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Analysis of Population Productivity Differences Among Tibetan Hulless Barley Varieties Under Fertilizer-Density Interactions

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Abstract: Addressing the critical constraints of low tillering survival rate and population productivity on yield improvement in hulless barley (Hordeum vulgare L. var. nudum) within the Qinghai-Tibet Plateau region, this study employed a two-factor split-plot design (4 fertilizer levels×3 planting densities×2 varieties) to systematically analyze the regulatory mechanisms of fertilizer-density interactions on tillering dynamics and population productivity. The results indicated that the jointing stage is the key period for tiller regulation. Path analysis revealed for the first time that the IAA (Indole-3-acetic acid)/ZT (Zeatin) ratio exerted the strongest direct effect on tiller number (path coefficient = 0.443). The FC3 treatment (N 75 kg/ha + P_2O_5 150 kg/ha) significantly promoted tillering, but hormonal responses differed markedly between varieties: High fertilizer (FC4) strongly induced ZT synthesis in Kunlun 14. Kunlun 15 maintained high IAA stability under FC3. Significant diminishing marginal returns were observed for nitrogen and phosphorus utilization. Kunlun 14 achieved peak nitrogen use efficiency (27.71%) and maximum yield (7808 kg/ha) under medium density (MD) combined with FC3. Kunlun 15 attained optimal nitrogen efficiency (24.26%) and high yield (7165 kg/ha) under low density (LD) with FC2, while excessive fertilization under high density resulted in negative agronomic efficiency. Optimization pathways for population structure revealed: Yield exhibited a highly significant positive correlation with seed setting rate (r = 0.962) and grain weight per spike, but a trade-off existed between effective panicle number and 1000-grain weight (r=-0.218*). For Kunlun 14, MD-FC3 synergistically increased panicle number and grain weight. For Kunlun 15, LD-FC2 expanded panicle number, whereas high density reduced grain weight per spike by 13.9% due to ZT/IAA imbalance. These findings elucidate fertilizer and density management strategies for enhancing tillering, panicle formation, and high-yield population structure establishment in hulless barley, providing both theoretical and practical foundations for rational tiller utilization and high-yield cultivation.**

Keywords: Tibetan hulless barley; Tillering dynamics; Fertilizer use efficiency; Population productivity

1 INTRODUCTION

Tibetan hulless barley (Hordeum vulgare Linn. var. nudum Hook. f.), as one of the primary grain-forage crops on the Qinghai-Tibet Plateau [1], plays an irreplaceable strategic role in regional food security. Over 60% of its yield supports staple food for Tibetan communities, while more than 35% is utilized for animal husbandry. However, the current average yield is over 30% lower than that of other cereal crops in China. The core bottlenecks limiting yield are the low survival rate of tillers and an imbalanced population structure [2].

Tillering is a crucial agronomic trait determining yield in gramineous crops [3-4]. The number of tillers formed and their survival rate directly influence the quality of the population structure. Regulating tillering to optimize population structure is therefore a vital step for achieving high yields [5-7]. The tillering capacity of a crop is primarily determined by its genotype but is also influenced by temperature [8], water, light [9], and cultivation management practices [10]. Among these, cultivation management practices exert significant regulatory

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effects on tiller initiation and survival, with sowing density and fertilization measures having particularly pronounced impacts [11-12]. Previous studies indicate that optimal planting density and fertilization rates are key techniques for regulating crop tillering [13-14]. An appropriate planting density can effectively utilize light energy and soil resources, ensuring normal individual plant development and coordinated population growth. This coordination unifies population dry matter accumulation, tillering, panicles per unit area, grains per spike, and 1000-grain weight, ultimately leading to high yield [15]. Rational fertilization can significantly improve the plant's internal nutrient metabolism and endogenous hormone levels, effectively promoting population growth—especially tiller initiation—resulting in a more rational population structure [16].

Nitrogen is an essential plant nutrient and a key component of proteins and amino acids [17]. Studies on barley by Li Jinyong et al [18]. demonstrated that the judicious application of fertilizer at the jointing-booting stage is a crucial measure for increasing yield and securing a successful harvest. Furthermore, research indicates that phosphorus fertilizer enhances tiller quantity in cereal crops and accelerates grain filling [19-20], making phosphorus a significant factor influencing wheat tillering. Appropriate increases in phosphorus application can promote tiller initiation and improve the survival rate of tillers in wheat [21].

Crop population productivity is closely related to crop growth, development, and cultivation management [22]. Sound fertilization and cultivation practices promote healthy crop growth and high yields, while poor practices can hinder development and reduce yield. Reasonably increasing planting density, coupled with nitrogen fertilizer application to mediate the conflict between individual plants and the population [23-24], can enhance both individual plant and population dry matter accumulation, increase grains per spike, and consequently lead to higher yields, effective tiller numbers, and nitrogen use efficiency [25-28].

Given the current lack of clarity regarding the regulatory roles and physiological characteristics of tiller survival and population productivity in Tibetan hulless barley varieties within China's Qinghai-Tibet Plateau region, this study selected different Tibetan hulless barley varieties as experimental materials. By investigating the interactive effects of varying planting densities and fertilizer combinations on Tibetan hulless barley tillering dynamics and population structure, the research aims to reveal the relationship between tiller initiation/survival and population productivity. It further seeks to identify fertilizer and density management strategies that promote tillering, increase panicle number, and establish high-yield population structures. The findings are expected to provide both theoretical and practical foundations for the rational utilization of tillering and high-yield cultivation practices in Tibetan hulless barley.

2 MATERIALS AND METHODS

2.1 EXPERIMENTAL MATERIALS

The tested Tibetan hulless barley varieties were Kunlun 14 [29] and Kunlun 15 [30], provided by the Tibetan hulless barley Research Laboratory, Institute of Crop Cultivation and Breeding, Academy of Agriculture and Forestry Sciences, Qinghai University.

Kunlun 14: A dual-purpose high-yielding grain and forage variety. Plant height: 109.53 ± 2.25 cm; Flag leaf length: 21.05 ± 0.38 cm; Leaf color: green; Leaf posture: drooping; Length of the first basal internode on the main stem: 2.73 ± 0.07 cm; Peduncle length: 38.55 ± 2.03 cm; Average tillers per plant: 2.20 ± 1.30; Spike posture: curved and drooping; Yield potential: 300–400 kg per mu (equivalent to 4500–6000 kg/ha); Good lodging resistance; Moderately resistant to barley stripe disease.

Kunlun 15: A high-yielding grain variety. Plant height: 87.65 ± 3.45 cm; Flag leaf length: 11.23 ± 0.22 cm; Leaf color: green; Leaf posture: erect; Length of the first basal internode on the main stem: 2.73 ± 0.07 cm; Peduncle length: 18.75 ± 1.77 cm; Average tillers per plant: 2.70 ± 1.42; Yield potential: 400–500 kg per mu (equivalent to 6000–7500 kg/ha); Lodging resistant; Strong disease resistance (to barley stripe disease and scald).

