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Comparison of Seed Tolerance to Low Temperature Between Praxelis Clematidea and Bidens Pilosa and Their Invasion Potential

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ABSTRACT

To investigate the response mechanisms of seeds of the invasive plants Praxelis clematidea and Bidens pilosa to low-temperature environments and their dispersal potential, this study used the paper culture method in petri dishes. Seeds were subjected to 25°C （room temperature）, 4 °C, 0 °C, and -20 °C for 3 and 6 months. After treatment, germination tests were conducted under suitable conditions, with freshly collected seeds serving as the control (CK). Seed germination and seedling growth indicators were measured to analyze the effects of temperature and treatment duration on seeds and seedlings of the two species. The results showed that germination and seedling growth indicators of both species decreased with longer treatment duration and increased with lower treatment temperatures, but all remained lower than those of the CK. After 6 months at room temperature, all indicators for both species dropped to zero. After 6 months at -20 °C, the germination rates of P. clematidea and B. pilosa decreased by 33.8% and 1.2%, respectively, compared with the CK, with the latter showing a significantly smaller reduction. After 6 months of low-temperature treatment, seedling height, root length, fresh weight, and root-to-shoot ratio of both species were lower than those after 3 months, though most differences were not significant. In conclusion, seeds of P. clematidea and B. pilosa have a certain tolerance to low-temperature environments and can still germinate and establish in new habitats under suitable conditions after low-temperature treatment. Among them, B. pilosa seeds exhibit stronger low-temperature tolerance and have a higher potential risk of northward dispersal.

KEYWORDS

Praxelis Clematidea; Bidens Pilosa; Low-Temperature Stress; Seed Germination; Seedling Growth.

1. INTRODUCTION

With increasing human activities, natural ecosystems have been subjected to many negative impacts, among which biological invasion has become a major global concern[1]. In China's diverse ecosystems, there are approximately 515 species of invasive alien plants, of which 260 occur in southeastern China [2], showing a gradual spread trend from southeast to northwest [3]. Plants of the Asteraceae family represent one of the most abundant groups of invasive species and have formed severe invasions in southern China [4].

Praxelis clematidea is an annual herb of the Asteraceae family. Its seeds are small with white pappus at the apex, enabling short-distance dispersal by wind, water, and insects, and can easily attach to objects or vehicles, achieving long-distance dispersal through human trade activities [5]. This species is native to South America and is now mainly distributed in Guangdong, Fujian, Hainan, Taiwan, and other parts of China [6]. P. clematidea has high adaptability, strong reproductive capacity, and

allelopathic effects. It has established populations in farmlands and orchards across many regions of southern China [7], disrupting the structure of native vegetation communities. Furthermore, P. clematidea has a strong ability to absorb soil nutrients. After invading habitats such as farmlands and orchards, it rapidly depletes soil fertility, reduces soil cultivability, and leads to reduced crop yield or quality degradation, causing serious economic losses. In 2014, P. clematidea was listed as an invasive plant by the State Environmental Protection Administration of China and included in the third batch of the List of Alien Invasive Species [8].

Bidens pilosa is an annual herb of the Asteraceae family, native to tropical America. Its achenes have awned pappi with barbs, allowing them to attach to humans, livestock, and goods, facilitating introduction into China. It is mainly distributed in Guangdong, Guangxi, and other regions [9]. B. pilosa is commonly found in wastelands and roadsides, distinguished by its white ligulate petals. It is a variety of Bidens bipinnata (also known as Bidens pilosa var. pilosa), which is often mistaken for B. pilosa without its white ligulate petals due to petal shedding. As an adult, B. pilosa exhibits strong phenotypic plasticity in response to light, temperature, and nitrogen, with rapid seed production, high seed yield, and high germination rates, quickly forming large, dense, monodominant plant communities in invaded areas [10]. After invasion, B. pilosa not only competes with native species for light, nutrients, and water but also often causes direct or indirect harm to neighboring species through allelopathy, severely damaging local ecosystems [11].

