



Effects of Water and Nitrogen Addition on the Seed Yield and Germination Characteristics of the Perennial Grass *Leymus chinensis* (Trin.) Tzvel

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The reproductive characteristics of plants are likely affected by climate change e.g., changes in precipitation patterns and nitrogen deposition, but few studies have examined the effects of these ecological agents of selection on the seed yield and germination characteristics of perennial grasses. Here, we conducted a multiple-year pot experiment with *Leymus chinensis*, a common perennial grass in the eastern region of the Eurasian steppe zone, which was grown under three water treatments with and without nitrogen addition. The seed yield of *L. chinensis* increased with precipitation and was highest (7.0 g/pot) under 747 mm of precipitation with nitrogen addition (10.5 g/m²). Seed yield was positively correlated with heading number, tiller number, and grain number per spike, and the heading number was a critical factor affecting seed yield. Seed germination percentage and the time to obtain 50% germination were affected by environmental cues experienced by the mother plants.

Keywords: *Leymus chinensis*, precipitation, nitrogen deposition, sexual reproduction, seed yield, seed germination

INTRODUCTION

Grasslands are among the most widely distributed terrestrial biomes globally, covering ca. 52.54 million km² of the terrestrial surface (Zhao et al., 2020). Grasslands play an important role in regional climates, biodiversity, conservation, the provision of ecosystem services, and socio-economic development (Zhao et al., 2015; Han et al., 2018; Nerlekar and Veldman, 2020). Grasslands have become seriously degraded because of climate change and human activities (Andrade et al., 2015; Shen et al., 2016; Wick et al., 2016; Zhou et al., 2020). The continual degradation of grasslands has caused a series of problems, including grassland desertification, biodiversity loss, and the decrease of carbon sinks capacity reduction, and these problems pose a threat to animal husbandry, ecological security, and sustainable development. The restoration of degraded grasslands thus require urgent attention (Man et al., 2016; Ma et al., 2018).

Given that the atmospheric deposition of biologically active nitrogen (N) has increased dramatically over the past few decades and precipitation patterns have changed, there has been increased research interest in examining the effects of N deposition and precipitation on the growth and reproduction of grass (Duan et al., 2019; Zhao et al., 2019). The addition of N has been shown to increase the height, population density, N concentration in tissues, photosynthetic rate, and water-use efficiency of plants (Pan et al., 2005; Ren et al., 2014). Ochoa-Hueso et al. (2014) suggested that

increases in precipitation can enhance plant productivity and thus potentially food production in water-limited ecosystems. Most studies examining the effects of elevated N deposition and altered precipitation on grasslands have focused on net primary productivity or vegetative plant reproduction. By contrast, few studies have examined the effects of N deposition and precipitation on the sexual reproduction of plants (Wu et al., 2011; Gajić et al., 2018; Huang et al., 2019; Zhao et al., 2019).

Regulation of water and N is one of the most effective methods for increasing the seed yield of grasses. Some studies have found that water and N can increase the supply of nutrients in plants, prevent floret degeneration, and increase the number of seeds (Islam et al., 2018; Liu et al., 2019; Wang et al., 2020). Kunstler et al. (2016) reported that a lack of precipitation reduced the number of plant tillers and the differentiation of spikes and florets. Li et al. (2015) found that the seed productivity of artificial grassland was significantly higher than that of natural grassland because of differences in nutrient conditions. Yang, (1989) reported that water and N can affect the development of seed-bearing organs in the ear of *Leymus chinensis*, and the residual effect of fertilization can enhance the seed yield of plants in the second year. Wang et al. (2013) found that N addition can increase the number of reproductive branches and promote the seed production of *L. chinensis*. Its ability to utilize and compete for nutrients and water resources depends on the stage of seed germination (Ghaderi-Far et al., 2010; Ma et al., 2012). However, few studies have examined the effects of nutrient addition and precipitation changes on the seed germination of maternal plants in semi-arid grassland.

