

Given the sharply continental climate of Northern Kazakhstan, optimizing seeding rates for regionally adapted varieties remains a critical research direction. The compactness of the plant habitus determines the required feeding area: the smaller the plant, the less space it occupies, which is important when defining optimal seeding rates (Rozhmina et al., 2020a; Pershakov, 2022). Understanding how different varieties respond to density stress under such conditions is essential for improving resource efficiency and maximizing yield.

Based on the synthesis of previous studies and preliminary observations, the present study was designed to test the following hypotheses:

### Hypotheses

1. Increasing seeding rate will increase plant density and height but negatively affect individual plant yield components (seed number per pod, 1000-seed weight) due to intensified intra-specific competition.
2. Flax varieties will differ significantly in photosynthetic activity, net photosynthetic productivity, overall productivity, and quality (oil and protein content), reflecting their distinct genetic potentials.
3. A significant variety × seeding rate interaction will be observed for key productivity and quality traits, indicating that optimal seeding rates are genotype-specific under the climate of Northern Kazakhstan.
4. Lower seeding rates may enhance individual plant performance, seed quality, and in some cases overall yield for specific varieties by reducing competitive stress and improving resource allocation.

## MATERIALS & METHODS

Scheme of the experiment on sowing oil flax and fiber flax in Northern Kazakhstan. The experiment was

laid out in Northern Kazakhstan to study the effect of seeding rate on the growth, development and productivity of different varieties of fiber flax. Experiment structure: The experiment included two blocks with different seeding rates: Block A – seeding rate 10 million pcs /ha. Block B – seeding rate 23 million pcs /ha. Each block included several flax varieties located in separate plots: Grant (A1), Lada (A2), Talar (A3), Kazakhstani Yantar (A4) – control, UF (A5). Each block (replication) contained all variety × seeding-rate combinations, randomly assigned to plots. The experimental plot size was 2 m<sup>2</sup> (1 m × 2 m). Plots were separated by narrow alleys to reduce border effects, and border rows were excluded from sampling. Each flax variety was sown at both seeding rates in each replication to allow direct comparison of density effects on yield formation.

Ecological testing of varieties and statistical data processing were carried out in accordance with generally accepted methods for conducting field agrotechnical experiments with oil crops. The mass of 1000 seeds was determined according to GOST 10842-89 (Lukomets, 2010). Observations and recording of phenological phases of vegetation (shoots, “Christmas trees”, budding, flowering, ripening), duration of interphase periods and the total vegetation period were carried out on the basis of the Field Experiment Methodology (Dospikhov, 1985) and methodological recommendations of the State Service for Agricultural Crop Testing (SCT) (Grigoriev, 1989). To determine the mass fraction of fat (oil) in flax seeds by extraction with organic solvents, the method specified in GOST 29033-91 is used (USSR State Committee for Quality Management and Standards, 1991). The Kjeldahl method is used to determine the protein content in flax seeds (USSR State Committee for Standards, 1984).

The present study involved varieties of oil flax and long-linen flax adapted to the climatic conditions of Kazakhstan. Ecological variety testing was carried out using varieties bred by Belarusian and Chinese breeders. Experimental work was carried out on plots of 2 m<sup>2</sup> with three repetitions in 2023-2024, where separate plots were provided for each variety and seeding rate. Correlation and statistical methods of analysis were used to assess yield and productivity. The obtained data were processed using specialized software packages for statistical analysis.

Thus, the applied methodological approaches provided a comprehensive assessment of the productivity and quality of flax products, guaranteeing the objectivity and reliability of the results obtained. Sowing took place in the Akmola region of Northern Kazakhstan, where climatic conditions are marked by sharp continentality. The relevant meteorological data for 2024 are shown in Fig. 1. Analysis of climate data for 2024 allows us to identify several significant characteristics.

### Temperature Conditions

In 2024, winter temperatures were on average lower than in the previous year, especially in January (minimum -17.3°C in the third ten-day period). More uniform temperature conditions were observed in spring, but they remained lower than in 2023, with a maximum in May in

the third ten-day period (14.5°C). Summer temperatures were also lower, with a peak in July in the first ten-day period (20.1°C). In September, temperatures continued to decrease to 8.4°C in the third ten-day period.