2.2 EXPERIMENTAL SITE DESCRIPTION

A fixed-site field experiment was conducted during the 2023 and 2024 growing seasons at the Germplasm Resource Innovation Experimental Base of the Academy of Agriculture and Forestry Sciences, located in Ershilipu Town, Xining City, Qinghai Province, China (Approx. 36°62'N, 101°77'E - Note: Coordinates likely represent 36.62°N, 101.77°E as minutes cannot exceed 59). The site is situated in the Huangshui River Basin irrigation area of eastern Qinghai Province, at an altitude of 2309.00 m. The soil type is classified as Kastanozem (Chestnut soil), with a bulk density of 1.50 g/cm^3 and a field water holding capacity of 15.20%. The topsoil (0-20 cm) had an organic matter content of 22.49 $g\ kg^{-1}$, total nitrogen content of 1.78 $g\ kg^{-1}$, and available phosphorus content of 37.48 $mg\ kg^{-1}$ (Table 1). To mitigate the adverse effect of spring drought on poor barley emergence, the experimental field received full irrigation before the topsoil froze after the autumn harvest (early November). The soil remained frozen during winter (mid-November to early March of the following year). Sowing was performed on the frozen soil surface during early spring (late March to early April). To simulate typical Tibetan hulless barley growing conditions, no supplemental irrigation was applied during the entire growing season. During the 2023 Tibetan hulless barley growing season (April to August), monthly rainfall was 295.6 mm, 321.6 mm, and 376.2 mm, respectively, with average temperatures of 14.7°C, 14.3°C, and 15.1°C, respectively. The baseline nutrient status of the 0–20 cm soil layer is presented in Table 1.

TABLE 1 BASIC PHYSICAL AND CHEMICAL PROPERTIES OF THE SOILS (0-20 CM SOIL LAYER) BEFORE SOWING

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Year	Organic matter/ (g·kg-1)	Total nitrogen /(g.kg-1)	Total phosphorus /(g·kg-1)	Total potassium /(g·kg-1)	Available nitrogen /(mg·kg-1)		Available phosphorus /(mg·kg-1)	Available potassium/(mg·kg -1)	pH
2023	13.02 ± 0.28	1.13 ± 0.01	1.50 ± 0.02	19.76 ± 0.25	72.96 ± 1.16		75.58 ± 1.93	313.0±3.74	8.48 ± 0.06
2024	20.34±0.09	1.01±0.03	1.27±0.03	23.80±0.12	43.63±5.12		22.96±4.12	179.33±21.63	8.21±0.03

2.3 EXPERIMENTAL DESIGN

The field experiment employed a two-factor split-plot design. Main Plots: Fertilization combinations (FC). Fertilizers used were urea [ω(N) = 46%] and diammonium phosphate (DAP) [ω(N) = 18%, ω(P_2O_5) = 46%]. Four FC levels were established based on conventional production practices: FC1 (CK): Control (No fertilizer), FC2 (Low fertilizer): Urea 37.5 kg/ha + DAP 75.0 kg/ha, FC3 (Production fertilizer): Urea 75.0 kg/ha + DAP 150.0 kg/ha, FC4 (Excessive fertilizer): Urea 150.0 kg/ha + DAP 300.0 kg/ha. Sub-Plots: Planting density. Three levels were established:

Low density (LD): Seeding rate 225 kg/ha, target seedlings established 2.80 million/ha, Medium density (MD): Seeding rate 262.5 kg/ha, target seedlings established 3.15 million/ha. High density (HD): Seeding rate 300 kg/ha, target seedlings established 3.60 million/ha.

This design resulted in 24 treatment combinations (4 FC × 3 Densities). The experiment was arranged in a randomized complete block design (RCBD) with three replications, totaling 72 experimental plots. Each plot measured 3 m in length. Sowing was performed with uniform row spacing of 0.20 m. Each plot contained 10 rows.

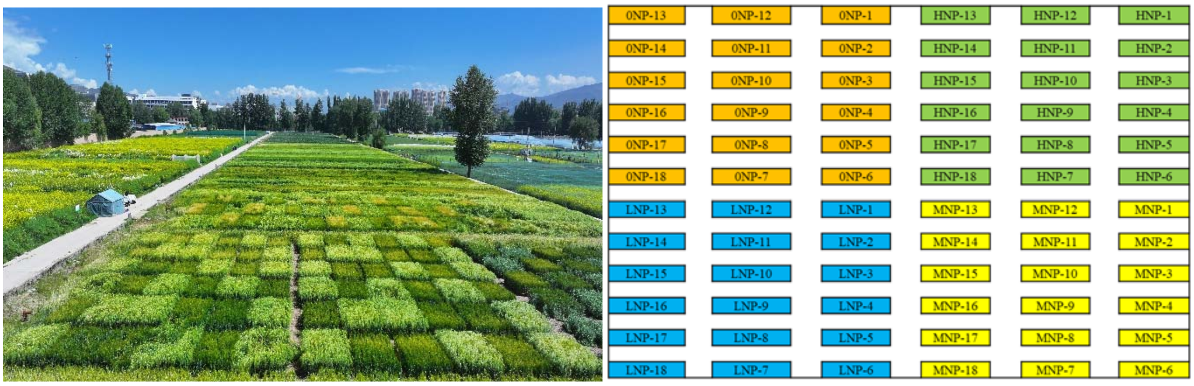

FIG. 1 EXPERIMENTAL DESIGN OF THE TEST SITE AND FRACTURE ZONE

Note: In figures: Orange = No fertilizer (FC1), Green = Low fertilizer (FC2), Blue = Production fertilizer (FC3), Yellow = Excessive fertilizer (FC4).

2.4 MEASUREMENTS AND M THODS

2.4.1 TILLER DYNAMIC MONITORING

Within each plot, a uniform plant growth area (0.5 m of two adjacent rows) was marked with stakes. Tiller counts were recorded every 5 days before the jointing stage, every 7 days after jointing, and once at maturity.

2.4.2 DETERMINATION OF PLANT ENDOGENOUS HORMONES

Samples were collected at the peak tillering stage. Fresh samples were taken from the tillering nodes, immediately frozen in liquid nitrogen, and stored at -80°C. The contents of auxin (IAA, Indole-3-acetic acid) and zeatin (ZT) were determined using High-Performance Liquid Chromatography (HPLC) [31]. Each sample was analyzed in triplicate, and the mean value was calculated.