To effectively control invasive alien plants and prevent their further spread, many scholars have predicted the potential distribution areas and dominant environmental variables of P. clematidea and B. pilosa [12-13]. Research indicates that B. pilosa is mainly distributed in tropical and subtropical regions between 15° and 30° north and south latitude [13], while P. clematidea is primarily distributed in tropical, subtropical, and certain warm temperate regions of China [14]. Both invasive plants show a tendency for further spread in China [12]. As plant propagules, seeds' strong adaptability facilitates individual survival in new habitats. The geographical distribution of alien plants is influenced by factors such as annual mean temperature, precipitation, extreme climate events, and annual accumulated temperature [15]. Low-temperature environments in invaded areas during winter pose a severe challenge for many alien plants originating from warm regions [16]. The ability to survive winter safely is a bottleneck limiting the successful invasion of many alien plants [14]. Therefore, studying the overwintering performance of invasive alien plant seeds is not only a key aspect of elucidating their invasion mechanisms but also an important basis for evaluating their invasiveness and potential distribution areas [17]. Seed germination is a critical stage in plant life history, and low temperature significantly affects seed germination and seedling growth [3]. Many studies have shown that low temperature is an important factor limiting the establishment of invasive species' population dominance in invaded areas [18-19].

Although previous studies have predicted the potential distribution areas of P. clematidea and B. pilosa and identified temperature as a key factor limiting their spread, comparative studies on the actual germination ability and seedling growth status of the two species' seeds after long-term low-temperature stress remain lacking. What are the true low-temperature tolerance thresholds of the seeds of these two invasive plants? Can the seeds germinate normally and establish seedling populations after low-temperature treatment? These key questions have not yet been experimentally verified. Therefore, this study simulated different low-temperature conditions (4 °C, 0 °C, -20 °C) and different treatment durations (3 months, 6 months), using room temperature treatment and fresh seeds as controls, to systematically compare the germination ability and seedling growth characteristics of P. clematidea and B. pilosa seeds after low-temperature stress. This experiment aims to explore the low-temperature tolerance ability of the two invasive plant seeds and their differences, reveal their potential for northward dispersal to cooler regions, and provide a scientific basis for the early monitoring and integrated control of P. clematidea and B. pilosa.

2. MATERIALS AND METHODS

2.1. Experimental Materials

Seeds of Praxelis clematidea and Bidens pilosa were collected on December 21, 2024, from an open wasteland beside National Highway 325 in Chikan District, Zhanjiang City, Guangdong Province. Healthy plants growing under full sunlight were selected, and mature, plump seeds were collected. After air-drying, the seeds were stored in self-sealing bags for later use.

2.2. Seed Treatment Methods

Four temperature treatments were set: room temperature (approximately 25 °C, referring to the annual mean temperature of Zhanjiang [20]), 4 °C, 0 °C, and -20 °C. Mature dry seeds of both species were each divided into four equal portions, placed into self-sealing bags, and stored in a refrigerator freezer (-20 °C), refrigerator compartments (4 °C and 0 °C), or room temperature environment. Treatment durations were divided into two gradients: 3 months and 6 months. After each treatment duration, seeds were taken from each temperature treatment for germination tests, with freshly collected seeds used as the control (CK).

2.3. Seed Germination Test

Germination tests were conducted on March 21, 2025 (after 3 months of treatment) and June 21, 2025 (after 6 months of treatment). From each temperature treatment, 120 plump seeds with specific gravity ≥ 1.0 were selected by water flotation. The seeds were disinfected by soaking in a 50-fold dilution of 10% sodium hypochlorite solution for 5 minutes, then rinsed three times with distilled water. The paper culture method in petri dishes was adopted. The disinfected seeds were evenly placed into sterile petri dishes lined with two layers of moist filter paper, with 30 seeds per dish and 4 replicates. An appropriate amount of distilled water was added to maintain humidity, and the dishes were covered and cultured at room temperature. Radicle protrusion of 2 mm through the seed coat was used as the criterion for seed germination. The number of germinated seeds was recorded daily, and the filter paper was replaced and distilled water added every other day. The experiment was terminated if all seeds became moldy or if no new germination occurred for three consecutive days. Fresh seeds (CK) and seeds treated for 6 months were subjected to germination tests using the same method.

2.3.1. Determination of Germination Indicators

Germination rate (%) = (Total number of germinated seeds / Total number of tested seeds) × 100%

Germination potential (%) = (Number of seeds germinated in the first 3 days / Total number of tested seeds) × 100%

Germination index = $\Sigma(Gt / Dt)$

Where Gt is the number of germinated seeds on day t (individuals), and Dt is the corresponding germination day (days).

2.3.2. Determination of Seedling Growth Indicators

On the final day of the experiment, seedling radicle length, hypocotyl length, plumule length, and fresh weight were measured. From each temperature treatment, five well-growing, representative seedlings were randomly selected from each of the four replicate petri dishes (20 seedlings per treatment in total). Radicle, hypocotyl, and plumule lengths (cm) were measured using an electronic vernier caliper, and seedling fresh weight (mg) was measured using an electronic analytical balance. Seedling height (hypocotyl + plumule), root length (radicle), and root-to-shoot ratio (root length/seedling height) were calculated.