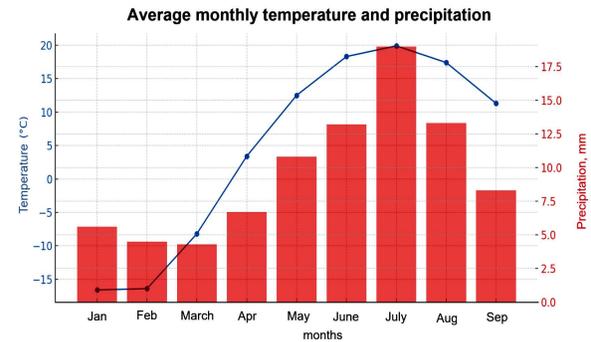


Fig. 1: Meteorological conditions of the area (2023-2024).

### Atmospheric Precipitation

Precipitation, the winter months of 2023 were characterized by a small amount, the maximum level was 13.5mm in January in the first ten-day period. In the spring, significant fluctuations were observed, the largest amount of precipitation was recorded in April in the second ten-day period (62.5mm). The summer period turned out to be predominantly dry, with rare precipitation, the maximum value of 7.4mm in June in the second ten-day period. In the fall, the amount of precipitation gradually decreased. In 2024, the winter period brought slightly more precipitation compared to 2023, especially in January in the first ten-day period (6.1mm). In spring, precipitation was moderate and more evenly distributed over the ten-day periods. Thus, the climate data reflected significant vertical variations in temperature and precipitation characteristics, which may have a direct impact on agronomic practices and crop yield formation.

### Statistical Analysis

Ecological testing of varieties and statistical data processing were carried out in accordance with generally accepted methods for field agrotechnical experiments with oil crops (Lukomets, 2010). All data were analyzed using a two-factor analysis of variance (ANOVA) with variety and seeding rate as fixed factors and block (replication) as a random factor. The linear model used was:

$$Y_{ijk} = \mu + B_k + V_i + S_j + (V \times S)_{ij} + \varepsilon_{ijk}$$

where  $Y_{ijk}$  is the observed value of the trait,  $\mu$  is the overall mean,  $B_k$  is the effect of the  $k$ -th block,  $V_i$  is the effect of the  $i$ -th variety,  $S_j$  is the effect of the  $j$ -th seeding rate,  $(V \times S)_{ij}$  is the interaction between variety and seeding rate, and  $\varepsilon_{ijk}$  is the random error term.

The assumptions of normality and homogeneity of variance were checked by Shapiro-Wilk and Levene tests, as well as by visual inspection of residual plots. Percentage data (germination, plant survival) were

arcsine square-root transformed when necessary; means are presented on the original scale. For each trait, effect sizes (partial eta-squared,  $\eta^2_p$ ) were calculated from the ANOVA sums of squares.

## RESULTS & DISCUSSION

Table 1 summarizes field germination, plant survival, and related stand-establishment parameters for different flax varieties grown at two seeding rates: 10 million seeds  $\text{ha}^{-1}$  (B1) and 23 million seeds  $\text{ha}^{-1}$  (B2). For each variety, the following indicators are presented:

**Seedling density (plants  $\text{m}^{-2}$ ):** The number of emerged seedlings per square meter after sowing, reflecting the achieved plant stand under each seeding rate.

**Field germination (%):** The proportion of emerged seedlings relative to the total number of seeds sown, serving as an indicator of sowing efficiency and early establishment success under field conditions.

**Number of plants before harvest (plants  $\text{m}^{-2}$ ):** The density of plants remaining in the field immediately prior to harvest, indicating stand persistence throughout the growing season.

**Plant survival (%):** The percentage of plants that survived from emergence to harvest, calculated relative to the initial seedling density, and reflecting varietal tolerance to biotic and abiotic stresses during crop development.