2.4.3 DETERMINATION OF PLANT AND SOIL NITROGEN CONTENT

Soil samples (0–20 cm depth) and aboveground plant parts (3 plants per plot) were collected during the tillering, flowering, and maturity stages. All samples were blanched at 105°C for 0.5 hours and then dried to a constant weight at 80°C. Plant samples were ground using a plant mill. Soil samples were ground and passed through a 40-mesh sieve. All processed samples were stored in sealed bags for subsequent analysis. Nitrogen content in plants and soil was determined using a

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Kjeldahl nitrogen analyzer [32]. The following nitrogen use efficiency indices were calculated [33-35]:

Nitrogen Partial Factor Productivity (PFP, kg kg^{-1}): PFP = Yield of N-fertilized plot / N application rate, Nitrogen Agronomic Efficiency (AE, kg kg^{-1}): AE = (Yield of N-fertilized plot - Yield of control plot (FC1)) / N application rate, Nitrogen Recovery Efficiency (RE, %): RE = [(Total N uptake in fertilized plot) - (Total N uptake in control plot (FC1))] / N application rate × 100%.

2.4.4 *Investigation Of Population Structure And Yield Components*

A fixed quadrat (0.5 m × 0.5 m = 0.25 m²) was established within a uniform plant growth area in each plot. The initial seedling count and panicle number were surveyed at the 3-leaf stage, jointing stage, and heading stage. At maturity, 10 random plants per plot were selected to determine: tillers per plant, effective panicles per plant, grains per panicle, grain weight per plant, and 1000-grain weight. The entire plot was harvested at maturity to determine plot yield. All measurements were performed in triplicate, and the mean value was used.

2.5 *Data Processing And Analysis*

Experimental data are presented as means. Data processing and statistical analysis were performed using Microsoft Excel 2010 and SPSS 26.2 (IBM Corp., Armonk, NY, USA). Graphs were generated using Origin 2023 (OriginLab, Northampton, MA, USA).

3 Results Analysis

3.1 *Interactive Effects Of Fertilization And Planting Density On Tillering Dynamics Of Tibetan Hulless Barley (Qingke)*

Field trials conducted over two years demonstrated that the number of tillers per plant of Tibetan hulless barley cultivar Kunlun 14 exhibited an initial increase followed by a subsequent decrease throughout its growth stages (Fig. 2 and 4). At the initial and peak tillering stages, the interactive effects of planting density and fertilization did not yield statistically significant differences in tiller number. However, at the jointing stage (ES), significant differences emerged among fertilizer treatments. The FC3 treatment (application of 75.0 kg/ha urea and 150.0 kg/ha diammonium phosphate) resulted in the highest tiller count, with planting density showing no significant influence at this stage. These findings indicate that the jointing stage is the critical period for promoting tiller survival and panicle formation, and that the FC3 fertilizer rate represents the optimal application level under the conditions of this study.

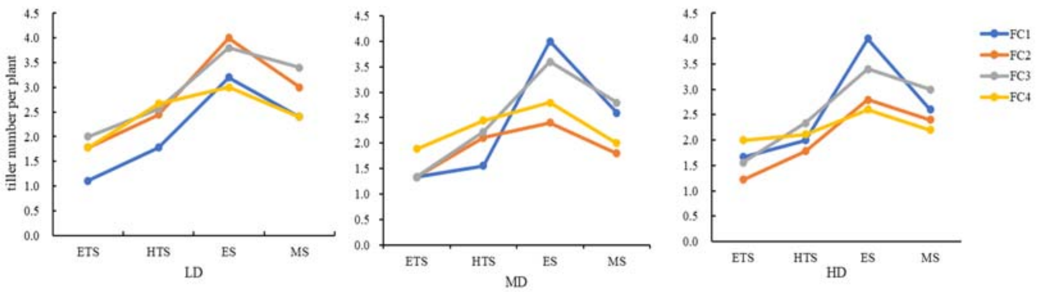

Fig. 2. Effect Of Different Fertilizer Application And Sowing Rates On Tiller Number At Different Fertility Stages Of Kunlun 14

Note: ETS, HTS, ES and MS in the figure represent the early tillering stage, full tillering stage, nodulation stage and maturity stage of barley, respectively, and LD, MD and HD represent low-density, medium-density and high-density planting, respectively, the same below.

As shown in Fig. 3, the dynamics of tiller number per plant in Tibetan hulless barley cultivar Kunlun 15 varied significantly across different growth stages. During the initial and peak tillering stages, tiller number declined under all four fertilizer treatments. Notably, the FC1 treatment (no fertilizer application) resulted in the highest tiller count under the interaction of fertilizer and planting density during these early stages, suggesting that the soil's inherent nutrient levels were sufficient to meet the requirements for initial tiller development. At the jointing and maturity stages, however, tiller number initially increased and then decreased across all fertilizer treatments. Furthermore, the highest tiller numbers at both stages were consistently observed in the FC3 treatment (75.0 kg/ha urea and 150.0 kg/ha diammonium phosphate) across all three planting densities (Fig. 4). Collectively, these results demonstrate that the FC3 treatment was optimal for promoting tiller survival, panicle formation, and maintenance in Kunlun 15.

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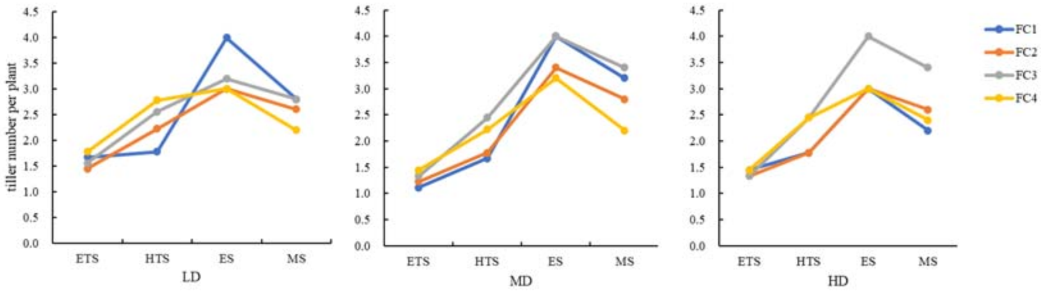

FIG. 3 EFFECT OF DIFFERENT FERTILIZER APPLICATION AND SOWING RATES ON TILLER NUMBER AT DIFFERENT FERTILITY STAGES OF KUNLUN 15