Leymus chinensis (Trin.) Tzvel (*L. chinensis*) is the dominant perennial, rhizomatous grass in the eastern region of the Eurasian steppe zone, including the Songnen grassland, which features an arid climate and has soils that are high pH and low in N (Wang et al., 2019). *L. chinensis* is considered the most appropriate grass for restoring degraded grasslands and establishing new grasslands in marginal areas. *L. chinensis* has a low heading percentage, low seed setting percentage, and low germination percentage, which severely limit its further utilization and seed yield (Shi et al., 2017). Thus, the low seed production capacity of *L. chinensis* is the main factor limiting its ability to be used for the establishment of large-scale artificial grasslands (Zhou and Yang, 2006; Wang et al., 2010).

Our previous study has shown that the aboveground biomass of *L. chinensis* increases with precipitation, and the aboveground biomass of *L. chinensis* was highest under 10.5 g/m² N addition and 747 mm of precipitation. Short-term N addition significantly affects leaf physiological traits but has no effect on morphological traits (Zhao et al., 2020). Whether the seed yield and germination characteristics of *L. chinensis* are altered after multiple years of water and N treatments has not yet been studied. Here, we characterized the effects of different water and N treatments on the sexual reproduction ability and seed germination of *L. chinensis*. We hypothesized that variation in the amount of precipitation and N addition would 1) alter the seed setting characteristics of *L. chinensis* and 2) affect the germination characteristics of the maternal plant seeds.

MATERIALS AND METHODS

Experimental Design and Sampling

The pot experiment was conducted in a movable rain shelter in Changchun, Jilin Province (124°18′–127°02′E, 43°05′–45°15′N, altitude of 250–350 masl). The site's mean annual temperature is 4.9°C, with an average temperature of 23°C in July and –16.4°C in January. The area features a temperate continental climate with a mean annual precipitation of 498.0 mm, maximum annual precipitation of 754.0 mm (1956, 50% higher than the mean), and minimum of 244.1 mm (1982, 50% lower than the mean) for the period 1953–2012. The experimental field was covered with black soil, which had a pH of 7.12, electrical conductivity of 0.73 dS/m, and soil organic carbon, N, and phosphorus (P) concentrations of 2.83%, 1.37 g/kg, and 0.67 g/kg, respectively (Zhao et al., 2019). The plastic plant pots (diameter: 30 cm, height: 30 cm) were filled with sieved soil from the 0–20 cm layer near the experimental field. Ten seedlings of *L. chinensis* were transplanted to each pot uniformly on June 01, 2016. Regular watering and weeding were carried out to ensure the normal growth of *L. chinensis*.

The water and N treatments began on June 01, 2017. There were three precipitation gradients and two nutrient levels (each with three replicates, 18 pots in total) to explore the effects of water, N, and the water × N interaction on the seed yield and germination characteristics of *L. chinensis*. The three precipitation gradients were mean annual precipitation (498 mm, W₂), 150% mean annual precipitation (747 mm, W₃), and 50% mean annual precipitation (249 mm, W₁). Underground water was used for irrigation (once every other day), and the concentrations of N, P, and potassium in underground water were below the limits of detection. The irrigation amount was 96, 193, and 289 ml/pot for W₁, W₂, and W₃, respectively. The two nutrient levels were control (N₀) and N addition (N₁). The amount of N was based on recommendations for alleviating nitrogen limitation in typical steppe (Bai et al., 2008; Bai et al., 2014). To avoid natural N input from wet deposition, all of *L. chinensis* plants were covered by a transparent polyvinylchloride roof on rainy days.