**Seeding rate: 10 million seeds  $\text{ha}^{-1}$  (B1).** At the lower seeding rate, significant varietal differences were observed in seedling density. The *Talar* variety exhibited the highest seedling density (585 plants  $\text{m}^{-2}$ ), whereas *Lada* recorded the lowest density (480 plants  $\text{m}^{-2}$ ). Field germination across all varieties ranged from 65 to 69%, indicating satisfactory emergence and effective stand establishment under this seeding rate. The number of plants remaining before harvest and overall plant survival were generally high, with only minor variation among varieties. For

instance, *Talar* showed a survival rate of 89%, reflecting strong adaptability and stability under moderate plant density.

**Seeding rate: 23 million seeds  $\text{ha}^{-1}$  (B2).** Increasing the seeding rate markedly enhanced seedling density across all varieties. Under this higher density, *Talar* again demonstrated the highest plant density, reaching 686 plants  $\text{m}^{-2}$ , confirming its superior emergence capacity and competitiveness under dense sowing conditions.

Field germination at 23 million pcs/ha is significantly higher than at 10 million pcs/ha, indicating that germination improves with a higher seeding rate. Plant numbers before harvest and plant survival remain high for all varieties, with *Lada* demonstrating the best survival rate at 95%. The survival rate is higher than 88% at both seeding rates, which indicates a good level of plant resistance in different conditions. UF1, with a seeding rate of 23 million pcs /ha, has high rates of seedling density and survival (survival rate - 92%). The table shows how changes in seeding rates affect the germination and survival characteristics of different flax varieties. The *Lada* variety demonstrates high survival at both seeding rates, and the *Talar* variety has the highest seedling density at a rate of 10 million pcs /ha. Increasing the seeding rate (up to 23 million pcs /ha) increases field germination, but also affects the density of plants in the field. Increase in seedling rate from 10\*\* to 23\*\* resulted in a corresponding increase in plant height across all varieties (Table 2). The tallest plants were recorded for UF1 (84.90cm) and *Lada* (84.57cm) at the higher seeding rate. However, the lowest plant height was observed in *grant* variety at 10\*\* (70.30cm) and this significantly differed ( $P < 0.05$ ) from other varieties. Additionally, the interaction between seeding rate and flax plant variety was significant, this indicates that all flax cultivar responds to increase in seeding rates. Higher seeding rate typically intensifies intra-specific competition, prompting plants to grow taller as they compete for sunlight.

**Table 1:** Field germination, plant density and survival of oil flax and flaxseed plants during the growing season

Variety	Seeding density, pcs/m <sup>2</sup>	Field germination, %	Number of plants before harvesting, pcs/m <sup>2</sup>	Plant survival rate, %
10 million pcs /ha – B <sub>1</sub>				
Grant	410	68	371	90
Lada	480	69	431	88
Talar	585	65	456	89
23 million pcs /ha – B <sub>2</sub>				
Grant	662	74	599	91
Lada	526	80	499	95
Talar	686	85	628	92
UF1	641	85	632	92

**Table 2:** Effect of seeding rate on the productivity of flax

Variety	Seeding rate ( $\times 10^6$ seeds $\text{ha}^{-1}$ )	Plant height (cm)	Productivity (t $\text{ha}^{-1}$ )	Number of productive stems	Seed number per pod	Weight-1000 (g)
TALAR	10	80.80 $\pm$ 5.5a	0.60 $\pm$ 0.08a	37.40 $\pm$ 3.1ab	8.5 $\pm$ 1.0a	7.0 $\pm$ 0.7a
	23	82.00 $\pm$ 3.0a	0.52 $\pm$ 0.1b	32.20 $\pm$ 1.7cd	6.6 $\pm$ 0.9bc	5.6 $\pm$ 0.0 bc
GRANT	10	70.30 $\pm$ 4.1b	0.52 $\pm$ 0.01b	31.80 $\pm$ 3.9a	8.0 $\pm$ 1.0a	6.7 $\pm$ 0.3a
	23	83.90 $\pm$ 1.6a	0.48 $\pm$ 0.03b	31.10 $\pm$ 1.1d	6.4 $\pm$ 0.8c	5.2 $\pm$ 0.1c
LADA	10	82.00 $\pm$ 6.5a	0.60 $\pm$ 0.03a	35.80 $\pm$ 4.5bc	7.8 $\pm$ 1.3ab	6.8 $\pm$ 0.3a
	23	84.57 $\pm$ 1.4a	0.49 $\pm$ 0.03b	31.70 $\pm$ 1.3d	5.9 $\pm$ 0.8c	5.3 $\pm$ 0.1bc
UF1	10	84.50 $\pm$ 4.8a	0.60 $\pm$ 0.04a	37.30 $\pm$ 1.7ab	8.1 $\pm$ 0.8a	5.8 $\pm$ 0.4b
	23	84.90 $\pm$ 2.1a	0.49 $\pm$ 0.02b	30.70 $\pm$ 0.8d	5.8 $\pm$ 0.6c	5.1 $\pm$ 0.1c
Variety (V)		**	**	ns	ns	**
Seeding rate (S)		**	**	**	**	**
V $\times$ S		**	**	**	ns	**