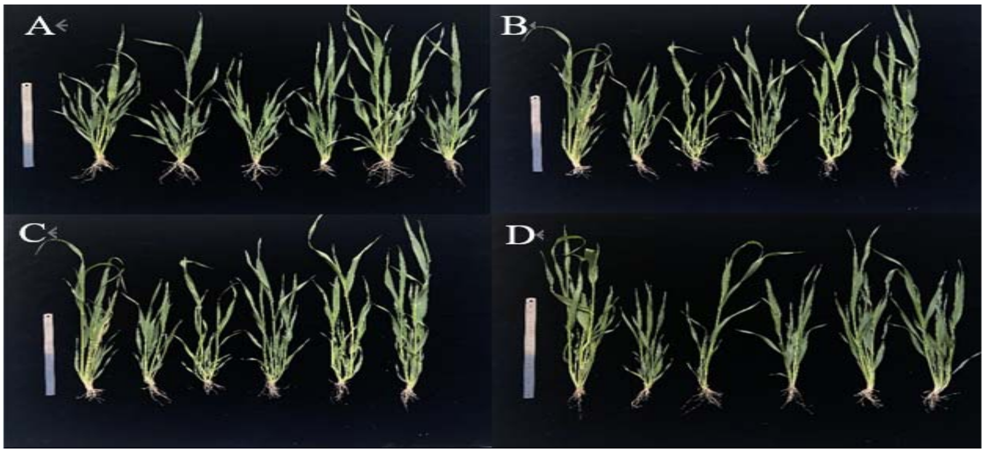

FIG. 4 FIELD DYNAMICS OF DIFFERENT FERTILIZER DENSITY COMBINATIONS ON BARLEY AT NODULATION STAGE

Note: As shown in Fig. 4, A, B, C and D represent the graphs of tiller dynamics at the nodulation stage of Kunlun 14 and 15 under the four fertilizer treatments of FC1, FC2, FC3 and FC4, respectively, from left to right sowing densities and varieties are KL14 (HD), KL15 (LD), KL14 (MD), KL15 (MD), KL14 (LD), and KL15 (HD)

3.2 *INTERACTIVE EFFECTS OF FERTILIZATION AND PLANTING DENSITY ON ENDOGENOUS HORMONES ASSOCIATED WITH TILLERING*

Plant endogenous hormones serve as critical signaling molecules governing plant growth and development, exerting vital physiological functions. During tiller differentiation in Tibetan hulless barley (Hordeum vulgare L. var. nudum Hook. f.), the contents of auxin (IAA), zeatin (ZT), and abscisic acid (ABA) in the young panicle play pivotal roles in tiller survival and panicle formation.

The results (Fig. 5) revealed that for cultivar Kunlun 14, ZT content was highest under the FC4 fertilizer treatment across all three planting densities. Regarding IAA content:Under the low-density (LD, 225.0 kg/ha) condition, the highest IAA content was observed with the FC2 treatment. Under the medium-density (MD) condition, the highest IAA content occurred with the FC4 treatment. Under the high-density (HD) condition, the FC3 treatment resulted in the highest IAA content. For cultivar Kunlun 15 (Fig. 6), ZT content peaked under the FC4 fertilizer treatment, regardless of planting density (LD, MD, or HD). Similarly, IAA content was highest under the FC3 fertilizer treatment across all three planting densities (LD, MD, and HD).

These findings indicate that the high-nitrogen-phosphorus FC4 fertilizer strongly stimulated ZT synthesis in both Tibetan hulless barley cultivars. In contrast, the optimal fertilizer treatment for maximizing IAA content in Kunlun 14 varied considerably with planting density, indicating complex regulation. Kunlun 15, however, exhibited a stable and favorable response to the moderate nitrogen-phosphorus FC3 fertilizer, achieving consistently higher IAA levels under different densities, which suggests superior environmental adaptability. This differential hormonal response provides a crucial physiological basis for developing variety-specific density and fertilization management strategies.

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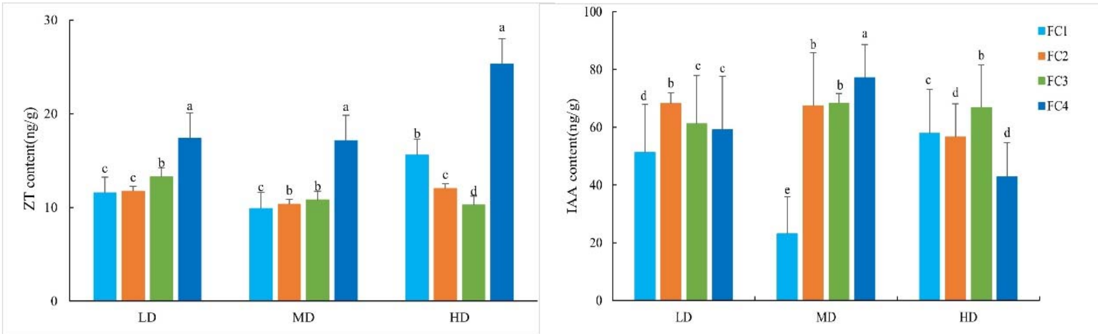

FIG. 5 EFFECTS OF FERTILIZER-DENSITY INTERACTIONS ON THE CHANGES OF ENDOGENOUS HORMONE CONTENTS IN KUNLUN 14

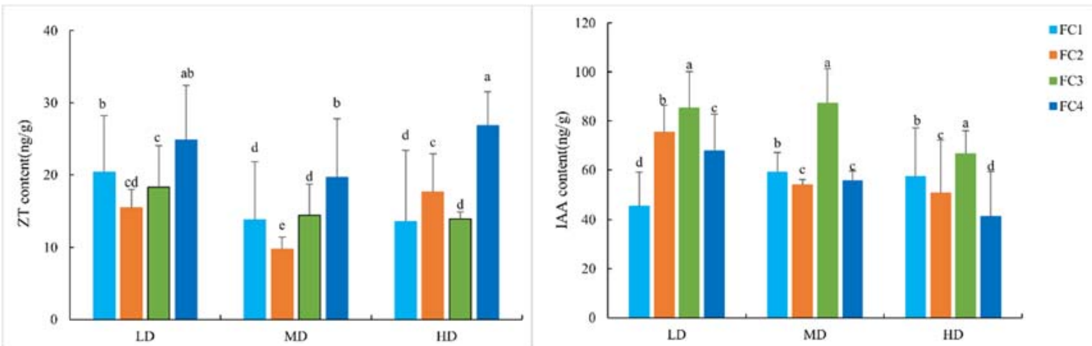

FIG. 6 EFFECTS OF FERTILIZER-DENSITY INTERACTIONS ON THE CHANGES OF ENDOGENOUS HORMONE CONTENTS IN KUNLUN 15

Path analysis results for tiller number in Tibetan hulless barley under different nitrogen fertilizer treatments, in relation to IAA, ZT, and the IAA/ZT ratio, are presented in Table 3.1. The relative importance of the influencing factors on tiller number, as determined by their correlation coefficients (which encompass both direct and indirect effects), was ranked as follows: ZT > IAA/ZT > IAA. The ranking based on the absolute values of the direct path coefficients was: IAA/ZT > ZT > IAA. This indicates that the IAA/ZT ratio exerted the strongest direct effect on tiller number. Furthermore, the primary indirect effect of the IAA/ZT ratio on tiller number was mediated predominantly through its interaction with IAA itself.

