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# Non-viviparous pre-dispersal seed germination in Amaranthaceae in the cold deserts of Central Asia

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In the broad context of understanding the relationship between timing of seed germination and adaptation of a plant species to its habitat, the purpose of this study was to purse an observation of pre-dispersal seed germination of *Salsola brachiata* (Amaranthaceae) in late winter 2021 in the Amaranthaceae species-rich cold deserts in northwest China (Central Asia). We searched for pre-dispersal germination in species of Amaranthaceae growing in sand dunes (S), salt deserts (SD) and gravel deserts (GD). We examined 69 species in 155 populations in autumn 2021 and 52 species in 12 populations in early spring 2022. No seeds of any of the 69 species germinated on the mother plants in autumn 2021, while 30 of 52 species (57.7%) did so during snowmelt in early spring 2022. The rank order of species with few to many seeds germinated on the mother plants was annuals (66.7%)>small shrubs (23.3%)>small trees (6.7%)>shrubs (3.3%). The number of species in S, SD, and GD with pre-dispersal germinated seeds was 16 of 27 (59.3%), 15 of 31 (48.4%), and 15 of 30 (50.0%), respectively. The high species occurrence of pre-dispersal germination in early spring suggested that it might be adaptive in the unpredictable-rainfall growing-season environment of the cold deserts of Central Asia, a center of diversity of Amaranthaceae. However, preliminary studies on seedling/juvenile survival of *S. brachiata* showed that those from post-dispersal soil-germinated seeds had the best survival, suggesting that pre-dispersal seed germination may be maladaptive.

KEYWORDS

cold desert, maladaptive, pre-dispersal seed germination, snowmelt, unpredictable-rainfall environment

## Introduction

Timing of seed germination plays a key role in the adaptation of plant species to their habitat, in particular because it affects the expression of life history traits and fitness components across the plant life cycle, e.g., seedling survival and seed production (Donohue et al., 2010; Postma and Ågren, 2022). The time of germination involves not only dormancy-break of the seeds but also their germination requirements after dormancy is broken. Thus, although dormancy may be broken germination will not occur unless the germination requirements of the seeds overlap with the environmental conditions in the habitat. Seed ecologists are interested in the requirements for both dormancy break and germination, and much attention has been given to the actual time of germination in the field because this provides insight into the relationship between the species and its habitat (Baskin and Baskin, 1972; Lu et al., 2014a,b, 2017, 2020; Maleki et al., 2022).

In late February 2021, the first author observed that some seeds attached to dead stems of *Salsola brachiata* (Amaranthaceae) growing in a cold desert of northern Xinjiang Province China (Central Asia) had germinated. At the time pre-dispersal seed germination was observed, the dead stems and seeds of this annual plant were very moist due to melting of the snow lodged on them. Subsequently, pre-dispersal seed germination was observed for other members of the Amaranthaceae growing in the cold desert, i.e., *Anabasis elatior*, *Atriplex micrantha*, and *Kochia prostrata*. These observations of pre-dispersal germination raised three questions. (1) How common is pre-dispersal germination among species of Amranthaceae in the cold deserts of northwest China? (2) Does pre-dispersal germination occur only in late winter/early spring during the time of snowmelt? (3) What is the consequence of pre-dispersal germination on seedling/ juvenile survival?

To address the first two questions, a field survey of numerous species of Amaranthaceae growing in these cold deserts was conducted in autumn 2021 and spring 2022. To address the question related to seedling survival, we monitored the survival of *S. brachiata* seedlings/juveniles resulting from pre-dispersal and post-dispersal (sown on soil) germination in spring 2022. We predicted that pre-dispersal germination (1) is limited to the snowmelt period of late winter/early spring when moisture in the habitat is high, and (2) many of the pre-dispersal seedlings fail to become established in the soil; that is, pre-dispersal seed germination is maladaptive.

The cold deserts in northern Xinjiang Province of China (Central Asia) are the main distribution area of Amaranthaceae species in the world (Mao, 1994). In this area, Amaranthaceae species include very common annual plants, semi-shrubs, and shrubs, but perennials and small trees are present. Also, species of Amaranthaceae are dominant or otherwise present in a diversity of habitat types (e.g., sand dune, salt desert, and gravel desert) [Xinjiang General Exploration Team of Chinese Academy of

Sciences (CAS), and Institute of Botany of CAS, 1978]. Thus, we determined the occurrence of pre-dispersal seed germination of Amaranthaceae species in sand dunes (S), gravel deserts (GD) and salt deserts (SD) in the cold deserts of northern Xinjiang at seed maturity in autumn and at the onset of the growing season (snowmelt) in late winter/early spring.

## Materials and methods

### The study area

The cold deserts in northern Xinjiang have a typical continental arid/semiarid climate with a low amount of precipitation and high evaporation (Lioubimtseva and Cole, 2006). Depending on location, mean monthly annual temperature ranges from 4.0°C to 9.0°C, and the range of mean temperatures of the coldest (January) and hottest (July) months is −32.8°C to −15.0°C and 25.0°C–40.5°C, respectively. Average annual precipitation (including rain and snow) is 160–300 mm, about two-thirds of which falls in spring and summer, and the snow that falls in winter begins to melt in March or April (Huang et al., 2017). Annual potential evaporation is 1,500–3,000 mm (Zhang et al., 2016). Additionally, rainfall is highly variable among seasons and years, but generally rainfall is higher in spring than in autumn (Su et al., 2007; Shi and Sun, 2008). Further, water from snowmelt increases soil water availability in spring (Bie et al., 2016).

Vegetation cover is about 30%, and the dominant plants are small trees (*Haloxylon* species), shrubs (*Calligonum*, *Caragana*, *Ephedra*, *Nitraria, Reaumuria*, and *Tamarix* species), semi-shrubs, and dwarf semi-shrubs (*Anabasis* and *Artemisia* species), but many annuals (e.g., *Agriophyllum* and *Salsola* species) and herbaceous perennials (e.g., *Allium* and *Astragalus* species) are present (Zhang et al., 2016; Li et al., 2020). The proportion of vegetation cover, especially for herbaceous annuals and herbaceous perennials, varies with precipitation, being strongly associated with inter-annual and intra-annual precipitation patterns (Zhang et al., 2016; Fang et al., 2019; Li et al., 2020). The cold deserts of northern Xinjiang, like those in other regions, have salt lakes and salt pans with associated halophytic vegetation (Soriano, 1983; Walter and Box, 1983; West, 1983).

### Survey of species with pre-dispersal seed germination

Species of Amaranthaceae are very common in the cold deserts in northern Xinjiang. Flowering occurs from early April to mid-September (Commissione Redactorum Florae Xinjiangensis, 1994), and fruits mature in late summer-early autumn [Xinjiang General Exploration Team of Chinese Academy of Sciences (CAS), and Institute of Botany of CAS, 1978]. Although some seeds are dispersed in autumn, many nondispersed seeds become

covered by snow and are not dispersed until spring. The mature fruit (utricle) with two permanently attached bracteoles is the dispersal/germination unit, and in the field they germinate in late winter/early spring.