Values are means  $\pm$  standard deviation ( $n = 3$ ). Within each column, means followed by different lowercase letters differ significantly at  $P < 0.05$  according to Tukey's HSD test. Variety (V), seeding rate (S), and their interaction (V  $\times$  S) were tested using two-way ANOVA. "\*\*\*\*" and "ns" indicate, respectively, highly significant ( $P < 0.01$ ) and non-significant ( $P \geq 0.05$ ) effects.

The seed number per pod exhibited variation across treatments and was influenced by variety and seeding rate, although the interaction effect was statistically non-significant ( $P > 0.05$ ). The highest seed number was observed in Talar at 10 plants/m<sup>2</sup> ( $8.5 \pm 1.0$ ), followed by UF1 ( $8.1 \pm 0.8$ ) and Grant ( $8.0 \pm 1.0$ ) at the same seeding rate. In contrast, increasing the seeding rate to 23 plants/m<sup>2</sup> resulted in a marked decrease in seed number across all varieties. For instance, Talar showed a reduction from 8.5 to 6.6 seeds per pod and Grant from 8.0 to 6.4 seeds per pod. These results support the hypothesis that low seeding rates promote better resource allocation per plant, thus enabling more efficient pod filling and seed development. The 1000-seed weight was significantly influenced by variety, seeding rate, and their interaction ( $P < 0.001$ ). The maximum seed weights were observed in Lada (6.8 g) and Grant (6.7 g) at 10 plants/m<sup>2</sup>, both statistically higher than their counterparts at the higher density. Conversely, the lowest values were recorded in UF1 and Grant at 23 plants/m<sup>2</sup> (5.1g). This reduction in seed weight at higher plant densities reflects reduced assimilate partitioning to individual seeds due to competition stress, which limits seed filling. The significant interaction effect suggests that some genotypes are more resilient to density stress, maintaining higher seed weight even under increased plant populations. These results corroborate earlier findings by Arslanoglu et al. (2022), Saroha et al. (2023) and Kaur et al. (2024).

While the number of productive stems per plant was not significantly affected by variety ( $P > 0.05$ ), it was significantly influenced by seeding rate ( $P < 0.05$ ) and its interaction with variety ( $P < 0.05$ ). The highest number of productive stems was recorded in Talar (37.4) and UF1 (37.3) at the lower seeding rate. In contrast, the lowest stem numbers were observed at 23 plants/m<sup>2</sup>, particularly in UF1 (30.7) and Lada (31.7). The significant interaction indicates that stem productivity response to seeding rate is genotype-specific, emphasizing the importance of varietal selection in optimizing stand density. Productivity was significantly affected by variety ( $P < 0.05$ ), seeding rate ( $P < 0.05$ ), and their interaction ( $P < 0.05$ ). The highest productivity ( $0.60 \text{ t ha}^{-1}$ ) was recorded in Talar, Lada, and UF1 at a seeding rate of 10 plants/m<sup>2</sup>. These values were significantly higher than those observed at the higher seeding rate (23 plants/m<sup>2</sup>), where productivity declined across all varieties. Productivity of Talar decreased from 0.60 to  $0.52 \text{ t ha}^{-1}$ , Lada from 6.0 to  $0.49 \text{ t ha}^{-1}$ , and UF1 from 0.60 to  $0.49 \text{ t ha}^{-1}$ . Similarly, Grant recorded  $0.52 \text{ t ha}^{-1}$  at 10 plants/m<sup>2</sup> and  $0.48 \text{ t ha}^{-1}$  at 23 plants/m<sup>2</sup>.