2.4. Data Processing and Analysis

Data were organized using Excel software. Variance analysis was performed using SPSS 19.0: One-way ANOVA was used to analyze differences among different treatments, with multiple comparisons conducted using the LSD method; Two-way ANOVA was used to analyze the interaction between low temperature and treatment duration. The significance level was set at $\alpha = 0.05$. Graphs were plotted using Origin 2018 software.

3. RESULTS AND ANALYSIS

3.1. Seed Germination Characteristics of Two Invasive Plants after Different Low-Temperature Treatments

The results of two-way ANOVA showed that the main effects of treatment time (ST) and temperature (LT) on the germination rate, germination potential, and germination index of Praxelis clematidea and Bidens pilosa seeds were all significant ($P < 0.05$), and the interaction between the two factors was also significant ($P = 0.000$), indicating that treatment time and temperature are the main factors affecting seed germination of the two invasive plants, and that there is a synergistic effect.

The germination rate, germination potential, and germination index of both plants showed highly consistent patterns (Figure 1). Under the same treatment time, as the treatment temperature decreased, all germination indicators of both seeds showed an increasing trend,表现为 -20 °C > 0 °C > 4 °C > room temperature, indicating that low-temperature treatment is beneficial for maintaining seed vigor, with the -20 °C treatment being the most effective. Under the same temperature, as treatment time prolonged, the germination indicators of both seeds under room temperature treatment decreased sharply: the germination rate of P. clematidea decreased from 43.3% to 0.8%, and that of B. pilosa decreased from 94.1% to 11.7% ($P < 0.05$). Although various indicators under low-temperature treatment also decreased, most did not reach a significant level ($P > 0.05$), indicating that low temperature can effectively slow down the decline of seed vigor, while long-term storage at room temperature leads to severe loss of seed vigor.

In terms of interspecific differences, B. pilosa exhibited better low-temperature tolerance than P. clematidea. After 6 months of treatment at -20 °C, the germination rate of P. clematidea decreased by 33.8% compared with CK, while that of B. pilosa decreased by only 1.2%. Furthermore, under various low-temperature treatments for 3 and 6 months, the cumulative germination rate of B. pilosa showed no significant difference from CK ($P > 0.05$), whereas that of P. clematidea was significantly reduced ($P < 0.05$). Regarding germination potential, after 6 months of treatment, the decrease for P. clematidea under 0 °C and -20 °C treatments was not significant compared with 3 months ($P > 0.05$), while that for B. pilosa decreased significantly ($P < 0.05$), indicating that the decline rate of P. clematidea seed vigor over time was slower than that of B. pilosa. Regarding germination index, under the 3-month treatment, the germination index of P. clematidea at 0 °C was significantly higher than that at 4 °C and room temperature ($P < 0.05$), while there were no significant differences among low-temperature treatments for B. pilosa ($P > 0.05$), further indicating that P. clematidea is more sensitive to low-temperature treatment, whereas B. pilosa maintains relatively stable germination ability over a wider temperature range.