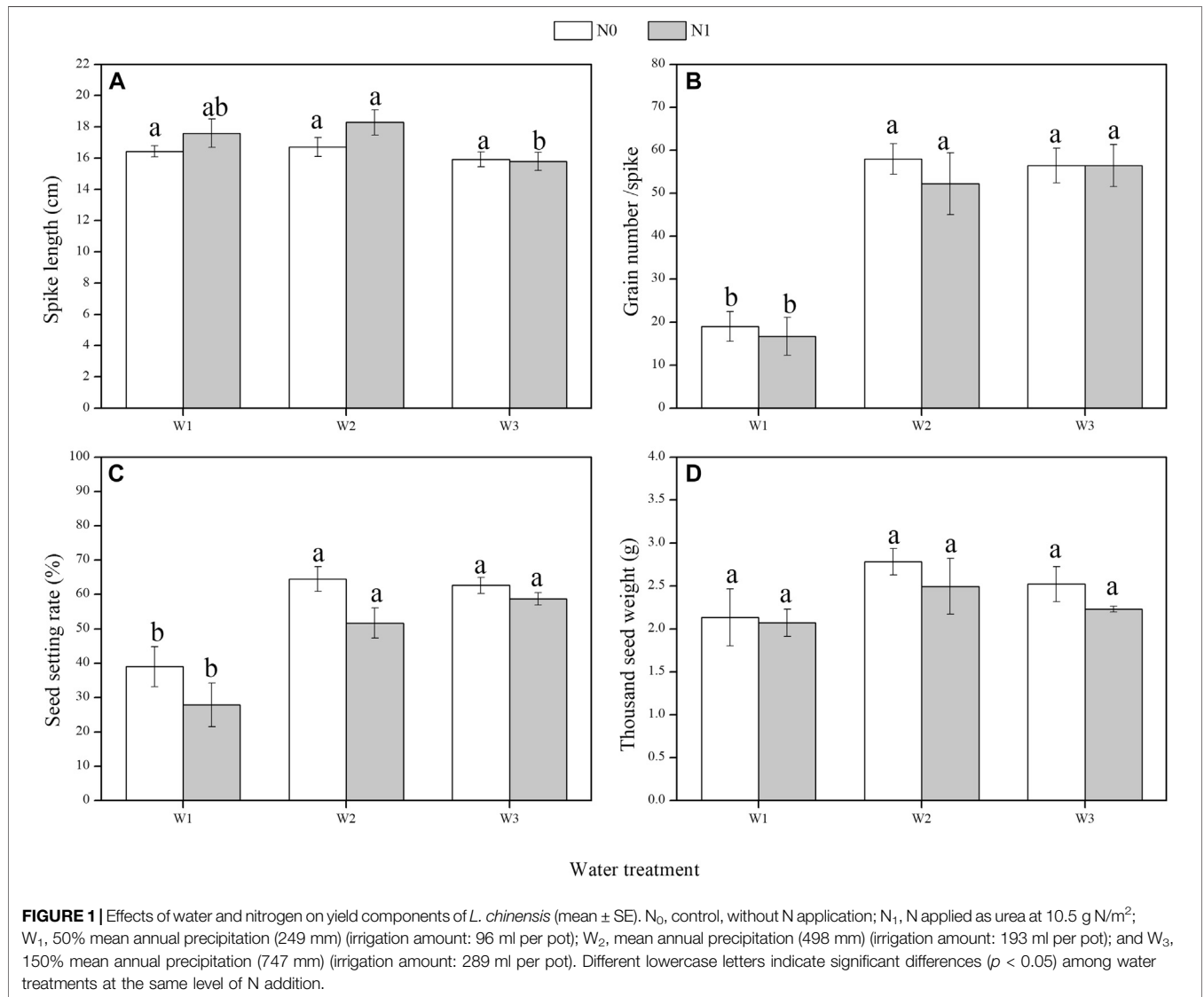
At the seed maturity stage on August 15, 2018, we determined the tiller number per pot and heading number per pot and measured the spike length, grain number per spike, and seed setting rate from nine randomly selected samples from each pot.