This consistent reduction in productivity with increasing seeding density is likely attributed to enhanced intra-specific competition for essential resources such as light, nutrients, and soil moisture. These findings align with the reports of Arslanoglu et al. (2022) and Ethridge et al. (2022), who observed that higher plant density restricts the capacity of individual flax plants to develop fully, thereby reducing yield components and final productivity. To achieve maximum yield, it is imperative to consider varietal characteristics and optimize the seeding rate in accordance with specific agrotechnical conditions. The oil and protein content of flax seeds was significantly affected by both

varietal differences and seeding rate, as well as their interaction, as confirmed by statistical analysis. The highest oil content across all treatments was recorded in the TALAR variety at a seeding rate of 23 plants/m<sup>2</sup>, reaching 41.14%, a value significantly higher than that of other combinations. Notably, LADA at 10 plants/m<sup>2</sup> and GRANT at 10 plants/m<sup>2</sup> also showed high oil levels of 40.80% and 40.22%, respectively. This highlights the genotype-specific nature of oil accumulation and the potential for certain varieties to maintain or even increase oil content under higher densities, as seen in Talar.

**Table 3:** Oil and protein content in flax seeds of different varieties at different seeding rates

Variety	Seeding rate ( $\times 10^6$ seeds ha <sup>-1</sup> )	Oils	Protein
TALAR	10	39.91 $\pm$ 1.5ab	18.24 $\pm$ 1.1ab
	23	41.14 $\pm$ 0.9a	19.08 $\pm$ 0.7a
GRANT	10	40.22 $\pm$ 1.6ab	18.71 $\pm$ 1.0ab
	23	40.25 $\pm$ 1.2ab	18.67 $\pm$ 0.8ab
LADA	10	40.80 $\pm$ 1.4b	18.69 $\pm$ 0.9ab
	23	38.48 $\pm$ 1.1b	18.22 $\pm$ 0.5ab
UF1	10	38.87 $\pm$ 1.6b	17.76 $\pm$ 0.8b
	23	39.92 $\pm$ 1.0ab	18.36 $\pm$ 0.5ab
Variety (V)		ns	ns
Seeding rate (S)		ns	ns
V $\times$ S		ns	ns

Values are means  $\pm$  standard deviation ( $n = 3$ ). Within each column, means followed by different lowercase letters differ significantly at  $P < 0.05$  according to Tukey's HSD test. Variety (V), seeding rate (S), and their interaction (V  $\times$  S) were tested using two-way ANOVA. "\*\*\*" and "ns" indicate, respectively, highly significant ( $P < 0.01$ ) and non-significant ( $P \geq 0.05$ ) effects.

A marked decline in oil content was observed with increased seeding rate in certain genotypes (Table 3). In the LADA variety, oil content dropped significantly from 40.80% at 10 plants/m<sup>2</sup> to 38.48% at 23 plants/m<sup>2</sup>, illustrating a sensitivity to higher plant density. These findings support previous reports from Canada and the United States, where increased planting densities resulted in reduced oil accumulation in flax seeds due to intensified competition for photosynthetically active radiation and soil nutrients. In Canadian research, oil content in flax seeds typically ranges between 38 and 42%, consistent with the values obtained in this study (Gubbels & Kenaschuk, 1989). This reduction in oil content in varieties like LADA under higher densities can be attributed to increased intra-specific competition for vital resources such as light and soil nutrients. Under crowded conditions, individual plants allocate more resources towards vertical growth to compete for sunlight, as evidenced by the general increase in plant height with higher seeding rates. This competitive struggle for light and nutrients ultimately impacts the plant's ability to produce and partition assimilates effectively for oil synthesis in the seeds. While direct evidence linking light competition specifically to reduced oil accumulation in flax was not explicitly identified in recent external literature, studies on other oilseed crops, such as oilseed rape, demonstrate that plant population density and nitrogen supply significantly influence leaf nitrogen distribution and carbon partitioning (Labra et al., 2020). These physiological adjustments can impact on the overall photosynthetic capacity and resource allocation efficiency, which are critical for seed oil production.