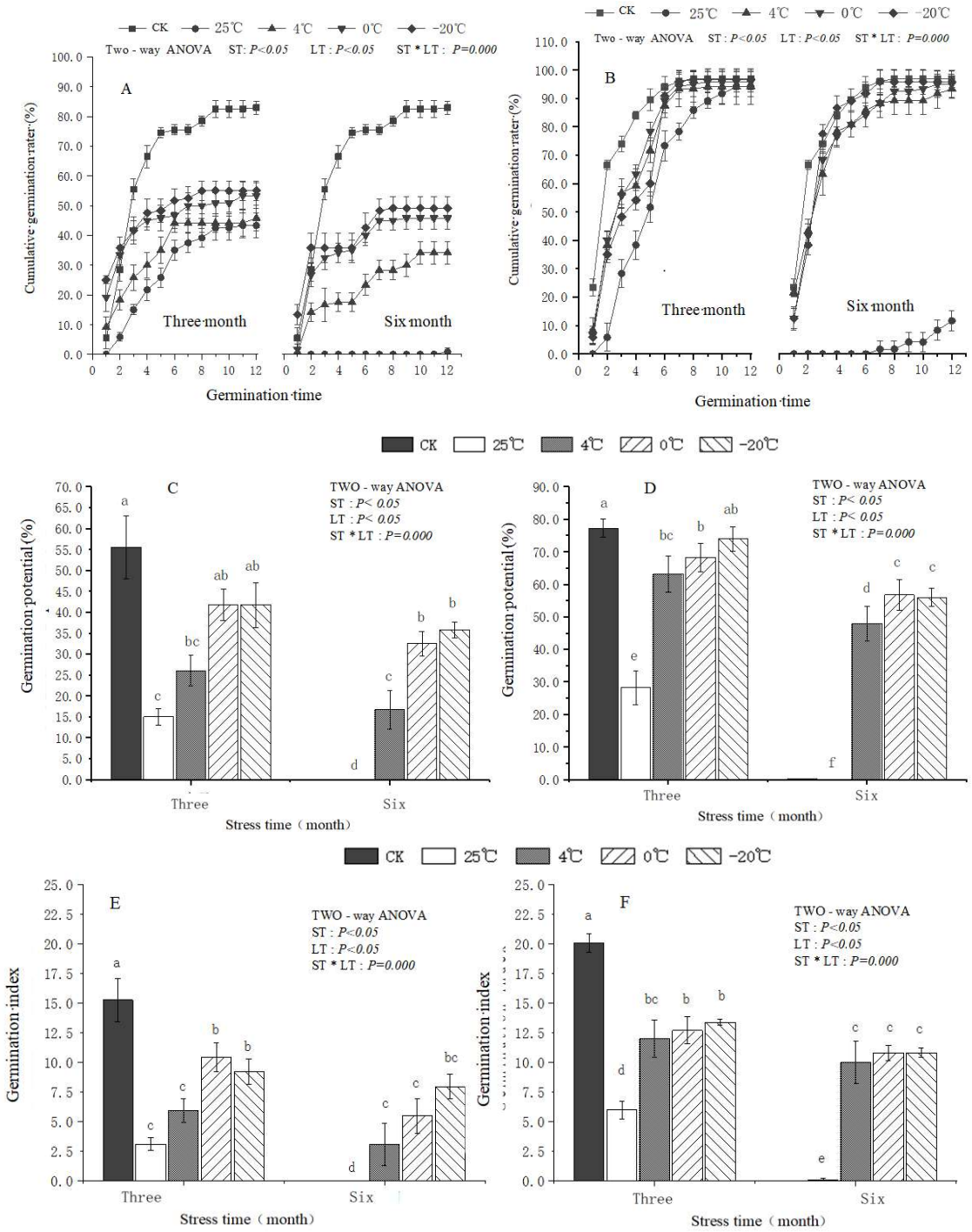


Fig 1 Effects of different temperatures and treatment durations on seed germination characteristics (cumulative germination rate, germination potential, and germination index) of Praxelis clematidea (A, C, E) and Bidens pilosa (B, D, F)

Notes: ST is the processing time, LT is the processing temperature; Different lowercase letters indicate significant differences between different treatments for the same invasive plant.