The objective of this part of the study was to survey the three kinds of typical habitats (i.e., S, GD, and SD) of Amaranthaceae species in the cold deserts of northern Xinjiang for pre-dispersal germination in autumn and spring. Thirty plants for each species were chosen haphazardly from each kind of habitat to observe pre-dispersal seed germination. If a plant of a species was observed with germinating seeds, the species was considered to have pre-dispersal seed germination. All species observed with pre-dispersal germination had few to many germinating seeds on the plants; especially the annual species had many germinating seeds. Only a few species, e.g., the trees *Haloxylon persicum* and *Haloxylon ammodendron,* had a relatively low number of seeds germinating on the plants, probably due to low snow cover on the branches and thus a low moisture level for the seeds. The number of species of Amaranthaceae with pre-dispersal seed germination was determined in each of the three kinds of habitats. Based on the Xinjiang General Exploration Team of Chinese Academy of Sciences (CAS), and Institute of Botany of CAS (1978), habitat types, life forms [i.e. annual herb (AH), shrub (S), semi-shrub (SS), or small tree (ST)] were recorded. For each species, pre-dispersal seed germination frequency (GF) was calculated as GF = GS/(GS + NGS), where GS and NGS are the number of sites with and without pre-dispersal seed germination, respectively. Information on geographical locations (i.e., longitude, latitude, and altitude) at the sampling sites was obtained using a GARMIN eTrex20 Global Positioning System (Jiaming Avionics Enterprise Management Co., Ltd., Shanghai, China).

### Autumn

Amaranthaceae species were observed for pre-dispersal germinated seeds in a total of 155 sites (i.e., 34, 62, and 59 for S, GD, and SD, respectively; Figure 1) between fruit ripening and before snowfall in late September to early November 2021.

### Spring

In the cold deserts of northern Xinjiang, temperatures increase quickly in early spring, and the snowmelt period is short. Seeds on mother plants can germinate during the short period of snow melting in late winter/early spring. Twelve sites (i.e., four, three, and five of S, GD, and SD, respectively Figure 1) were evaluated during the short snowmelt period from early March to early April 2022. For each species, type of habitat and life form were recorded, and GF was calculated as described above.

## Growth and development stages of seedlings

Growth and development stages of seedlings from pre-dispersal seed germination were monitored for each species

until seedling detachment from their mother plant and establishment in the soil.

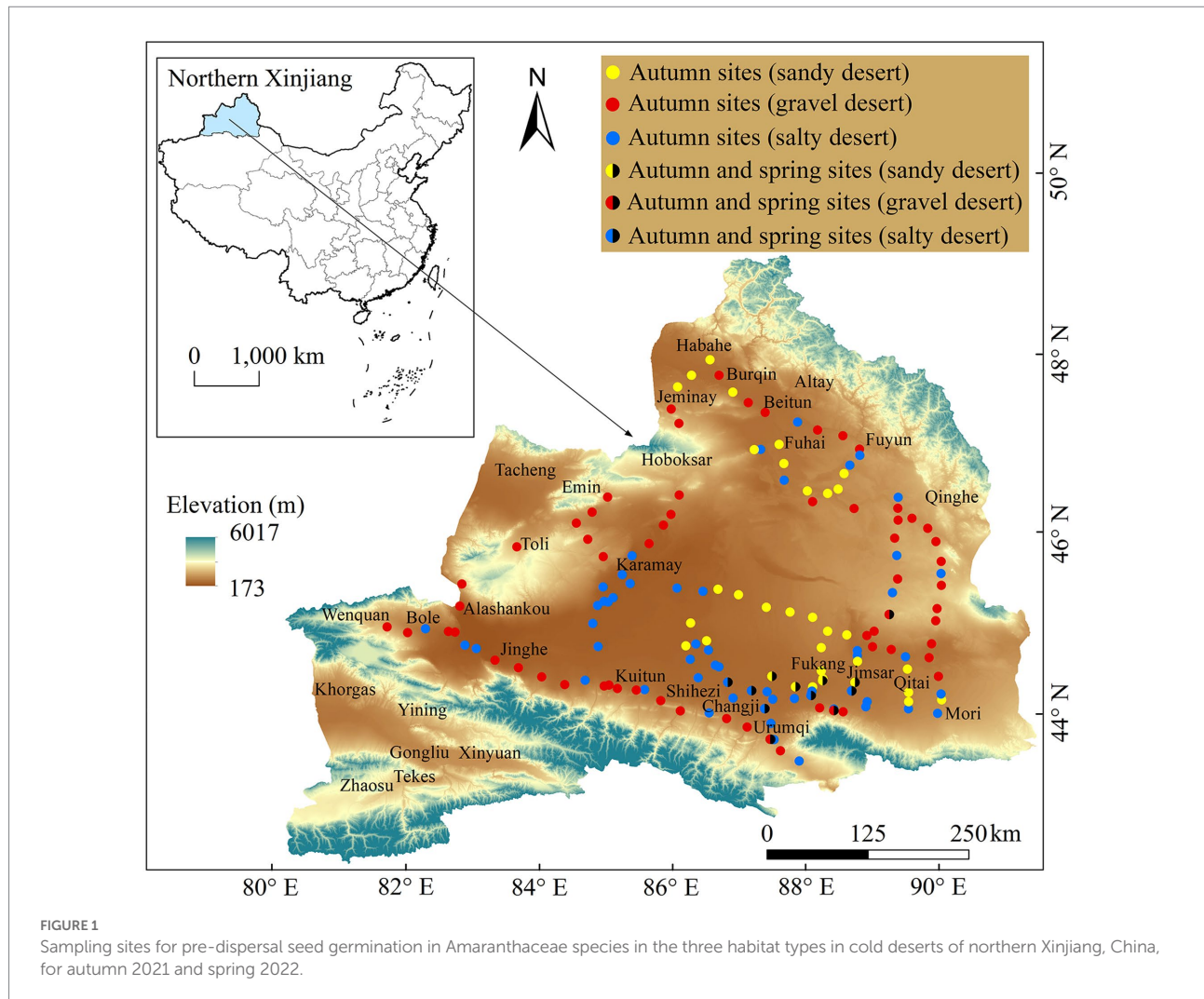## Survival and growth of *Salsola brachiata* seedlings/juveniles

The objective of this part of the study was to do a preliminary evaluation of seedling/juvenile survival in an experimental garden. On 1 November 2021, 100 dead plants of *Salsola brachiata* with mature fruits were collected from a natural population on Yamalic Hill, a suburb of Urümqi city near the southern edge of the cold deserts of northern Xinjiang, China (43°48′ N, 87°34′ E, 966 m a.s.l.). These plants were transplanted to bare soil in a 0.5 m × 1.0 m plot in the experimental garden located on the campus of Xinjiang Agricultural University, Urümqi, China, about 3 km from the population site. During snowmelt in early March 2022, seedlings from (1) pre-dispersal germinated seeds (S1), (2) soil-germinated seeds that had dispersed in autumn and thus under snow all winter (S2), and (3) soil-germinated seeds that were dispersed during snowmelt in spring 2022 (S3) were monitored for survival.