TABLE 2 RESULTS OF FLUX ANALYSIS OF BARLEY TILLER NUMBER WITH IAA, ZT, AND IAA/ZT UNDER DIFFERENT NITROGEN FERTILIZER TREATMENTS

Factors	Correlation coefficients	Direct path coefficients	Indirect path coefficients		
			IAA	ZT	IAA/ZT
IAA	-0.141	0.208		-0.011	0.172
ZT	-0.058	0.309	-0.018		-0.183
IAA/ZT	-0.088	0.443	-0.039	-0.262	

3.3 *INTERACTIVE EFFECTS OF FERTILIZATION AND PLANTING DENSITY ON FERTILIZER ABSORPTION AND UTILIZATION IN TIBETAN HULLESS BARLEY*

3.3.1 *Characteristics Of Nitrogen Fertilizer Absorption And Utilization In Different Tibetan Hulless Barley Cultivars*

Under the interactive treatments of different fertilization levels and planting densities, nitrogen uptake in both Tibetan hulless barley cultivars increased in the fertilized treatments compared to the unfertilized control (Tables 3 and 4).For both Kunlun 14 and Kunlun 15: Nitrogen use efficiency (NUE) decreased with increasing fertilizer application under low-density (LD) and medium-density (MD) planting conditions. Conversely, NUE increased with increasing fertilizer application under the high-density (HD) condition.The highest NUE for Kunlun 14 (27.71%) was achieved under the MD-FC3 treatment.The highest NUE for Kunlun 15 (25.93%) occurred under the HD-FC3 treatment.

Additionally: Nitrogen partial factor productivity (PFPN) for both cultivars decreased with increasing fertilizer application. The highest PFPN values for both cultivars were observed under the MD-FC2 treatment (188.14 kg kg^{-1} for Kunlun 14 and 191.09 kg kg^{-1} for Kunlun 15).The highest nitrogen agronomic efficiency (NAE) for Kunlun 14 (14.47 kg kg^{-1}) was found under the HD-FC2 treatment. The highest NAE for Kunlun 15 (10.36 kg kg^{-1}) occurred under the MD-FC2 treatment. Based on the analysis presented in the tables, moderate fertilizer application combined with reduced planting density enhanced nitrogen fertilizer absorption and utilization efficiency in both tested Tibetan hulless barley cultivars.

Table 3 Characteristics Of Nitrogen Fertilizer Utilization Of Kunlun 14 Under Different Fertilizer Density Transport Treatments

Seeding density	Fertilization treatment	Total nitrogen uptake（kg hm-2）	Nitrogen use efficiency（%）	Agronomic efficiency of nitrogen fertilizer（kg kg-1）	Nitrogen fertilizer is more productive（kg kg-1）
LD	FC1	119.89±2.65 d	0	0	0
	FC2	127.94±3.43 c	21.46±1.23 a	7.12±1.21 b	175.95±13.12 a
	FC3	133.69±4.43 b	18.41±0.32 b	12.39±0.12 a	96.81±9.21 b
	FC4	141.52±6.32 a	14.42±0.87 c	2.38±0.08 c	44.59±7.32 c
MD	FC1	128.69±4.32 d	0	0	0
	FC2	137.14±6.54 c	22.53±1.21 b	12.69±1.32 a	188.14±9.12 a
	FC3	149.47±7.54 b	27.71±1.09 a	7.54±0.26 b	90.21±10.21 b
	FC4	159.36±8.65 a	20.44±0.87 c	2.24±0.28 c	45.51±6.34 c
HD	FC1	126.95±6.43 d	0	0	0
	FC2	134.21±6.43 c	19.36±0.32 b	14.47±2.32 a	185.99±18.43 a
	FC3	142.56±8.32 b	20.81±1.32 a	8.76±1.21 b	94.51±9.32 b
	FC4	157.56±9.34 a	20.40±0.91 a	3.19±0.32 c	46.07±7.43 c

Table 4 Characteristics Of Nitrogen Fertilizer Utilization Of Kunlun 15 Under Different Fertilizer Density Transport Treatments

Seeding density	Fertilization treatment	Total nitrogen uptake（kg hm-2）	Nitrogen use efficiency（%）	Agronomic efficiency of nitrogen fertilizer（kg kg-1）	Nitrogen fertilizer is more productive（kg kg-1）
	FC1	121.35±12.21 d	0	0	0

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LD	FC2	130.45±16.21 c	24.26±1.21 a	6.86±1.09 a	189.15±19.21 a
	FC3	138.72±18.22 b	23.16±1.03 a	-0.08±0.06 c	91.06±10.21 b
	FC4	145.38±19.21 a	16.02±1.98 b	0.43±0.98 b	46.01±10.21 c
MD	FC1	120.87±10.21 d	0	0	0
	FC2	129.53±17.21 c	23.09±2.01 a	10.36±1.21 a	191.09±20.21 a
	FC3	137.53±18.31 b	22.21±1.67 a	-3.84±0.34 b	86.52±12.32 b
	FC4	154.67±19.21 a	22.53±1.32 a	-3.53±0.76 b	41.64±9.21 c
HD	FC1	125.14±16.21 d	0	0	0
	FC2	131.29±19.21 c	16.41±1.98 b	8.91±0.06 a	172.13±19.31 a
	FC3	144.59±17.21 b	25.93±2.21 a	1.38±1.21 b	102.99±16.32 b
	FC4	162.34±18.32 a	24.82±1.38 a	-1.19±0.45 c	39.61±12.32 c

3.3.2 Characteristics Of Phosphorus Fertilizer Absorption And Utilization In Different Tibetan Hulless Barley Cultivars

Under the interactive treatments of different planting densities and fertilizer application rates, total phosphorus uptake in both Tibetan hulless barley cultivars increased in the fertilized treatments compared to the unfertilized control (Tables 5 and 6). The highest phosphorus uptake for both Kunlun 14 and Kunlun 15 was observed under the HD-FC4 treatment. Phosphorus use efficiency (PUE) decreased with increasing fertilizer application for both cultivars. The highest PUE for Kunlun 14 (18.37%) occurred under the HD-FC2 treatment. The highest PUE for Kunlun 15 (11.64%) was achieved under the LD-FC2 treatment. Both phosphorus agronomic efficiency (PAE) and phosphorus partial factor productivity (PFPp) decreased with increasing fertilizer application. For Kunlun 14, the highest PAE (7.23 kg kg^{-1}) and PFPp (92.99 kg kg^{-1}) were both observed under the HD-FC2 treatment. For Kunlun 15, the highest PAE (5.18 kg kg^{-1}) and PFPp (95.54 kg kg^{-1}) were both recorded under the MD-FC2 treatment.