3.2. Seedling Growth of Two Invasive Plants from Seeds after Different Low-Temperature Treatments

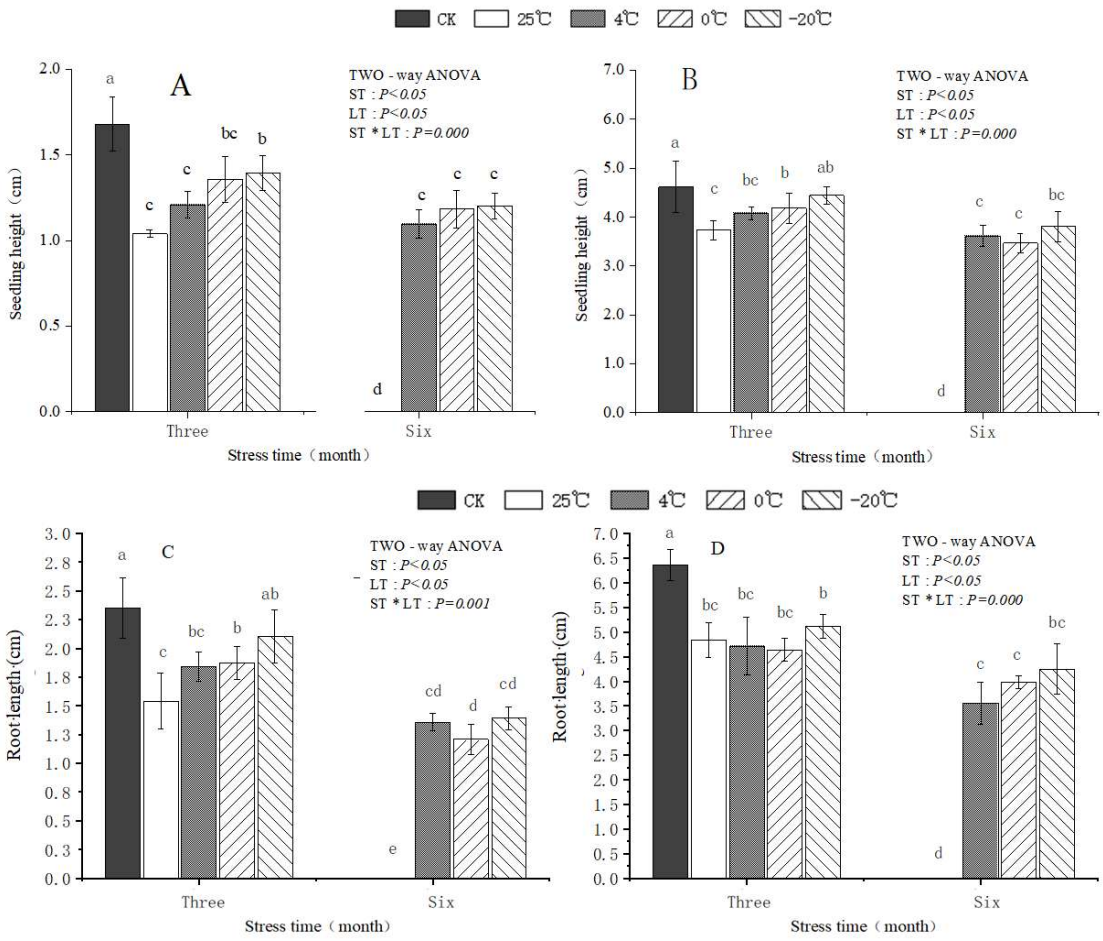
The results of two-way ANOVA showed that the main effects of treatment time and temperature on seedling height, root length, fresh weight, and root-to-shoot ratio were all significant ($P < 0.05$), and the interaction between the two factors was also significant ($P = 0.000$ or $P = 0.002$), indicating that

treatment time and temperature also affect the growth of seedlings derived from seeds after germination.

3.2.1. Effects of Low-Temperature Treatment on Seedling Height, Root Length, and Fresh Weight

Under the same treatment time, as the treatment temperature decreased, the seedling height, root length, and fresh weight of both species showed an increasing trend (Figure 2). After 3 months of treatment, the root length of P. clematidea seedlings under the -20 °C treatment showed no significant difference from CK ($P > 0.05$), and the seedling height and fresh weight of B. pilosa under the -20 °C treatment also showed no significant difference from CK ($P > 0.05$). However, after 6 months of treatment, all growth indicators of both species were significantly lower than those of CK ($P < 0.05$), but under low-temperature treatments, all indicators were significantly higher than those under room temperature treatment ($P < 0.05$). This indicates that seeds treated with low temperature have less loss of internal nutrients, leading to better seedling growth in the later stage.

As treatment time prolonged, the seedling height, root length, and fresh weight of both species decreased. However, under low-temperature treatments, the decreases were mostly not significant ($P > 0.05$), whereas under room temperature treatment, the decreases were sharp. Notably, the fresh weight of B. pilosa seedlings after 3 months of low-temperature treatment showed no significant difference from CK, indicating strong recovery ability. In contrast, the root length of P. clematidea was more sensitive to treatment time, with root length decreasing significantly under most treatments ($P < 0.05$).