The S1 seedlings were from seeds that germinated on the transplanted dead mother plants and then after about 2–3 days had fallen to the soil. Ten fallen S1 seedlings were transplanted into each of three subplots of a 0.3 m × 0.5 m plot.

On Yamalic Hill, we observed that some seeds of *S. brachiata* were naturally dispersed during autumn (before snowfall) and in winter and the next spring. To ensure that there were seeds on the soil in the garden, we sowed seeds on the soil and on the snow surface. For S2 seedlings, 1,000 seeds were sown on soil in a 0.3 m × 0.5 m plot on 1 November 2021. When S2 seedlings emerged in spring, the plot was divided three smaller plots to monitor survival; there were 20, 15, and 15 seedlings in each of the three smaller plots. For S3 seedlings, 1,000 seeds were sown on the snow surface in a 0.3 m × 0.5 m plot on 24 February 2022. After S3 seedlings emerged, the plot was divided three smaller plots to monitor survival; there were 20, 15, and 15 seedlings in each of the three smaller plots. Thus, there was one plot each for S1, S2, and S3 seedlings/juveniles, and each plot was divided into three 0.16 × 0.10 m plots.

The S1 seedlings were monitored from the time they fell to the soil (6 March 2022) until they reached the four-leaf stage (6 April 2022). Since the S2 seedlings were covered by deep snow, and we could not determine the time of germination; we only saw them on 6 March after the snow had melted. Seeds for the S3 seedlings that were sown on the snow surface did not germinate until all the snow had melted (6 March), and then the seeds were on the soil surface. S2 and S3 seedlings were monitored from the time of germination (3 March 2022) until they reached the four-leaf stage (6 April 2022). In the experimental garden, seedlings were subjected to natural temperature and soil moisture conditions.

Another set of S1, S2, and S3 seedlings was marked with toothpicks to which different colors of thread were tied. After 0 (day of marking), 3, 6, 11, 16, 21, and 27 days of growth, five S1, S2, and S3 seedlings each were harvested and their roots washed

**FIGURE 1**
Sampling sites for pre-dispersal seed germination in Amaranthaceae species in the three habitat types in cold deserts of northern Xinjiang, China, for autumn 2021 and spring 2022.

free of soil. Then, the seedlings were oven-dried at 80°C for 48 h, and the dry mass of each seedling was determined by weighing using an electronic-balance (0.0001 g). The four-leaf stage at 27 days of growth was considered to be the end of the seedling establishment stage.

## Data analysis

Correlative analyses were used to determine the relationship between pre-dispersal seed germination and germinating season (i.e., autumn or spring), between pre-dispersal seed germination and habitat type (i.e., S, GD, and SD), and between pre-dispersal seed germination and life form (i.e., AH, S, SS, and ST). One-way ANCOVAs were used to analyze differences in final survival percentage and dry mass at the 4-leaf stage of S1, S2, and S3 seedlings of *Salsola brachiata*, with initial seedling size (i.e., dry mass) as a covariate to minimize the effects of variation in initial size among seedlings on survivorship. All data analyses were

performed with the software SPSS 19.0 (SPSS Inc., Chicago, IL, United States). Values are means ± 1SE.

## Results

### Autumn survey of pre-dispersal seed germination

In autumn 2021, we observed 69 species in 25 genera of Amaranthaceae in the three habitats (S, 37 species in 17 genera; GD, 51 species in 19 genera; and SD, 51 species in 21 genera). In the three habitats, trends for number of species of each life form were the same. Frequency of both annual herb (AH) and shrub (SH) life forms was the highest, and the rank order of life forms [i.e. annual herb (AH), shrub (SH), semi-shrub (SS), or small tree (ST)] in the three habitats was: S, [AH (25) > SS (9) > ST (2) > SH (1)]; GD, [AH (34) > SS (13) > SH (3) > ST (1)]; and SD, [AH (32) > SS (15) > SH (3) > ST (1)]. In autumn 2021, no species exhibited pre-dispersal seed germination in any of the three habitat types (Table 1).

TABLE 1 Pre-dispersal seed germination (or not) in Amaranthaceae species (in various subfamilies of Amaranthaceae) in the cold deserts of northern Xinjiang in both autumn 2021 and spring 2022 and reports in the literature of very fast germination occurring in the species of Amaranthaceae surveyed in this study.

| Habitat type | Species | Subfamily | Life form | Fast germination (References) | Pre-dispersal seed germination (or not) | | GF |
|---|---|---|---|---|---|---|---|
| | | | | | Autumn | Spring | |
| Sand dunes | | | | | | | |
| | *Agriophyllum squarrosum* | Corispermeoideae | AH | — | ○ | ○ | 0/2 |
| | *Anabasis aphylla* | Salsoloideae | SS | Peng (2020) | ○ | ● | 1/2 |
| | *Atriplex patens* | Atriplicioideae | AH | — | ○ | ○ | 0/1 |
| | *Bassia dasyphylla* | Camphorosmeoideae | AH | Parsons (2012) and Liu et al. (2013) | ○ | ● | 2/4 |
| | *Ceratocarpus arenarius* | Corispermeoideae | AH | — | ○ | ● | 3/4 |
| | *Chenopodium album* | Chenopodioideae | AH | Yao et al. (2010) | ○ | ○ | 0/1 |
| | *Corispermum lehmannianum* | Corispermeoideae | AH | — | ○ | ○ | 0/1 |
| | *Girgensohnia oppositiflora* | Salsoloideae | AH | — | ○ | ● | 1/1 |
| | *Halogeton glomeratus* | Salsoloideae | AH | Parsons (2012) and Liu et al. (2013) | ○ | ● | 1/1 |
| | *Halostachys caspica* | Salicornioideae | SS | — | ○ | ○ | 0/1 |
| | *Haloxylon ammodendron* | Salsoloideae | ST | Parsons (2012) and Liu et al. (2013) | ○ | ● | 2/4 |
| | *Haloxylon persicum* | Salsoloideae | ST | Parsons (2012) and Liu et al. (2013) | ○ | ● | 1/1 |
| | *Horaninovia ulicina* | Salsoloideae | AH | — | ○ | ● | 3/4 |
| | *Kochia laniflora* | Camphorosmeoideae | AH | — | ○ | ○ | 0/1 |
| | *Kochia scoparia* | Camphorosmeoideae | AH | Parsons (2012) and Liu et al. (2013) | ○ | ● | 1/1 |
| | *Krascheninnikovia ceratoides* | Corispermeoideae | SH | — | ○ | ● | 1/2 |
| | *Petrosimonia sibirica* | Salsoloideae | AH | — | ○ | ○ | 0/1 |
| | *Salsola brachiata* | Salsoloideae | AH | Wang et al. (2007) | ○ | ● | 3/3 |
| | *Salsola collina* | Salsoloideae | AH | — | ○ | ○ | 0/1 |
| | *Salsola foliosa* | Salsoloideae | AH | — | ○ | ● | 1/3 |
| | *Salsola heptapotamica* | Salsoloideae | AH | — | ○ | ● | 2/3 |
| | *Salsola nitraria* | Salsoloideae | AH | — | ○ | ● | 3/4 |
| | *Salsola ruthenica* | Salsoloideae | AH | Parsons (2012) and Liu et al. (2013) | ○ | ● | 3/4 |
| | *Suaeda acuminata* | Suaedioideae | AH | Parsons (2012) and Liu et al. (2013) | ○ | ○ | 0/1 |
| | *Suaeda glauca* | Suaedioideae | AH | — | ○ | ● | 1/2 |
| | *Suaeda microphylla* | Suaedioideae | SS | — | ○ | ○ | 0/1 |
| | *Suaeda pterantha* | Suaedioideae | AH | — | ○ | ○ | 0/1 |
| Gravel deserts | | | | | | | |
| | *Anabasis brevifolia* | Salsoloideae | SS | — | ○ | ○ | 0/1 |
| | *Anabasis elatior* | Salsoloideae | SS | Han et al. (2011) | ○ | ● | 2/2 |
| | *Anabasis salsa* | Salsoloideae | SS | — | ○ | ● | 1/1 |
| | *Atriplex aucheri* | Atriplicioideae | AH | Wei et al. (2003) | ○ | ● | 1/1 |
| | *Atriplex cana* | Atriplicioideae | SS | — | ○ | ○ | 0/1 |
| | *Atriplex micrantha* | Atriplicioideae | AH | Liu and Wei (2007) | ○ | ● | 1/1 |
| | *Atriplex tatarica* | Atriplicioideae | AH | — | ○ | ○ | 0/2 |
| | *Ceratocarpus arenarius* | Corispermeoideae | AH | — | ○ | ● | 2/2 |