**Table 4:** Photosynthetic and net productivity of photosynthesis of different varieties of flax depending on the seeding rate

Variety	Seeding rate ( $\times 10^6$ seeds ha <sup>-1</sup> )	Photosynthetic Productivity (PP) in thousands of m <sup>2</sup> /ha/day	Net Photosynthetic Productivity (NPP) in g/m <sup>2</sup> ·day
TALAR	10	1060.7 $\pm$ 1.3c	4.23 $\pm$ 0.0a
	23	1061.7 $\pm$ 1.5c	4.20 $\pm$ 0.0a
GRANT	10	1446.2 $\pm$ 1.2b	1.74 $\pm$ 0.1d
	23	1446.0 $\pm$ 1.6b	1.76 $\pm$ 0.0d
LADA	10	1554.0 $\pm$ 2.3a	3.17 $\pm$ 0.0b
	23	1553.2 $\pm$ 1.1a	3.11 $\pm$ 0.1b
UF1	10	963.99 $\pm$ 2.7d	2.48 $\pm$ 0.1c
	23	961.00 $\pm$ 1.9e	2.52 $\pm$ 0.2c
Variety (V)		**	**
Seeding rate (S)		ns	ns
V $\times$ S		**	ns

Values are means  $\pm$  standard deviation (n = 3). Within each column, means followed by different lowercase letters differ significantly at P<0.05 according to Tukey's HSD test. Variety (V), seeding rate (S), and their interaction (V  $\times$  S) were tested using two-way ANOVA. "\*" and "ns" indicate, respectively, highly significant (P<0.01) and non-significant (P $\geq$ 0.05) effects

The negative impact of increased plant density on individual plant yield components was evident across varieties. The 1000-seed weight, a crucial indicator of seed filling, was significantly reduced at higher plant densities for Lada, Grant, and UF1. This decline reflects reduced assimilate partitioning to individual seeds due to competition stress, which limits seed filling. This phenomenon is a direct consequence of altered source-sink relationships. In dense stands, the increased number of competing sinks (seeds) per unit area, coupled with potentially reduced photosynthetic output per plant due to mutual shading and nutrient depletion, leads to an insufficient supply of photo-assimilates to each developing seed. Consequently, seed size and weight are diminished. Research on soybean highlights how assimilate supply during early seed development profoundly influences flower and pod abortion and subsequently affects the potential seed growth rate during the seed filling phase. Low assimilate supply can force plants to adjust by increasing flower/pod abortion and shortening the lag phase to ensure a minimum assimilate per pod/seed (Ali et al., 2022). Although this specific mechanism was observed in soybean, the underlying principle of assimilate competition affecting seed development is widely applicable to other oilseed crops like flax, where seed filling is a critical determinant of final yield and quality.

In contrast to oil content, protein concentration tended to increase with higher seeding rates. In the TALAR variety, protein content increased from 18.24% at 10 plants/m<sup>2</sup> to 19.08% at 23 plants/m<sup>2</sup>, while in UF1, values rose from 17.76% to 18.36% across the same density range. This inverse relationship between oil and protein content may reflect a shift in carbon and nitrogen partitioning, where dense plant stands enhance nitrogen assimilation but reduce the synthesis of carbon-rich compounds like oil. This trade-off between oil and protein synthesis is a well-documented physiological response in many oilseed crops. Under conditions of heightened competition, plants may prioritize nitrogen uptake and protein synthesis, which are essential for structural components and enzyme production, over the energy-intensive process of oil accumulation. Studies on other crops, such as soybean, have shown that nitrogen fertilization can reduce seed oil concentration (Tamagno et al., 2018). Furthermore, optimizing nutrient management, such as phosphorus application, can influence carbon and

nitrogen assimilation, thereby impacting seed yield and quality in flax (Xie et al., 2023). These findings underscore the delicate balance in resource allocation and the need to understand how different environmental factors and management practices modulate this balance in flax.