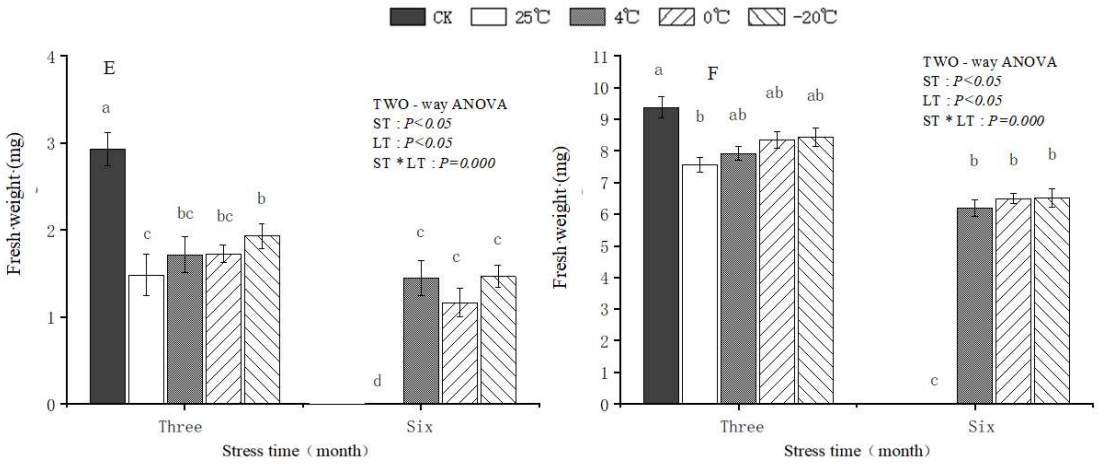


Fig 2 Effects of different temperatures and treatment durations on the seedling growth (seedling height, root length and fresh weight) of Praxelis clematidea (A, C, E) and Bidens pilosa (B, D, F)

Notes: ST is the processing time, LT is the processing temperature; Different lowercase letters indicate significant differences between different treatments for the same invasive plant.

3.2.2. Root-to-Shoot Ratio of Seedlings of Two Invasive Plants from Seeds after Different Low-Temperature Treatments

The root-to-shoot ratio reflects the biomass allocation strategy of seedlings under stress. Under the same treatment time, as the treatment temperature decreased, the root-to-shoot ratio of seedlings of both species generally showed an increasing trend, but all were significantly lower than that of CK ($P < 0.05$) (Figure 3). After 3 months of treatment, there was no significant difference in root-to-shoot ratio among treatments for P. clematidea ($P > 0.05$), while the root-to-shoot ratio of B. pilosa under the -20 °C treatment was significantly higher than that under other low-temperature treatments ($P < 0.05$). After 6 months of treatment, the root-to-shoot ratios of both species under low-temperature treatments were significantly higher than that under room temperature treatment ($P < 0.05$).

As treatment time prolonged, the root-to-shoot ratios of both species decreased significantly ($P < 0.05$), with the most drastic decrease occurring under room temperature treatment. Notably, after 6 months of treatment, the root-to-shoot ratios of B. pilosa under 4 °C and 0 °C treatments were slightly less than 1, while those of P. clematidea under all low-temperature treatments were greater than 1. This indicates that P. clematidea coordinates its biomass allocation under low-temperature stress, prioritizing investment in root growth (root-to-shoot ratio > 1), thereby exhibiting a more stress-resistant biomass allocation strategy. In contrast, root growth of B. pilosa is relatively inhibited after long-term low-temperature treatment.

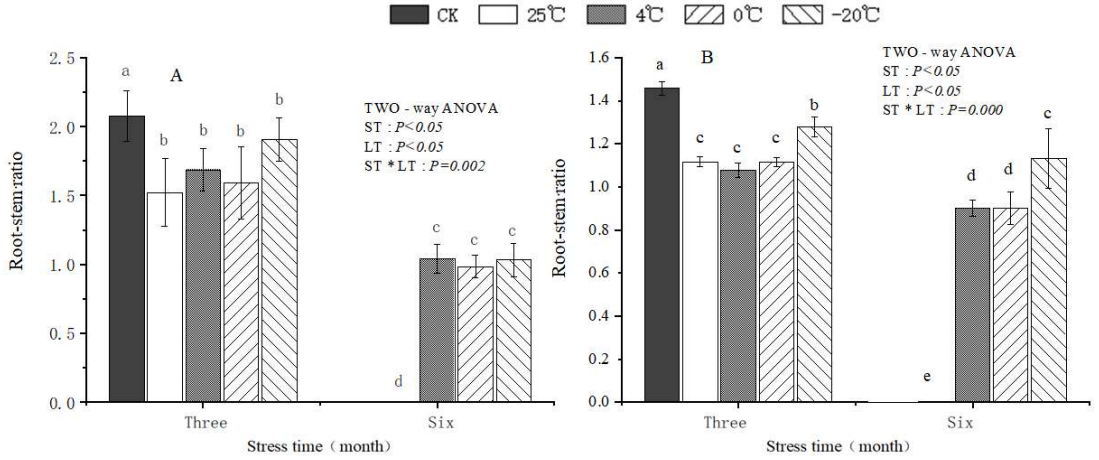


Fig 3 Effects of different temperatures and treatment durations on seeding root-stem ratio of Praxelis clematidea (A) and Bidens pilosa (B)

Notes: ST is the processing time, LT is the processing temperature; Different lowercase letters indicate significant differences between different treatments for the same invasive plant.