*(Continued)*

TABLE 1 (Continued)

| Habitat type | Species | Subfamily | Life form | Fast germination (References) | Pre-dispersal seed germination (or not) | | GF |
|---|---|---|---|---|---|---|---|
| | | | | | Autumn | Spring | |
| | *Chenopodium album* | Chenopodioideae | AH | Yao et al. (2010) | ○ | ○ | 0/1 |
| | *Chenopodium glaucum* | Chenopodioideae | AH | — | ○ | ○ | 0/1 |
| | *Girgensohnia oppositiflora* | Salsoloideae | AH | — | ○ | ○ | 0/1 |
| | *Halogeton arachnoideus* | Salsoloideae | AH | — | ○ | ○ | 0/1 |
| | *Halogeton glomeratus* | Salsoloideae | AH | Parsons (2012) and Liu et al. (2013) | ○ | ● | 2/3 |
| | *Haloxylon ammodendron* | Salsoloideae | ST | Parsons (2012) and Liu et al. (2013) | ○ | ○ | 0/1 |
| | *Iljinia regelii* | Salsoloideae | SS | — | ○ | ○ | 0/1 |
| | *Kochia prostrata* | Camphorosmeoideae | SS | Parsons (2012) and Liu et al. (2013) | ○ | ● | 1/2 |
| | *Kochia scoparia* | Camphorosmeoideae | AH | Parsons (2012) and Liu et al. (2013) | ○ | ○ | 0/1 |
| | *Krascheninnikovia ceratoides* | Corispermeoideae | SH | — | ○ | ○ | 0/2 |
| | *Nanophyton erinaceum* | Salsoloideae | SS | — | ○ | ● | 2/2 |
| | *Petrosimonia sibirica* | Salsoloideae | AH | — | ○ | ● | 1/1 |
| | *Salsola affinis* | Salsoloideae | AH | Wei et al. (2007), Parsons (2012) and Liu et al. (2013) | ○ | ● | 2/2 |
| | *Salsola arbuscula* | Salsoloideae | SS | — | ○ | ○ | 0/1 |
| | *Salsola brachiata* | Salsoloideae | AH | Wang et al. (2007) | ○ | ● | 2/3 |
| | *Salsola dshungarica* | Salsoloideae | SS | — | ○ | ● | 1/1 |
| | *Salsola foliosa* | Salsoloideae | AH | — | ○ | ○ | 0/1 |
| | *Salsola heptapotamica* | Salsoloideae | AH | — | ○ | ● | 1/1 |
| | *Salsola nitraria* | Salsoloideae | AH | — | ○ | ● | 1/1 |
| | *Salsola rosacea* | Salsoloideae | AH | — | ○ | ● | 1/1 |
| | *Salsola ruthenica* | Salsoloideae | AH | Parsons (2012) and Liu et al. (2013) | ○ | ○ | 0/1 |
| | *Suaeda pterantha* | Suaedioideae | AH | — | ○ | ○ | 0/1 |
| Salty deserts | | | | | | | |
| | *Anabasis aphylla* | Salsoloideae | SS | — | ○ | ● | 2/2 |
| | *Anabasis elatior* | Salsoloideae | SS | Han et al. (2011) | ○ | ○ | 0/1 |
| | *Anabasis patens* | Salsoloideae | AH | — | ○ | ● | 1/1 |
| | *Anabasis tatarica* | Salsoloideae | AH | — | ○ | ○ | 0/2 |
| | *Atriplex aucheri* | Atriplicioideae | AH | Wei et al. (2003) | ○ | ● | 1/2 |
| | *Bassia hyssopifolia* | Camphorosmeoideae | AH | — | ○ | ● | 1/2 |
| | *Camphorosma monspeliaca* | Camphorosmeoideae | SS | — | ○ | ● | 1/1 |
| | *Ceratocarpus arenarius* | Corispermeoideae | AH | — | ○ | ○ | 0/1 |
| | *Chenopodium album* | Chenopodioideae | AH | Yao et al. (2010) | ○ | ○ | 0/1 |
| | *Girgensohnia oppositiflora* | Salsoloideae | AH | — | ○ | ● | 1/1 |
| | *Halocnemum strobilaceum* | Salicornioideae | SS | — | ○ | ○ | 0/1 |