Germination Experiment

The germination test was carried out in an incubator (Harbin, China) using 9-cm diameter Petri dishes lined with two layers of filter paper that were saturated with 6 ml of distilled water. The incubation regime consisted of alternating cycles of 12 h of light (fluorescent and incandescent white light of 54 μmolm⁻²s⁻¹) and high temperature (28°C) and 12 h of darkness and low temperature (16°C). Water was added to the dishes when necessary to ensure that they were continuously moist. The dishes were distributed randomly in the incubator, and their positions changed daily. Each water and N treatment was replicated nine times, with 25 seeds were used in each

TABLE 1 | Results of two-way ANOVAs for the effects of water, nitrogen and their interactions on yield components of *L. chinensis*.

| Factor | d.f. | Grain number/spike | | | Seed setting rate (%) | | | Thousand seed weight (g) | | | Seed yield (g/pot) | | |
|--------------|------|--------------------|---------|-------|-----------------------|--------|-------|--------------------------|--------|-------|--------------------|---------|--------|
| | | MS | F | p | MS | F | p | MS | F | p | MS | F | p |
| Water (W) | 2 | 2882.228 | 227.434 | 0.004 | 1353.127 | 41.123 | 0.024 | 0.428 | 16.870 | 0.056 | 44.581 | 129.712 | <0.001 |
| Nitrogen (N) | 1 | 32.895 | 2.596 | 0.248 | 389.087 | 11.825 | 0.075 | 0.205 | 8.080 | 0.105 | 3.727 | 10.844 | 0.006 |
| W × N | 2 | 12.673 | 0.210 | 0.814 | 32.905 | 0.512 | 0.612 | 0.025 | 0.166 | 0.849 | 2.264 | 6.588 | 0.012 |



replication. Seeds were considered to be germinated upon emergence of the radicle. Germination was recorded every day for 28 days. The time to 50% germination (in days) was calculated from the germination times of all germinated seeds.

Germination percentage (GP) was calculated using the equation:

$$GP = (n/N) \times 100 \tag{1}$$

where n is the number of germinated seeds at the end of the test, and N is the total number of seeds kept for germination.

The time to obtain 50% germination (T_{50}) was calculated using the equation (Farooq et al., 2005):

$$T_{50} = t_i + \frac{\left(\frac{N}{2} - Ni\right)(t_j - t_i)}{(Nj - Ni)} \tag{2}$$

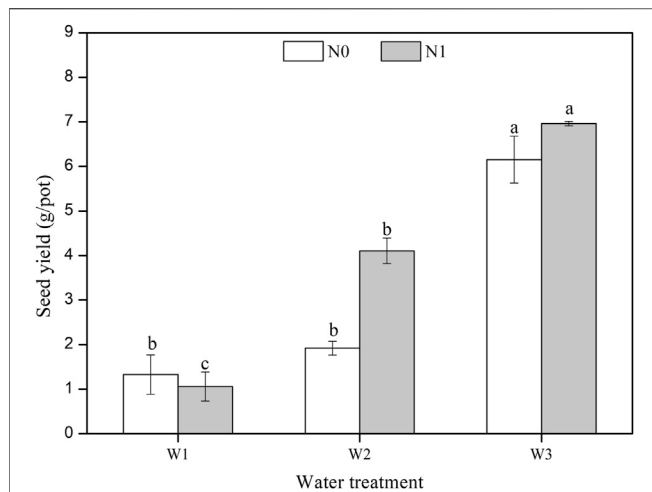


FIGURE 2 | Effects of water and nitrogen on seed yield of *L. chinensis* (mean ± SE). N₀, control, without N application; N₁, N applied as urea at 10.5 g N/m²; W₁, 50% mean annual precipitation (249 mm) (irrigation amount: 96 ml per pot); W₂, mean annual precipitation (498 mm) (irrigation amount: 193 ml per pot); and W₃, 150% mean annual precipitation (747 mm) (irrigation amount: 289 ml per pot). Different lowercase letters indicate significant differences ($p < 0.05$) among water treatments at the same level of N addition.

where N is the final number of germinated seeds, N_j and N_i are the cumulative numbers of seeds germinated by adjacent counts at times t_j and t_i, respectively, when N_i < N/2 < N_j.