Table 5 Characteristics Of Phosphate Fertilizer Utilization Of Kunlun 14 Under Different Fertilizer Intensive Management Treatments

Seeding density	Fertilization treatment	Total phosphorus uptake（kg hm-2）	Phosphate fertilizer use efficiency(%)	Agronomic efficiency of phosphate fertilizers（kg kg-1）	Phosphate fertilizers are more productive（kg kg-1）
LD	FC1	30.21±3.12 d	0	0	0
	FC2	38.38±1.21 c	10.89±0.65 a	3.56±0.32 b	87.97±5.12 a
	FC3	48.11±2.53 b	11.93±0.54 a	6.19±1.12 a	48.40±3.21 b
	FC4	51.46±1.97 a	7.08±0.32 b	1.19±0.65 c	22.29±2.31 c
MD	FC1	41.48±4.32 d	0	0	0
	FC2	54.86±3.21 c	17.84±1.08 a	6.31±0.32 a	92.87±5.32 a

	FC3	59.79±3.02 b	12.21±0.53 b	3.77±0.26 b	47.03±3.22 b
	FC4	63.74±2.12a	7.42±0.86 c	1.11±0.28 c	22.75±2.08 c
HD	FC1	42.57±2.32 d	0	0	0
	FC2	56.35±2.03 c	18.37±1.21 a	7.23±0.65 a	92.99±6.43 a
	FC3	59.88±2.73 b	11.54±1.06 b	4.38±0.05 b	47.26±3.23 b
	FC4	66.18±3.21 a	7.87±0.41 c	1.59±0.12 c	23.04±2.87 c

TABLE 6 CHARACTERISTICS OF PHOSPHATE FERTILIZER UTILIZATION OF KUNLUN 15 UNDER DIFFERENT FERTILIZER INTENSIVE MANAGEMENT TREATMENTS

Seeding density	Fertilization treatment	Total phosphorus uptake（kg hm-2）	Phosphate fertilizer use efficiency（%）	Agronomic efficiency of phosphate fertilizers（kg kg-1）	Phosphate fertilizers are more productive（kg kg-1）
LD	FC1	30.41±2.35 d	0	0	0
	FC2	39.14±3.03 c	11.64±1.03 a	3.43±0.32 a	94.57±7.12 a
	FC3	41.62±3.43 b	7.47±0.32 b	-0.04±0.08 c	45.53±6.01 b
	FC4	43.61±2.82 a	4.40±0.87 c	0.22±0.05 b	23.01±2.31 c
MD	FC1	31.26±2.12 d	0	0	0
	FC2	38.86±3.09 c	10.13±0.32 a	5.18±0.43 a	95.54±6.32 a
	FC3	41.26±4.57 b	6.67±0.49 b	-1.92±0.26 b	42.26±4.22 b
	FC4	46.40±5.65 a	5.05±0.87 c	-1.77±0.08 c	20.82±3.08 c
HD	FC1	35.04±3.53 d	0	0	0
	FC2	42.01±3.48 c	9.29±0.42 a	4.45±0.65 a	86.07±4.43 a
	FC3	46.27±2.76 b	7.49±0.32 b	0.69±0.05 b	41.50±4.39 b
	FC4	51.94±5.37 a	5.63±0.21 c	-0.59±0.02 c	19.81±2..87 c

3.4 *INTERACTIVE EFFECTS OF FERTILIZER RATE AND SOWING DENSITY ON YIELD AND POPULATION PRODUCTIVITY IN HIGHLAND BARLEY*

Fertilizer rate and sowing density significantly influenced both grain yield and its components in the highland barley cultivar ‘Kunlun 14’ (Table. 7). Grain yield was significantly affected by both factors, exhibiting an initial increase followed by a decline across the ranges tested. The highest grain yield under low (LD, 225 kg/ha), medium (MD, 262.5 kg/ha), and high (HD, 300 kg/ha) sowing densities was consistently achieved at the FC3 fertilizer level. Maximum grain yield (7807.79 kg/ha) was recorded under the MD density with FC3 fertilization. All

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fertilizer treatments resulted in significantly higher yields relative to the unfertilized control (FC1). The greatest yield increase (42.06%) occurred under MD density with FC2 fertilization compared to FC1. Without fertilization (FC1), yield showed an initial increase and subsequent decrease with increasing sowing density. In contrast, yield under FC3 fertilization reached its maximum at all three densities tested.

Yield components (panicles per m², productive panicles per m², grain weight per panicle, 1000-grain weight) also displayed an initial increase followed by a decrease in response to increasing fertilizer rate and sowing density. At the same fertilizer level, MD density significantly increased productive panicles per m² and 1000-grain weight by 1.57% and 2.36%, respectively, compared to LD density, but decreased panicles per m² and grain weight per panicle by 3.97% and 2.16%, respectively. HD density significantly increased panicles per m², productive panicles per m² and 1000-grain weight by 9.86%, 0.75% and 2.63%, respectively, compared to LD, while reducing grain weight per panicle by 5.14%. At the same density level, FC2 fertilization significantly enhanced all yield components relative to FC1: panicles per m² (+3.28%), productive panicles per m² (+23.80%), grain weight per panicle (+20.21%), and 1000-grain weight (+5.58%). FC3 fertilization significantly increased productive panicles per m² (+37.5%), grain weight per panicle (+8.48%), and 1000-grain weight (+2.62%) compared to FC1, while panicles per m² showed a minor but significant increase (+0.76%).

These results demonstrate a significant interaction between fertilizer rate and sowing density. Yield optimization required adjusting sowing density according to fertilizer availability: reducing density when fertilizer was limited (FC1, FC2) and increasing density when ample fertilizer (FC3) was applied. The optimal combination for maximizing grain yield in 'Kunlun 14' highland barley was medium sowing density (MD, 262.5 kg/ha) coupled with high fertilizer application (FC3).

TABLE 7 YIELD CHARACTERISTICS OF KUNLUN 14 UNDER DIFFERENT FERTILIZER DENSITY OPERATIONS

Seeding density	Fertilization treatment	Plant height	Number of spikes(106)	Number of effective spikes	Weight of grains per ear	thousand grain weight	yield (kg/hm2)
LD	FC1	115.26±7.03 c	3.77±0.05 c	3.69±0.90 c	3.25±0.16 d	52.33±0.23 d	5389.92±162.47 c
	FC2	114.34±5.78 c	4.27±0.11 b	4.00±1.25 b	3.28±0.16 d	51.83±3.29 d	6509.36±486.17 b
	FC3	110.80±3.11 d	4.06±0.17 c	4.25±0.75 b	3.88±0.37 b	54.15±3.56 c	7246.39±129.76 a
	FC4	121.54±5.83 a	3.51±0.36 d	3.94±1.15 c	4.39±0.46 a	56.93±2.74 b	7238.06±129.77 a
MD	FC1	112.20±6.88 d	3.87±0.19 c	3.06±1.22 d	3.24±0.14 d	53.13±0.44 c	5496.08±441.68 d
	FC2	113.66±5.42 c	3.59±0.07 d	4.63±1.41 a	3.96±0.03 b	56.91±0.99 b	7159.68±182.49 b
	FC3	111.10±4.47 d	3.62±0.19 d	4.75±1.01 a	3.41±0.32 d	52.51±2.05 d	7807.79±542.34 a
	FC4	110.06±3.05 d	3.91±0.08 c	3.69±1.50 c	3.87±0.47 b	57.78±2.59 a	6825.08±352.52 c
HD	FC1	109.84±6.51 d	4.24±0.17 b	3.25±1.14 d	3.06±0.24 d	53.19±1.07 c	5661.72±441.75 d
	FC2	117.52±6.43 b	4.41±0.19 a	3.75±1.89 c	4.24±0.95 a	58.77±0.91 a	6301.48±592.49 c
	FC3	119.42±7.14 b	4.29±0.16 b	4.75±1.49 a	3.07±0.56 d	56.14±1.09 b	7395.36±287.75 a