*(Continued)*

TABLE 1 (Continued)

| Habitat type | Species | Subfamily | Life form | Fast germination (References) | Pre-dispersal seed germination (or not) | | GF |
|---|---|---|---|---|---|---|---|
| | | | | | **Autumn** | **Spring** | |
| | *Halogeton glomeratus* | Salsoloideae | AH | Parsons (2012) and Liu et al. (2013) | ○ | ● | 2/4 |
| | *Halostachys caspica* | Salicornioideae | SH | — | ○ | ○ | 0/3 |
| | *Kalidium caspicum* | Salicornioideae | SS | Parsons (2012) and Liu et al. (2013) | ○ | ○ | 0/1 |
| | *Kalidium foliatum* | Salicornioideae | SS | — | ○ | ○ | 0/2 |
| | *Kochia laniflora* | Camphorosmeoideae | AH | — | ○ | ○ | 0/1 |
| | *Krascheninnikovia ewersmannia* | Corispermeoideae | SH | — | ○ | ○ | 0/1 |
| | *Petrosimonia sibirica* | Salsoloideae | AH | — | ○ | ● | 4/4 |
| | *Salicornia europaea* | Salicornioideae | AH | — | ○ | ○ | 0/1 |
| | *Salsola affinis* | Salsoloideae | AH | Wei et al. (2007), Parsons (2012) and Liu et al. (2013) | ○ | ● | 1/1 |
| | *Salsola brachiata* | Salsoloideae | AH | Wang et al. (2007) | ○ | ● | 1/2 |
| | *Salsola collina* | Salsoloideae | AH | — | ○ | ● | 1/1 |
| | *Salsola foliosa* | Salsoloideae | AH | — | ○ | ● | 2/2 |
| | *Salsola heptapotamica* | Salsoloideae | AH | — | ○ | ● | 5/5 |
| | *Salsola nitraria* | Salsoloideae | AH | — | ○ | ○ | 2/2 |
| | *Salsola ruthenica* | Salsoloideae | AH | Parsons (2012) and Liu et al. (2013) | ○ | ● | 1/1 |
| | *Suaeda acuminata* | Suaedioideae | AH | Parsons (2012) and Liu et al. (2013) | ○ | ○ | 0/3 |
| | *Suaeda glauca* | Suaedioideae | AH | — | ○ | ● | 1/2 |
| | *Suaeda microphylla* | Suaedioideae | SS | — | ○ | ○ | 0/3 |
| | *Suaeda physophora* | Suaedioideae | SS | Parsons (2012) and Liu et al. (2013) | ○ | ○ | 0/2 |
| | *Suaeda salsa* | Suaedioideae | AH | Parsons (2012) and Liu et al. (2013) | ○ | ○ | 0/1 |

AH, annual herb; SH, shrub; SS, semi-shrub; ST, small tree; —, not reported; ●, pre-dispersal seed germination; ○, no pre-dispersal seed germination; GF, pre-dispersal seed germination frequency for each species in each habitat type = GS/(GS + NGS), where GS and NGS are the number of sites with and without pre-dispersal seed germination, respectively.

## Spring survey of pre-dispersal seed germination

At the 12 sites in early spring 2022, we found 52 species in 23 genera in 5 subfamilies of Amaranthaceae: S, 27 species in 17 genera; GD, 30 species in 14 genera; and SD, 31 species in 17 genera. Thirty-three of the 52 species (63.5%) were in subfamily Salsoloideae. Trends for number of species for each life form in S, GD, and SD in spring 2022 were the same as those in autumn 2021.

In early spring 2022, when the snow was melting, 30 species (57.7%) exhibited pre-dispersal seed germination (Table 1; Figure 2). The number of species with pre-dispersal seed germination in S, GD, and SD was 16 (59.3%), 15 (50.0%) and 15 (48.4%), respectively (Table 1; Figure 2). Genera with highest number of species with pre-dispersal seed germination were

*Salsola* (9), *Anabasis* (3), and *Atriplex* (3) (Figure 3A). In early spring, the number of species with pre-dispersal seed germination varied with life form: annuals (66.67%) > small shrubs (23.33%) > small trees (6.67%) > shrubs (3.33%) (Figure 3B). Thirteen species (43.33%) with pre-dispersal seed germination were found in two or more habitats (Figure 3C): S, 8 (50.0%); GD, 6 (40.0%); and SD, 5 (33.3%) (Table 1).

Correlation analysis also showed that the relationship between pre-dispersal seed germination and germination season (autumn vs. spring) was significantly negative ($r = -0.98$, $p < 0.05$). Pre-dispersal seed germination was found in the three habitat types (S, GD, and SD) and in the four life forms (AH, S, SS, and ST). The relationships between pre-dispersal seed germination and habitat type and between pre-dispersal seed germination and life form were nonsignificantly negative ($r = -0.01$, $p = 1.00$) and positive ($r = 0.01$, $p = 0.91$), respectively.
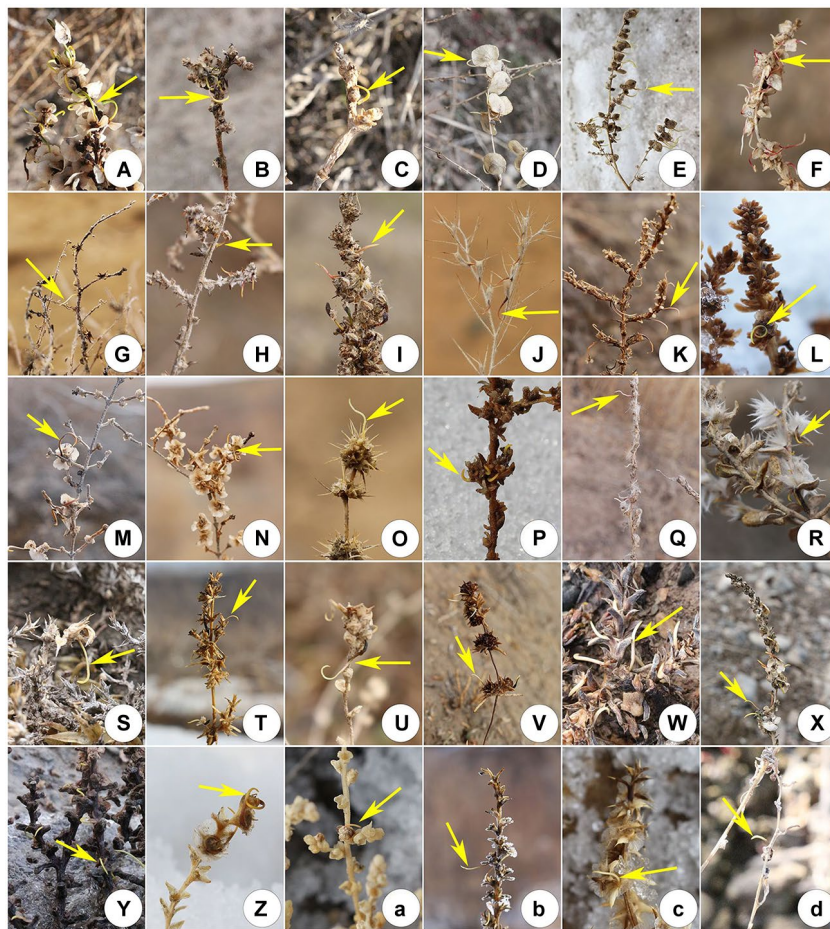
**FIGURE 2**
Pre-dispersal seed germination of 30 Amaranthaceae species in cold deserts of northern Xinjiang during snow-melting in early spring 2022.
**(A)** *Anabasis aphylla*; **(B)** *A. elatior*; **(C)** *A. salsa*; **(D)** *Atriplex aucheri*; **(E)** *A. micrantha*; **(F)** *A. patens*; **(G)** *Bassia dasyphylla*; **(H)** *B. hyssopifolia*;
**(I)** *Camphorosma monspeliaca*; **(J)** *Ceratocarpus arenarius*; **(K)** *Girgensohnia oppositiflora*; **(L)** *Halogeton glomeratus*; **(M)** *Haloxylon*
*ammodendron*; **(N)** *H. persicum*; **(O)** *Horaninovia ulicina*; **(P)** *Kochia prostrata*; **(Q)** *K. scoparia*; **(R)** *Krascheninnikovia ceratoides*; **(S)** *Nanophyton*
*erinaceum*; **(T)** *Petrosimonia sibirica*; **(U)** *Salsola affinis*; **(V)** *S. brachiata*; **(W)** *S. collina*; **(X)** *S. dshungarica*; **(Y)** *S. foliosa*; **(Z)** *S. heptapotamica*; **(a)** *S.*
*nitraria*; **(b)** *S. rosacea*; **(c)** *S. ruthenica*; **(d)** *Suaeda glauca*.