Statistical Analyses

Generalized linear model (GLM) was used to analyze the effects of water, N, and the water × N interaction on seed yield, yield components, GP and T₅₀, where water and N served as fixed factors and block as a random effect. Analysis of variance, followed by Duncan’s test, was used to compare means among treatments. Pearson’s correlation coefficients were used to analyze the relationships between yield components and other related characters. Differences were considered statistically significant at *p* values of 0.05. All the analyses were performed in SPSS 20.0 software program (SPSS Inc., Chicago, Illinois, United States).

RESULTS

Seed Yield and Components

The grain number per spike and seed setting rate were significantly affected by water ($F = 227.434, p < 0.01$; $F = 41.123, p < 0.05$; **Figures 1B,C; Table 1**). There was no significant difference in the spike length between N treatments under the same precipitation treatment (**Figure 1A**). Under N₁, the spike length of *L. chinensis* was 13.7% lower under W₃ compared with W₂. Grain number per spike and seed setting rate were lower under W₁ than under W₂ and W₃. Under the same precipitation treatment, the seed setting rate and thousand seed weight of *L. chinensis* were higher under N₀ than N₁ (**Figures 1C,D**).

The seed yield per pot of *L. chinensis* was significantly affected by water, N, and the water × N interaction ($F = 129.712, p < 0.001$;

TABLE 2 | The correlation among yield components and other related characters.

| Factor | X ₁ | X ₂ | X ₃ | X ₄ | X ₅ |
|----------------|----------------|----------------|----------------|----------------|----------------|
| X ₂ | 0.507* | — | — | — | — |
| X ₃ | -0.166 | -0.427 | — | — | — |
| X ₄ | 0.335 | -0.065 | -0.053 | — | — |
| X ₅ | 0.137 | -0.273 | 0.143 | 0.583* | — |
| Y | 0.566* | 0.594** | -0.267 | 0.701** | 0.192 |

X₁, Tiller number; X₂, Heading number; X₃, Spike length; X₄, Grain number/spike; X₅, Thousand seed weight; Y, Seed yield. Correlation coefficients calculated by the Pearson two-tailed test; *and ** indicate significant correlation at the 0.05 and 0.01 levels, respectively.

TABLE 3 | Results of two-way ANOVAs for the effects of water, nitrogen and their interactions on germination and T₅₀ of *L. chinensis*.

| Factor | d.f. | Germination percentage (%) | | | T ₅₀ (d) | | |
|--------------|------|----------------------------|-------|-------|---------------------|-------|-------|
| | | MS | F | p | MS | F | p |
| Water (W) | 2 | 134.222 | 1.189 | 0.457 | 18.841 | 3.318 | 0.232 |
| Nitrogen (N) | 1 | 0.889 | 0.008 | 0.937 | 9.315 | 1.64 | 0.329 |
| W × N | 2 | 112.889 | 4.536 | 0.034 | 5.679 | 1.778 | 0.211 |

$F = 10.844, p < 0.01$; $F = 6.588, p < 0.05$; **Table 1**). Seed yield significantly increased with precipitation. The highest seed yield was observed under N₁W₃ (7.0 g/pot). Plants under N₁W₂ produced two-fold more seeds than the plants under N₀W₂. The seed yield was 13.2% higher under N₁W₃ than under N₀W₃ (**Figure 2**). The water × N interaction had a positive effect on the seed yield of *L. chinensis*.

Significant positive correlations were observed between seed yield and tiller number ($R^2 = 0.566, p < 0.05$). There was a significant positive correlation between seed yield and heading number ($R^2 = 0.594, p < 0.01$, **Table 2**). Tiller number had a smaller effect on seed yield compared with heading number. There was a significant positive correlation between tiller number and heading number ($R^2 = 0.507, p < 0.05$). Significant positive correlations were observed between seed yield and grain number per spike ($R^2 = 0.701, p < 0.01$). There was a negative, but non-significant, correlation between spike length and seed yield. Significant positive correlations were observed between thousand seed weight and grain number per spike ($R^2 = 0.583, p < 0.05$).