During the study, the parameters of photosynthetic productivity and net photosynthetic productivity were analyzed across four flax varieties under two seeding rates. Statistical analysis revealed significant differences among flax varieties in terms of both PP and NPP (Table 4). Additionally, a significant interaction between variety and seeding rate was observed, whereas the seeding rate itself did not significantly influence the traits. These results underscore the dominant role of genetic factors in determining productivity, as well as the importance of variety-specific responses to planting density. The highest PP values were recorded in the LADA variety at both seeding rates, significantly exceeding those of other genotypes. GRANT ranked second in PP, followed by TALAR and UF1, the latter showing the lowest PP. These differences reflect variation in the genotypes' capacity for light interception and assimilation. Despite its lower Photosynthetic Productivity, the TALAR variety exhibited the highest NPP at both seeding rates, indicating superior efficiency in converting photosynthates into dry matter. In contrast, GRANT, despite high Photosynthetic Productivity, had the lowest NPP, suggesting higher respiratory losses or reduced carbon allocation to structural biomass. UF1 showed intermediate NPP values, while LADA ranked second in NPP. The observed inverse relationship between PP and NPP in some genotypes highlights the need to evaluate both total photosynthetic output and the efficiency of assimilate use when selecting for high-yielding flax varieties. These findings suggest that TALAR and LADA hold promise for breeding programs aimed at improving both photosynthetic performance and biomass productivity under varying seeding conditions.

The pronounced genotype-specific responses observed in this study emphasize the critical role of genetic factors and their interaction with environmental conditions and agronomic practices. Our results align with recent multi-environment studies on flax, which consistently highlight the significant influence of both genetic and environmental factors on seed yield, oil content, and fatty acid composition (Čeh et al., 2020; Kaur et al., 2024). For example, a comprehensive evaluation of

thousands of linseed accessions across multiple environments in India revealed a wide range of variability in oil content (from 30.14 to 45.96%), underscoring the strong genetic control over this trait and its plasticity across different growing conditions (Kaur et al., 2024). Similarly, research in Kazakhstan emphasizes the necessity of understanding how diverse flax varieties respond to various growth conditions to optimize oil and fiber quality (Yelnazarkyzy et al., 2024). This underscores the importance of conducting ecological variety testing in specific climatic zones to identify locally adapted genotypes, as highlighted by Kazakhstan's leading role in oilseed flax production and ongoing breeding efforts (Kassenov, 2025). The concept of genotype-by-environment interaction is further supported by studies on similar oilseed crops like *Camelina*, which demonstrate that GxE effects significantly shape seed oil composition and content, highlighting the environmental plasticity of these traits (Brock et al., 2020). Therefore, optimal seeding rates and management strategies are inherently genotype-specific and must be tailored to local agro-ecological conditions to maximize both yield and quality.

A key limitation of the current study is its focus on a single site and two growing seasons (2023–2024). While providing valuable insights for this specific continental climate, the findings may not be universally applicable without further validation across diverse environments. Multi-environment trials are crucial for identifying stable genotypes and robust agronomic practices that perform consistently under varying climatic and soil conditions (Lambrecht et al., 2023). The influence of environmental factors such as temperature, precipitation, and soil type can significantly alter plant growth and resource allocation, leading to different optimal seeding rates and varietal performances in other regions. For instance, studies examining the impact of genotype and location on seed yield and oil composition in linseed indicate that environmental conditions play a substantial role in shaping the final product quality (Čeh et al., 2020). Similarly, the quality of oil and fiber in various flax varieties is significantly influenced by growth conditions (Yelnazarkyzy et al., 2024). Therefore, while our study provides a foundational understanding for Northern Kazakhstan, its generalizability is enhanced when corroborated by similar research conducted across a broader range of environmental contexts. Future research should aim to expand the geographical and temporal scope of such studies to develop more generalized recommendations for flax cultivation.

The study contributes to a better understanding of the factors influencing flax productivity and provides recommendations for optimizing agronomic practices to maximize yield and product quality.