## Stages in development of pre-dispersal germinated seedlings

Development of seedlings from the pre-dispersal germinated seeds for each of the 30 species was similar and can be divided into four stages: (I) the radicle initially emerged between the bracteoles; (II) the radicle completed emergence and hypocotyl emerged between the bracteoles; (III) the cotyledons mostly emerged through the bracteoles; and (IV) seedlings dropped to the soil surface. The development stages of seedlings from pre-dispersal germinated seeds of *Anabasis elatior*, *Atriplex patens*, *Kochia prostrata*, and *Salsola heptapotamica* are shown in Figure 4.

When the pre-dispersal germinated seedlings fell from the mother plants, their cotyledons were fully expanded, but at this time the cotyledons of the seedlings that germinated on the soil had not unfolded.
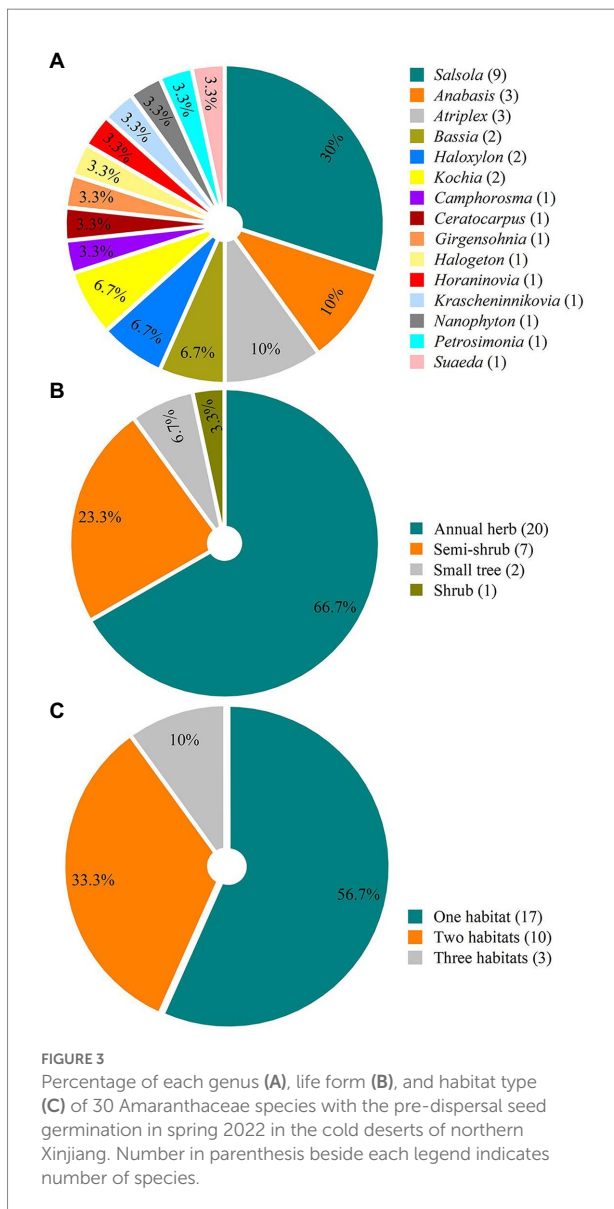
## Survival and growth of *Salsola brachiata* seedlings/juveniles

Final survival of S1 seedlings/juveniles (56.7%) was significantly lower than that of S2 (86.0%) and S3 (84.0%), which did not differ significantly from each other (Figure 5A). The final dry mass of the three types of seedlings did not differ significantly for each other ($p = 0.19$; Figure 5B).

## Discussion

Our prediction that pre-dispersal seed germination is limited to the snowmelt period in spring was supported. At the time of snowmelt in spring, pre-dispersal germination of seeds of various species of Amaranthaceae was documented in sand dunes, gravel deserts, and salt deserts, but no pre-dispersal germination was

**FIGURE 3**
Percentage of each genus **(A)**, life form **(B)**, and habitat type **(C)** of 30 Amaranthaceae species with the pre-dispersal seed germination in spring 2022 in the cold deserts of northern Xinjiang. Number in parenthesis beside each legend indicates number of species.