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	FC4	112.82±4.41 d	4.21±0.08 b	4.25±1.16 b	3.67±0.54 c	52.80±3.93 d	7265.85±372.29 ab
ANOVA	FC	ns	ns	**	**	ns	ns
	D	ns	**	ns	ns	ns	ns
	FC×D	*	**	*	ns	*	*

Note: Different letters in the same column indicate that the differences between different fertilizer application rates at each sowing density treatment are significant at the P<0.05 level; *, ** are significant at the P<0.05 and P<0.01 levels, respectively, and ns denotes that the level of significance has not been reached; the following table is the same as the table below.

As presented in Table 8, grain yield of highland barley cultivar 'Kunlun 15' exhibited an overall declining trend with increasing fertilizer rates and sowing densities, although yield peaks were observed under specific treatment combinations. Across low (LD, 225 kg/ha), medium (MD), and high (HD) sowing densities, maximum yields consistently occurred at the FC2 fertilizer level (urea 37.5 kg/ha + diammonium phosphate 75 kg/ha), with the highest recorded yield (7165.82 kg/ha) achieved under LD × FC2. Compared to the unfertilized control (FC1), fertilizer application significantly enhanced yields under both LD and MD densities (yield increments: 27.80%-34.08% for LD; 21.52%-38.00% for MD). In contrast, FC3 fertilization under HD density resulted in a 2.09% yield reduction relative to FC1. Yield progressively declined with increasing sowing density in the absence of fertilizer.

These findings demonstrated that the combination of elevated fertilizer rates and high sowing densities significantly suppressed grain yield. Consequently, reducing fertilizer input was beneficial under high-density conditions, whereas supplementary fertilization promoted yield gains at low density. Yield components displayed differential responses: Panicles per m² consistently decreased with increasing fertilizer rates and sowing densities. Productive tillers per plant exhibited a unimodal response (initial increase followed by decrease) to incremental fertilizer and density levels. Both grain weight per panicle and 1000-grain weight increased with higher fertilizer application but declined with elevated sowing density.

TABLE 8 YIELD CHARACTERISTICS OF KUNLUN 15 UNDER DIFFERENT FERTILISER DENSITY OPERATIONS

Seeding density	Fertilization treatment	Plant height (cm)	Number of spikes(106)	Number of effective spikes	Weight of grains per ear(g)	Thousand grain weight(g)	Yield (kg/hm2)
LD	FC1	93.34±6.13 a	3.18±0.12 a	3.50±0.95 d	2.63±0.67 d	47.15±1.23 c	5343.71±218.21 b
	FC2	88.58±3.65 c	2.88± 0.08 c	4.01±1.23 c	2.73±0.78 d	47.09±1.98 c	7165.05±276.45 a
	FC3	92.54±5.23 b	2.86±0.02 d	4.81±0.98 a	3.09±0.68 c	50.88±2.01 a	6829.5±298.56 b
	FC4	91.54±2.74 b	2.88±0.23 c	4.50±1.67 b	3.39±0.79 a	52.80±2.42 a	6900.6±198.98 b
MD	FC1	87.96±4.32 d	3.35± 0.12 a	4.06±1.56 c	2.96±0.54 d	50.59±2.17 a	5140.31±213.56 b
	FC2	89.52±3.21 c	2.91±0.14 b	3.44±1.01 d	3.02±0.23 c	47.41±2.54 c	7093.82±251.32 a
	FC3	93.32±1.98 a	3.16±0.09 a	4.56±1.97 b	3.33±0.78 b	48.49±2.65 b	6488.85±231.48 c
	FC4	88.64±3.16 c	2.84±0.11 d	4.00±1.17 c	3.06±1.01 c	47.84±2.98 c	6246.45±213.67 d
HD	FC1	93.32±2.12 a	3.11±0.08 a	3.25±0.67 d	3.17±0.78 b	49.29±2.14 b	6069.05±215.31 d

	FC2	91.74±3.46 b	3.09±0.14 b	4.44±0.57 b	2.85±0.36 d	46.59±1.78 d	6454.95±228.31 c
	FC3	94.98±5.37 a	2.96±0.17 b	5.44±1.75 a	2.79±0.76 d	46.20±2.43 d	6224.71±142.31 d
	FC4	94.46±4.28 a	2.91±0.09b	4.63±0.99 b	3.52±0.65 a	50.47±2.17 a	5941.82±173.54 d
ANOVA	FC	ns	*	**	**	ns	ns
	D	ns	**	ns	ns	ns	ns
	FC×D	*	*	*	ns	*	*

Synergistic Mechanisms of Yield Formation in Highland Barley under Fertilizer-Density Interaction (Table 9). Analysis of key yield-related traits revealed that grain yield was strongly dependent on two synergistic processes: Grain setting rate exhibited an extremely significant positive correlation with yield (r=0.962**,p<0.01). Grain weight per panicle was also positively correlated with yield (r=0.516**,p<0.01). Notably, productive panicles per unit area showed a significant positive correlation with yield (r=0.397*,p<0.05) but displayed negative associations with both 1000-grain weight (r=−0.218*,p<0.05) and grain setting rate (r=−0.036). This indicated that excessive population expansion likely triggered competition for photosynthetic assimilates, thereby suppressing grain development and confirming a fundamental trade-off between panicle number and grain weight.

Endogenous hormone dynamics further elucidated this trade-off: The ZT/IAA ratio (zeatin-to-auxin) positively correlated with productive panicles (r=0.333 * ,p<0.05), suggesting zeatin dominance enhanced tiller survival and panicle formation. Conversely, IAA negatively correlated with ZT (r=−0.359*, p<0.05), and ZT/IAA was strongly negatively linked to IAA (r=−0.614**, p<0.01), demonstrating their antagonistic roles in regulating source-sink partitioning. Conclusion: Maximizing yield necessitates resolving the conflict between panicle number and sink capacity. Strategic fertilizer-density management—particularly modulating the ZT/IAA balance—can synergistically optimize panicle density, grain setting efficiency, and panicle filling.