## Conclusion

This study offers valuable insights into the genotype-specific responses of flax varieties to varying seeding densities within the sharply continental climate of Northern Kazakhstan, underscoring the critical interplay among genetics, agronomic practices, and environmental

conditions. Our findings indicate that while photosynthetic potential and net photosynthetic productivity are largely variety-specific and exhibit less sensitivity to changes in seeding rate, other crucial yield components and seed quality attributes, such as oil and protein content, are significantly influenced by the interaction between variety and seeding density. For maximizing overall productivity and yield, our research showed that the Talar, Lada, and UF1 varieties consistently achieved their highest productivity at a lower seeding rate of 10 million pcs/ha. Specifically, Talar and Lada both yielded  $0.60\text{t ha}^{-1}$ , and UF1 also reached  $0.60\text{t ha}^{-1}$  under this density. This suggests that a lower plant population allows for superior resource allocation to individual plants, thereby fostering higher individual yield components like seed number per pod and 1000-seed weight. The Grant variety also showed slightly higher productivity at 10 million pcs/ha, yielding  $0.52\text{ t ha}^{-1}$ , although its overall productivity remained lower than that of the other tested varieties. Optimizing seed quality, particularly oil and protein content, revealed more complex and genotype-dependent responses. The TALAR variety achieved its highest oil content of 41.14% and protein content of 19.08% at the higher seeding rate of 23 million pcs/ha. This indicates Talar's capacity to maintain or even enhance quality under increased planting density. In contrast, the LADA variety exhibited its highest oil content of 40.80% at the lower seeding rate of 10million pcs/ha, with a notable decrease at the higher seeding rate of 23million pcs/ha, indicating its sensitivity to higher densities. Its protein content was also marginally higher at the lower density. The GRANT variety showed relatively stable oil content (approximately 40.2%) and protein content (around 18.7%) across both seeding rates, suggesting it is less responsive to density variations in these quality traits. Similarly, the UF1 variety experienced an increase in both oil content (39.92%) and protein content (18.36%) at the higher seeding rate of 23 million pcs/ha, a response similar to Talar. Regarding photosynthetic efficiency, the LADA variety consistently recorded the highest Photosynthetic Productivity values at both seeding rates, reaching  $1554.0 \pm 2.3$  at 10 million pcs/ha and  $1553.2 \pm 1.1$  at 23 million pcs/ha. This highlights Lada's superior capability in light interception and assimilation. Despite having lower Photosynthetic Productivity, the TALAR variety displayed the highest Net Photosynthetic Productivity at both seeding rates ( $4.23 \pm 0.0$  at 10 million pcs/ha and  $4.20 \pm 0.0$  at 23million pcs/ha). This indicates Talar's exceptional efficiency in converting photosynthates into dry matter. These findings suggest that both Talar and Lada hold significant promise for breeding programs focused on improving photosynthetic performance and biomass productivity. The study confirmed that varietal characteristics are a decisive factor in flax productivity under continental climatic conditions. While the seeding rate did not significantly impact photosynthetic potential and net photosynthetic production, a notable interaction between variety and seeding rate was observed for overall productivity and seed quality traits, further emphasizing the genotype-specific nature of optimal planting densities. To optimize

crop performance, resource efficiency, and the quality of flax production in similar sharply continental climates, growers should carefully consider the specific characteristics and intended use of each flax variety. For maximizing seed yield, a lower seeding rate of approximately 10 million pcs/ha is generally recommended for varieties such as Talar, Lada, and UF1. However, if the primary objective is to achieve higher oil and protein content, particularly for varieties like Talar and UF1, a higher seeding rate of approximately 23 million pcs/ha might prove more beneficial. For the Lada variety, maintaining oil content optimization would still favor the lower density. These genotype-specific recommendations allow for more precise and effective agronomic management, moving beyond generalized seeding guidelines and enabling tailored cultivation strategies.

## DECLARATIONS

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**Author's Contribution:** RY: Supervision, Conceptualization, experimental design, data collection, statistical analysis, manuscript drafting, review and editing. GS: methodology development, data interpretation, manuscript review and editing. All authors have read and approved the final manuscript.

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