found in these habitats in autumn. To our knowledge this is the first report of pre-dispersal seed germination in Amaranthaceae or of early survival of seedlings/juveniles of Amaranthaceae with pre-dispersal germination.
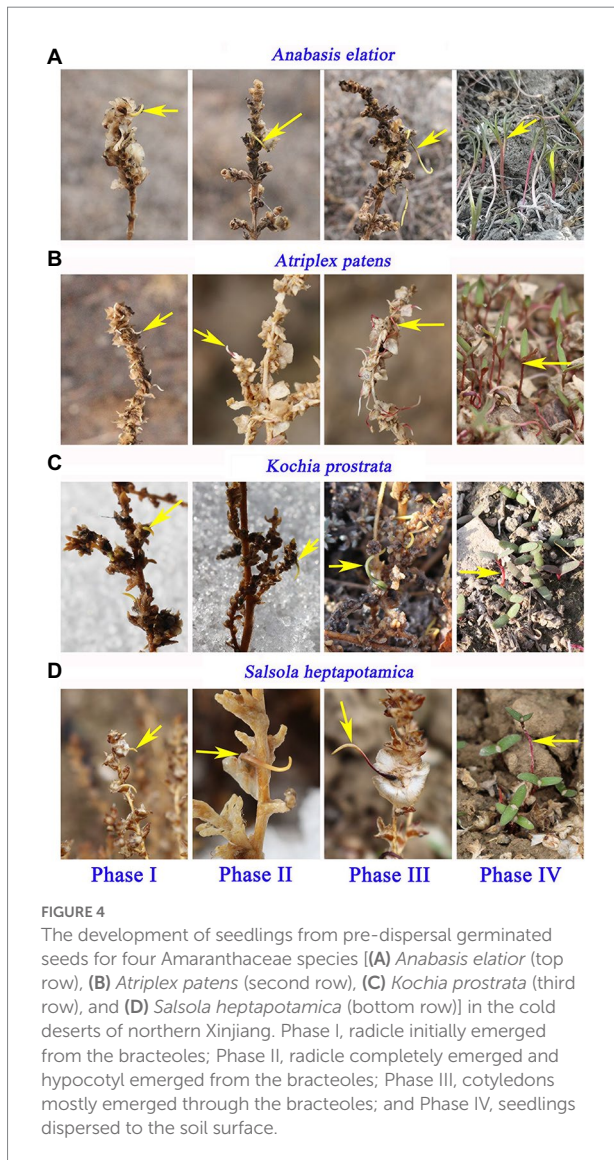
Pre-dispersal seed germination as reported here for various species of Amarnathaceae is not vivipary *sensu stricto*. That is, it is not (sexually-based) true vivipary or cryptovivipary such as occurs in mangroves (Goebel, 1905; Guppy, 1906, 1912; Sussex, 1975; Tomlinson, 1986; Elmqvist and Cox, 1996; Leck and Outred, 2008) in which the embryo does not go through a "rest period" between completion of embryogeny and germination. Growth of the embryo in mangroves is continuous into the seedling stage of the life cycle, and the seeds are desiccation intolerant (recalcitrant).

On the other hand, seeds of Amaranthaceae in our study are desiccation tolerant (orthodox) in storage behavior. Subbiah et al. (2019) did not list any species of Amaranthaceae in their global list of recalcitrant-seeded species. And pre-dispersal seed germination in the Amaranthaceae species certainly is not (asexually-based) pseudo-vivipary (*sensu* Elmqvist and Cox, 1996) in which sexual propagules [caryopses (seeds)] in an inflorescence are replaced, in whole or in part, by asexual (vegetative) propagules, as occurs, for example, in various species of grasses and particularly in those growing at high latitudes and altitudes (e.g., Wycherley, 1953; Moore and Doggett, 1976; Lee and Harmer, 1980; Alsos et al., 2013; Lo Medico et al., 2018).

Another term used to refer to germination of sexually-produced seeds while they are still on the mother plant is pre-harvest sprouting (PHS), which is common in seeds (grains) of cereals, i.e., barely, maize, oats, rice, rye, sorghum, and wheat (all of which have orthodox storage behavior), and causes much economic loss to farmers in many parts of the world. PHS refers to a phenomenon in which developing grains germinate viviparously (precociously) on the mother plant prior to harvest. The primary cause of PHS is lack of dormancy of the grain under humid/wet environmental conditions (e.g., Eyster, 1931; Neill et al., 1987; Lund et al., 2001; Paulsen and Auld, 2004; Rodríguez et al., 2015; Singh et al., 2021; Sohn et al., 2021). However, whereas the cereal grains that germinate viviparously do not go through a rest period before they germinate, seeds of the Amaranthaceae species in our study go through an extended autumn → late winter/early spring rest period (quiescence, dormancy) before they germinate on the mother plant.

Seeds of some species of Amaranthaceae are nondormant at maturity, e.g., the brown seeds of the dimorphic species *Suaeda aralocaspica* (Wang et al., 2008). However, even in species with nondormant seeds, no pre-dispersal germination occurs in late autumn. An important reason for lack of pre-dispersal (and even post-dispersal) germination in autumn in the cold deserts of Central Asia is lack of rainfall during autumn (Lu et al., 2022). Another reason for lack of germination in autumn is that freshly-matured seeds have physiological dormancy, e.g., two of the three seed morphs of *Atriplex centralasiatica* (Wang et al., 2020), two of three seed morphs of *Salsola affinis* (Wei et al., 2008), one of four seed morphs of *S. brachiata* (Baskin et al., 2014), the black seed morph of the dimorphic *Suaeda aralocaspica* (Wang et al., 2008), and both the two basicarps and the aerial dispersal units of *Ceratocarpus arenarius* (Lu et al., 2013).

Pre-dispersal germination in spring requires that some seeds remain on the mother plant over winter. Although seeds may be dispersed in mid-to late autumn, many are not dispersed, probably (at least in part) because they become covered by snow. Thus, two cohorts of seeds from the same mother plants are present in spring: seeds dispersed to the soil
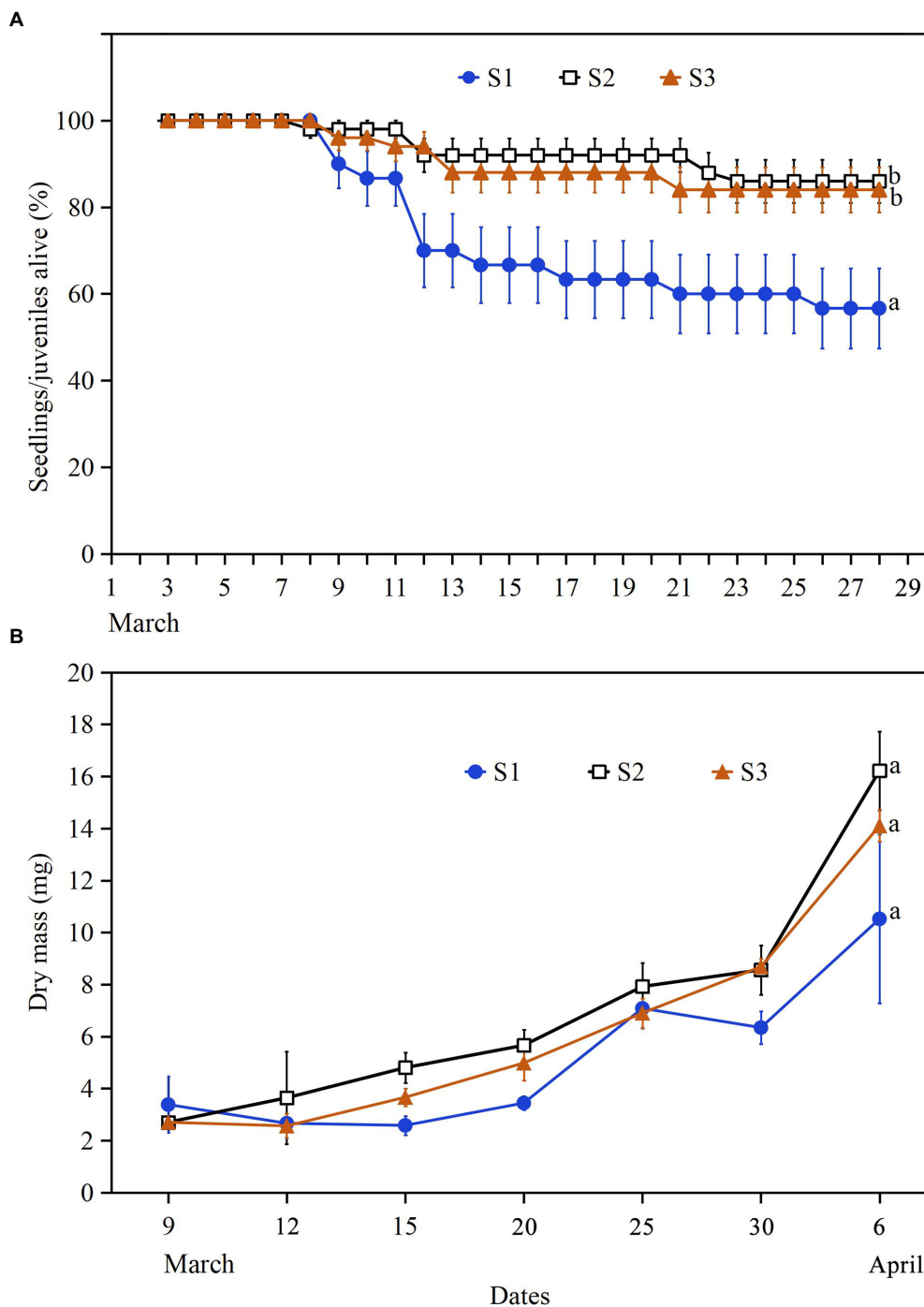
**FIGURE 4**
The development of seedlings from pre-dispersal germinated seeds for four Amaranthaceae species [**(A)** *Anabasis elatior* (top row), **(B)** *Atriplex patens* (second row), **(C)** *Kochia prostrata* (third row), and **(D)** *Salsola heptapotamica* (bottom row)] in the cold deserts of northern Xinjiang. Phase I, radicle initially emerged from the bracteoles; Phase II, radicle completely emerged and hypocotyl emerged from the bracteoles; Phase III, cotyledons mostly emerged through the bracteoles; and Phase IV, seedlings dispersed to the soil surface.