TABLE 9 CORRELATION BETWEEN ENDOGENOUS HORMONES, YIELD AND CONSTITUTIVE FACTORS UNDER FERTILIZER AND DENSITY

factor	Number of effective spikes	Kernel weight	Thousand-grain weight	Yield	Fertility	ZT	IAA	ZT/IAA
Number of effective spikes	1							
Kernel weight	0.037	1						
Thousand-grain weight	-0.218	-0.063	1					
Yield	0.397*	0.516**	-0.069	1				
Fertility	-0.036	0.467**	-0.003	0.962**	1			
ZT	0.227	-0.092	-0.183	0.103	0.014	1		
IAA	-0.039	-0.060	-0.076	0.188	0.265	-0.359*	1	
ZT/IAA	0.333*	0.036	-0.016	-0.115	-0.167	0.442**	-0.614**	1

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Note: Different letters in the same column indicate that the differences between different fertilizer application rates at each sowing density treatment are significant at the P<0.05 level; *, ** are significant at the P<0.05 and P<0.01 levels, respectively, and ns denotes that the level of significance has not been reached.

4 DISCUSSION

4.1 *TILLERING DYNAMICS DRIVEN BY NITROGEN AND GENOTYPE*

Tillering—a cornerstone of high-yield population architecture in highland barley—was predominantly governed by nitrogen fertilization rather than sowing density. Both cultivars exhibited a unimodal response (increase followed by decrease) to nitrogen escalation, with Kunlun 14 peaking under high nitrogen (HN) and Kunlun 15 under medium nitrogen (MN). The jointing stage emerged as a critical window for tiller survival, necessitating genotype-specific nitrogen optimization: 150 kg/ha urea + 300 kg/ha diammonium phosphate for Kunlun 14 versus 75 kg/ha urea + 150 kg/ha diammonium phosphate for Kunlun 15. Genetic divergence in tillering capacity under identical nitrogen levels underscored intrinsic physiological adaptations.

4.2 *HORMONAL CROSSTALK MODULATES TILLER DEVELOPMENT*

Endogenous hormone profiling revealed cultivar-dependent strategies: Kunlun 14 prioritized zeatin (ZT) accumulation under high-NP conditions (FC4), accelerating cell division for tiller initiation. Kunlun15 upregulated auxin (IAA) under medium-NP (FC3), potentially suppressing excessive tillering. Path analysis confirmed the IAA/ZT ratio (direct path coefficient: 0.443) as the dominant regulator of tiller number, validating synergistic hormone control over tiller fate. Elevated ZT/IAA under dense planting exacerbated inter-plant competition, reducing grain filling efficiency—a key constraint in high-yield populations.

4.3 *NITROGEN-USE EFFICIENCY: TRADE-OFFS UNDER DENSITY STRESS*

TABLE 10 NITROGEN UTILIZATION DIVERGED SHARPLY BETWEEN CULTIVARS

Cultivar	Optimal Combination	NUE Metric	Value
Kunlun 14	MD + FC3	N recovery efficiency	27.71%
Kunlun 15	LD + FC2	Partial factor productivity (PFPN)	189.15 kg·kg^{-1}

Density-induced light competition disproportionately impaired Kunlun 15’s PFPN under HD (39.61 vs. 46.07 kg·kg^{-1} in Kunlun 14), likely due to reduced photoassimilate partitioning to grains.

Remarkably, Kunlun 15’s high agronomic efficiency (17.38 kg·kg^{-1}) under HD-FC3 suggested nitrogen-mediated osmotic adjustment enhanced stress resilience.

4.4 *PHOSPHORUS EFFICIENCY: DIMINISHING RETURNS AND CULTIVAR NICHES*

Total phosphorus uptake increased linearly with fertilization, but efficiency metrics (recovery efficiency, agronomic efficiency) declined—exemplifying diminishing returns. Key contrasts emerged: Kunlun 14 maximized P recovery (18.37%) under high density + medium P (HD-FC2). Kunlun 15 achieved peak P agronomic efficiency (5.18 kg·kg^{-1}) under medium density + medium P (MD-FC2). Negative agronomic efficiency under FC3 highlighted severe yield penalties from phosphorus excess, urging precision P management.

4.5 *YIELD ARCHITECTURE: BALANCING SOURCE-SINK RELATIONS*

Yield formation hinged on harmonizing population structure and nutrient allocation: Kunlun 14: Medium density (MD) + High fertilizer (FC3) synergized panicle density (4.75×10^6/ha) and grain weight (3.88 g/panicle), leveraging enhanced 1000-grain weight (56.93 g) under high nitrogen. Kunlun 15: Low density (LD) + Medium fertilizer (FC2) optimized panicle number (4.44×10^6/ha), but high nitrogen suppressed 1000-grain weight (46.20g), indicating inferior remobilization efficiency. The antagonism between ZT/IAA-driven tillering and canopy-level light capture emphasized hormonal fine-tuning for sink-source coordination. Kunlun 14's superior soil nutrient mining capability further validated its adaptability to variable fertility.

4.6 PRACTICAL IMPLICATIONS

For Kunlun 14: Adopt 262.5 kg/ha sowing density + 75 kg/ha urea + 150 kg/ha diammonium phosphate to maximize yield (7807.79 kg/ha) and N recovery (27.71%). For Kunlun 15: Use 225 kg/ha sowing density + 37.5 kg/ha urea + 75 kg/ha diammonium phosphate to balance yield (7165.05 kg/ha) and PFPN (189.15 kg·kg^{-1}), mitigating environmental nitrogen loss.

5 CONCLUSIONS

To resolve the dual constraints of low productive tiller survival and suboptimal population architecture in Tibetan highland barley, a split-plot experiment revealed three key mechanisms governing tiller dynamics and yield formation under synergistic fertilizer-density interactions:

(1) Phenological determinism—The jointing stage (Zadoks stage 3) was identified as a critical window for tiller survival, with FC3 fertilization (75 kg/ha urea + 150 kg/ha diammonium phosphate) maximizing productive tillers across both cultivars.

(2) Hormonal governance—Tillering was directly controlled by the IAA/ZT balance (direct path coefficient: 0.443), exhibiting genotype-specific responses: Kunlun 14 demanded FC4 fertilization to elevate zeatin (ZT) synthesis for accelerated cell division, while Kunlun 15 optimized auxin (IAA) homeostasis under FC3 to mitigate tiller abortion.

(3) Yield-nutrient synergy—Kunlun 14 achieved peak yield (7808 kg/ha) and maximized nitrogen recovery efficiency (27.71%) under medium density (262.5 kg/ha) + FC3 by synergizing panicle density (4.75×10^6/ha) and grain weight (3.88 g/panicle), whereas Kunlun 15 required low density (225 kg/ha) + FC2 to balance high yield (7165 kg/ha) with superior partial factor productivity of nitrogen (PFPN: 189.15 kg/kg), thereby minimizing inter-plant competition. These results establish cultivar-tailored frameworks for precision field management in high-altitude agroecosystems.

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