4. DISCUSSION

After maturation and air-drying, low-temperature freezing treatment of seeds simulates the overwintering habitat of seeds under ideal conditions [21]. Low temperature and dryness can reduce seed respiration and inhibit lipid peroxidation within seeds, maintaining seed vigor at a relatively high level for a certain period, during which seeds are essentially in a state of secondary dormancy [22]. Dry low-temperature treatment plays an important role in prolonging seed lifespan and improving seed germination rate, although the temperature tolerance range varies among different plant species [23]. In contrast, seed vigor is greatly lost under room temperature storage [24]. The results of this study are highly consistent with the above theories.

4.1. Effects of Low-Temperature Treatment on Seed Germination

This study showed that under the same treatment time, as the treatment temperature decreased, the cumulative germination rate, germination potential, and germination index of Praxelis clematidea and Bidens pilosa seeds all increased, but remained lower than those of CK. For both seeds under the 3-month and 6-month treatments, seed vigor was optimal at -20 °C and 0 °C. This result is consistent with the findings of Hong Lan et al. [18] on Bidens pilosa and Guo Yupin et al. [25] on clover, indicating that low-temperature treatment has universal applicability for maintaining seed vigor in Asteraceae invasive plants. This may be because low temperature inhibits internal metabolic activities of seeds, reduces respiration rate, and decreases the consumption of storage materials such as soluble sugars, proteins, and fats [22]. At the same time, low temperature can inhibit membrane lipid peroxidation, protect the integrity of cell membrane structures, and thus delay seed aging [23]. In this study, the -20 °C treatment was the most effective, possibly because lower temperatures more effectively inhibit endogenous enzyme activity in seeds, causing seeds to enter a deeper state of dormancy, thereby maximizing the preservation of seed vigor.

This study found that the reduction in germination of B. pilosa seeds after low-temperature treatment was significantly smaller than that of P. clematidea. After 6 months of treatment at -20 °C, the germination rate of P. clematidea decreased by 33.8% compared with CK, while that of B. pilosa decreased by only 1.2%. This difference may be related to the morphological structure and physiological characteristics of the two seeds. Cheng Biqiang et al. [26] conducted experiments on seed germination and storage of 100 tropical plant species and found that small and very small seeds were more tolerant to low temperature or drought. However, in this study, although P. clematidea seeds are smaller than B. pilosa seeds, their cold tolerance was weaker, indicating that seed size is not the sole determinant of cold tolerance. A more likely explanation is that B. pilosa seeds have a thicker seed coat structure, which more effectively prevents low-temperature damage to the embryo, or that their seeds contain higher concentrations of cryoprotective substances such as soluble sugars and proline, which help maintain cellular structural stability under low-temperature stress [27]. This mechanism requires further verification.

4.2. Effect of Treatment Duration on Seed Vigor

As treatment duration prolonged, the seed vigor of both P. clematidea and B. pilosa decreased under the same low-temperature conditions, with the most drastic decrease occurring under room temperature treatment. This is consistent with the findings of Xin Xueyan [24], mainly because under room temperature, seeds have strong respiration, rapid nutrient consumption, and are susceptible to microbial infection, leading to seed mold and loss of vigor.

This study found that under low temperature, the germination potential of P. clematidea and the germination index under -20 °C treatment decreased less over time than those of B. pilosa, indicating that the decline rate of P. clematidea seed vigor over time was slower. This phenomenon may be related to the smaller volume of P. clematidea seeds—small seeds more easily achieve temperature equilibrium under low-temperature conditions, resulting in more uniform and stable intracellular metabolic activities [26]. Additionally, P. clematidea seeds may possess a stronger antioxidant enzyme system (such as superoxide dismutase and catalase), enabling more effective scavenging of reactive oxygen species generated under low-temperature stress [28].

However, this study also revealed a seemingly contradictory phenomenon: although P. clematidea seed vigor declines more slowly, its absolute germination rate after low-temperature treatment is lower than that of B. pilosa. This result suggests that low-temperature tolerance of seeds comprises two different dimensions: one is the ability to maintain vigor during low-temperature storage ("storage tolerance"), and the other is the ability to resume germination after low-temperature treatment ends ("germination recovery ability"). P. clematidea performs better in the first dimension, while B. pilosa is stronger in the second dimension. The physiological basis of this difference warrants further investigation.