surface and covered by snow and seeds not dispersed and still attached to dead stems of mother plants that are covered by snow.

The number of plants with seeds remaining on them the following spring varied with the life form and habitat type (Table 1). For example, in the S habitat type only a few seeds remained on the small trees (*Haloxylon ammodendron* and *Haloxylon persicum*) and the shrub (*Krascheninnikovia ceratoides*), while many seeds remained on the annuals (*Ceratocarpus arenarius* and *Salsola brachiata*) and semi-shrubs (*Anabasis aphylla* and *Suaeda microphylla*). Likewise, for the same species the number of seeds remaining on the plants varied in habitat types. For example, in *Haloxylon ammodendron* some seeds of this species remained on the mother plants in S, while no seeds remained on the plants in GD.

The seeds attached to the dead stems of mother plants are the first ones exposed to increasing temperatures in spring (and to high moisture levels due to melting snow), and they germinate rapidly. Nondormant seeds that can germinate in <24 h from the beginning of imbibition to radicle emergence are said to be "very fast germinating" (Parsons, 2012; Liu et al., 2013; Parsons et al., 2014; Kadereit et al., 2017). At maturity, seeds with very fast germination are characterized by fully developed and often chlorophyllous embryos, and they occur in taxa whose fresh seeds are either nondormant or have nondeep physiological dormancy (Parsons, 2012; Liu et al., 2013). Liu et al. (2013) used the term "cryptoviviparous-like" to describe seeds with very fast germination. Based on available literature, very fast germination is mainly found in stressful, highly dynamic and pioneer habitats, where it reduces chances of seedling mortality (Karrenberg et al., 2002; Gutterman, 2003). Of the 49 species reported to have very fast germinating seeds, 27 (55%) are in the Amaranthaceae (Parsons, 2012; Parsons et al., 2014; Kadereit et al., 2017). Thirteen of the 30 species with pre-dispersal germination in our study have been reported to have very fast germination (Table 1). Five species (i.e., *Chenopodium album*, *Kalidium caspicum*, *Suaeda acuminata*, *Suaeda physophora*, and *Suaeda salsa*) have been reported to have very fast germination, but we did not find pre-dispersal germination for them in spring 2022. One possible reason is that the plants of these five "winter-upright" species are too tall to have good snow cover, and thus seeds did not have the high moisture level required for germination.

More plants of *S. brachiata* from the post-dispersal germinated seeds survived to the four-leaf stage than those from the pre-dispersal germinated seeds. In the cold deserts of Central Asia, rainfall is highly variable among seasons and years, but generally rainfall is higher in spring than in autumn (Wang et al., 2006). Further, snowmelt increases water availability in spring, which promotes seedling establishment (Lu et al., 2014a,b; Bie et al., 2016). It seems reasonable that pre-dispersal germination in a low rainfall year would result in earlier establishment/growth of seedlings from pre-dispersal than those from post-dispersal germinating seeds. Further, although many seedlings from pre-dispersal germinating seeds die, their seed production per plant could be higher than that of those from post-dispersal germinating seeds (*sensu* Wang et al., 2010). The lower survival percentages of plants from pre-dispersal than post-dispersal germinating seeds suggests that pre-dispersal germination may be maladaptive, but more studies are needed.

In conclusion, the results from our study raise several questions. For example, are the seeds with and without pre-dispersal germination the same size and have the same degree of dormancy? In the achene-dimorphic species *Grindelia squarrosa* (Asteraceae), only disc achenes had pre-dispersal germination, i.e., no ray achenes germinated; disc achenes are less dormant than ray achenes (Pliszki and Górecki, 2021). Additionally, what might be the effect of

**FIGURE 5**
Percentages (mean±SE) of seedlings/juveniles alive **(A)** and dry mass of seedlings **(B)** of *Salsola brachiata* in spring 2022. S1, seedlings from plant-germinated seeds; S2, seedlings from soil-germinated seeds that dispersed before snow in autumn 2021; S3, seedlings from soil-germinated seeds that dispersed in winter 2021 and at snowmelt in early spring 2022. Different lowercase letters indicate significant differences in final percentage survival **(A)** or final dry mass **(B)** of S1, S2, and S3 seedlings.

climate change on the life history, ecology, and demography on Amaranthaceae species with pre-dispersal germination in the cold deserts, especially with regard to amount and frequency of precipitation? These questions need to be addressed by future research.

# Data availability statement

The original contributions presented in the study are included in the article, further inquiries can be directed to the corresponding author.

## Ethics statement

No specific permits were required for the described field studies. The locations are not privately-owned or protected in any way, and the field studies did not involve endangered or protected species.

## Author contributions

JL and DT conceived and designed the experiments. JL, WL, and JH performed data collection. JL analyzed the data. JL, DT, CB, and JB wrote the manuscript. All authors contributed to the article and approved the submitted version.

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## Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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