Seed Germination

The GP of *L. chinensis* was significantly affected by the water × N interaction ($F = 4.536, p < 0.05$, **Table 3**). The GP ranged from 80.0% under N₁W₂ to 94.7% under N₁W₃. The lowest T₅₀ was observed under N₁W₁, and T₅₀ was 23.7 and 29.9% lower under N₁W₁ compared with N₁W₂ and N₁W₃, respectively (**Figure 3A**).

Under N₁, T₅₀ increased with precipitation. Under N₀, T₅₀ increased from 8.8 days under W₁ to 13.4 days under W₂ (**Figure 3B**). The water conditions experienced by the mother plant affected T₅₀ in the progeny. T₅₀ was lower and higher in the progeny under W₁ and W₃, respectively, compared with W₂.

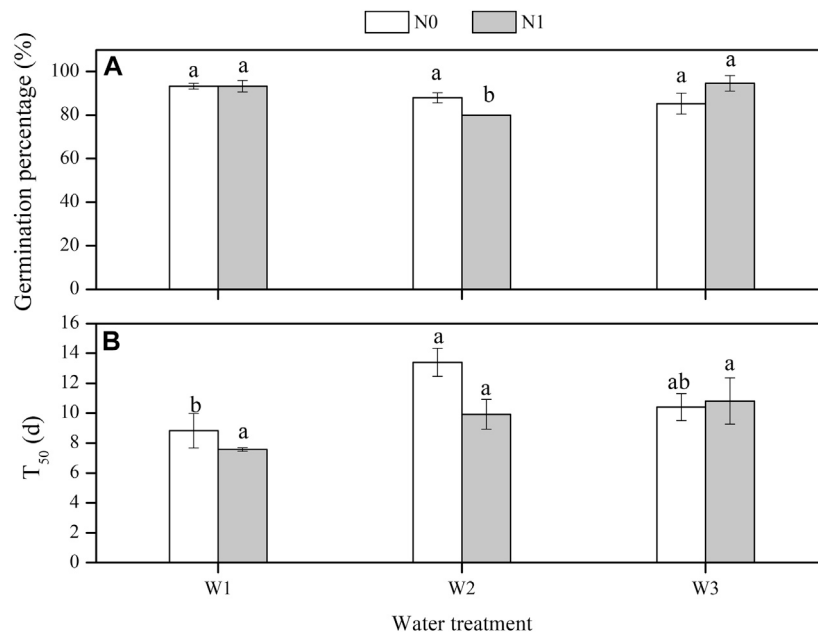


FIGURE 3 | Effects of water and nitrogen on germination percentage and T_{50} of *L. chinensis* (mean \pm SE). N₀, control, without N application; N₁, N applied as urea at 10.5 g N/m²; W₁, 50% mean annual precipitation (249 mm) (irrigation amount: 96 ml per pot); W₂, mean annual precipitation (498 mm) (irrigation amount: 193 ml per pot); and W₃, 150% mean annual precipitation (747 mm) (irrigation amount: 289 ml per pot). Different lowercase letters indicate significant differences ($p < 0.05$) among water treatments at the same level of N addition.

DISCUSSION

Seed Yield

In this study, the water supply had a major effect on the seed yield (Table 1). The grain number per spike and seed setting rate in *L. chinensis* varied depend on water supply. The increase in the tiller number, heading number, and number grain per spike all contributed to the increase in seed production. Plants under W₃ produced 4.6-fold more seeds than plants under W₁ with no fertilizer input (Figure 2). The results were consistent with those of Main et al. (2014) showing that the heading number of *Gossypium* spp. decreases under water deficiency. The heading number of *Zoysia japonica*, *Agropyron cristatum*, and *Psathyrostachys juncea* increases significantly under a suitable level of N application (Tandoh et al., 2019; Qasim et al., 2020; Zanon et al., 2020). However, our findings are inconsistent with a previous study conducted in Brazil showing that the seed yield of grass was not greatly affected by water (Canto et al., 2020).