4.3. Effects of Low-Temperature Treatment on Seedling Growth and Adaptive Strategies

Seedling height, root length, fresh weight, and root-to-shoot ratio not only reflect seedling quality but also indicate plant adaptability to the environment [29]. Seedlings respond to external environmental changes by altering their biomass allocation, which is a self-adjustment strategy of plants in response to environmental changes [29].

This study showed that for seedlings germinated from seeds of P. clematidea and B. pilosa after low-temperature treatment, all growth indicators under the same treatment time decreased compared with CK, but the reduction in growth indicators of seedlings from low-temperature-treated seeds was smaller than that from room temperature treatment. This is because low-temperature-treated seeds experience less loss of internal nutrients, providing sufficient storage materials for early seedling growth upon germination [22]. In contrast, under room temperature treatment, seeds have higher respiratory consumption, leading to substantial depletion of storage materials and resulting in weak seedling growth after germination.

In terms of interspecific differences, this study found that after 3 months of treatment, the seedling height and fresh weight of B. pilosa under -20 °C treatment, and the root length of P. clematidea under -20 °C treatment, showed no significant differences from CK, indicating that short-term (3 months) low-temperature treatment has limited effects on seedling growth after germination, and both species can recover well. This result corroborates the findings of Chen Wen et al. [19] on the temperature response of seed germination in five Asteraceae invasive plants.

As treatment duration extended to 6 months, the root-to-shoot ratios of B. pilosa seedlings germinated from seeds under 4 °C and 0 °C treatments were slightly less than 1, while those of P. clematidea under all low-temperature treatments were greater than 1. This indicates that P. clematidea adopts a more proactive biomass allocation strategy under low-temperature stress—prioritizing investment in root growth (root-to-shoot ratio > 1) to enhance the absorption capacity of water and nutrients, thereby laying the foundation for later growth [29]. In contrast, the root growth of B. pilosa is relatively inhibited after long-term low-temperature treatment, and it may rely more on the recovery ability of aboveground growth. This finding echoes the conclusions of Pan Yumei et al. [30] comparing the growth characteristics of Bidens pilosa and native species under different light and water conditions, indicating that invasive plants can improve survival and competitiveness under stress by adjusting biomass allocation.

4.4. Relationship between Low-Temperature Tolerance and Invasion Potential, and Research Prospects

In summary, seeds of P. clematidea and B. pilosa can tolerate severe winter cold in invaded areas (down to -20 °C) for a certain period. After the cold passes and environmental conditions become suitable, the seeds can germinate and grow normally. This result is similar to the findings of Li Jie et al. [21] on the overwintering performance of Xanthium italicum and Xanthium spinosum seeds, indicating that seed overwintering ability is one of the key traits for successful invasion of cold regions by alien plants.However, this study also raises a question worth pondering: since seeds of both species can tolerate low temperatures of -20 °C, why have P. clematidea and B. pilosa not yet broken out and spread on a large scale in regions with severe cold climates (such as northern China)? Possible reasons include the following:

First, limitations at the seedling establishment stage. Low temperature not only affects seed germination but also significantly affects seedling establishment and growth [31]. This study found that although seeds can tolerate -20 °C low temperature, all growth indicators of seedlings germinated after 6 months of treatment were significantly lower than those of CK, indicating that long-term low-temperature storage causes irreversible damage to seedling vigor. Under natural conditions, seeds after overwintering also face environmental stresses such as variable spring temperatures and late spring cold spells, which may further limit successful seedling establishment.

Second, limitations of growing season length. Northern regions have short frost-free periods and low effective accumulated temperatures. Even if seeds can germinate, seedlings may not have sufficient growing time to complete their life cycle before winter arrives [14].

Whether seeds can tolerate variable spring temperatures and successfully disperse after germination at suitable temperatures has not been verified in this paper. Studies by Chang Bowen et al. [31] on peanut and Wen Riyu et al. [32] on quinoa have shown that low-temperature stress significantly affects the physiological and biochemical characteristics of seedlings (such as chlorophyll content, antioxidant enzyme activity, membrane permeability, etc.). Future research can be pursued in the following directions: (1) measure the physiological and biochemical indicators of seedlings of the two species under low-temperature stress to reveal their molecular and physiological mechanisms of cold tolerance; (2) conduct field overwintering experiments to verify the ecological validity of laboratory simulation results; (3) combine climate models to predict the potential dispersal range of the two invasive plants under climate change scenarios.

CONFLICTS OF INTEREST

The authors declare that they have no conflict of interest.

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