The results of this study indicate that water and N affect the number of germinated seeds of *L. chinensis* in the following year. At the end of the growing season, a large number of buds in the underground bud bank germinated, and the apical meristem of the progeny began to transform from vegetative branches into reproductive branches, many of which reached the spikelet differentiation stage. Hence, water and N treatment in the previous year has a strong effect on the spikelet differentiation of *L. chinensis* (Ryle, 2010; Taliman et al., 2019).

The results of this study showed that N addition can improve the grain number per spike and seed yield (Table 1). This might stem from the fact that N is a major component of nucleic acids and

protoplasm. The extra protein produced under N addition allows the plant leaves to grow larger and hence have a larger surface available for photosynthesis (Zhang et al., 2016). Water can promote nutrient absorption in *L. chinensis*, which enhances photosynthetic capacity, provides energy for reproductive development, promotes the differentiation of spikes and florets, and reduces the number of aborted spikes and florets. Saeidnia et al. (2018) recorded that water stress reduces the seed yield of *Bromus inermis* by 38%. A sufficient supply of water and N can prevent nutrient competition between seeds and other organs after spikelet and floret differentiation, thereby increasing the grain number per spike and seed setting rate (He et al., 2017; Kaisermann et al., 2017; Cohen et al., 2021).

Seed yield is the product of the heading number and the reproductivity of reproductive branches per plant. In this study, water significantly increased the seed yield of *L. chinensis*, which was consistent with the results of previous research (Wang et al., 2010; Chen et al., 2013; Gao et al., 2020). N might promote tillering, the accumulation of dry matter, and seed yield by affecting flower bud development and seed production (Hrdlickova et al., 2011; Wang et al., 2017; Wang et al., 2019; Yang et al., 2019). Additionally, N might be involved in the expression of some flowering genes, as on-off cycles in gene expression are positively correlated with N fertilization levels; thus, N fertilization can effectively increase seed yield (Miyazaki et al., 2015).

Seed Germination

Seed germination is a critical phase in the plant life cycle. Seeds harvested from plants grown in different maternal environments may vary in their ability to germinate under the same germination

conditions (Nguyen et al., 2021). As shown in **Figure 3A**, fewer seeds harvested from plants grown under W_2 germinated compared with those harvested from plants grown under W_1 and W_3 with N addition. The shortest T_{50} in this study was observed under N_1W_1 , which indicated that N application significantly shortened the germination time of seeds. The addition of N fertilizer to the mother plants promoted the germination of seeds (Alboresi et al., 2005). The mother plant has a substantial influence on seed traits, such as GP (Singh et al., 2017; Geshnizjani et al., 2019). The environmental cues (e.g., soil moisture and nutrients) the mother plant experiences can lead to variation in seed quality even within the same genotype (Van Der Weele et al., 2000).

CONCLUSION

In conclusion, seed yield was highest when plants had a high tiller number, heading number, and grain number per spike. Therefore, water and N need to be carefully managed to optimize seed production. The highest seed yield (7.0 g/pot) of *L. chinensis* was observed under N_1W_3 . Decreases or increases in precipitation in treatments without N addition shortened the germination time of the produced seeds.

DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article/**Supplementary Materials**, further inquiries can be directed to the corresponding authors.

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AUTHOR CONTRIBUTIONS

D-DZ conceived and designed the experiments, performed the experiments, analyzed the data, prepared figures and/or tables, authored or reviewed drafts of the paper, and approved the final draft. H-YM conceived and designed the experiments, authored or reviewed drafts of the paper, and approved the final draft. LW conceived and designed the experiments, authored or reviewed drafts of the paper, and approved the final draft. S-YL performed the experiments, prepared figures and/or tables, and approved the final draft. W-WQ, M-YM and J-BX performed the experiments, authored or reviewed drafts of the paper, and approved the final draft.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fenvs.2021.704097/full#supplementary-material>

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