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Competition / colonization trade off in the invasive annual grass Aegilops tauschii based on seed position effects

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Abstract

Aegilops tauschii is an invasive grass with seed position effects in wheat (*Triticum aestivum*) fields, and its presence results in decreased grain yield. Competition between the invasive *A. tauschii* and wheat was reported in several studies, however, seed position effects in *A. tauschii* haven't been taken into account. In the present study, seeds from three diaspore positions in compound spike and two/three seed positions in diaspore of *A. tauschii* and seeds of *T. aestivum* were mono- and mixed cultured under different planting ratios. For both species, plant height, number of tillers per plant, number of seeds per plant and mass of seeds per plant were counted and measured after maturation. Also, relative competitive intensity (RCI) and relative performance in interspecific pairs and intraspecific pairs (LnRR□inter/intra) were determined. Plant height of *A. tauschii* increased, while number of tillers, number of seeds and seed mass per plant decreased as diaspore/seed position on *A. tauschii* increased under both mono- and mixed culture conditions. Plant height of *T. aestivum* decreased, while number of tillers, number of seeds and seed mass per plant increased as diaspore/seed positions of *A. tauschii* increased in mixed culture. Regardless of seed position, competitive ability of *A. tauschii* was higher than that of *T. aestivum*. Intraspecific competition intensity was higher than interspecific competition intensity in *A. tauschii* while it was the opposite in *T. aestivum*. In most cases for *A. tauschii*, growth indicators were highest while RCI was the lowest in the mixed culture ratio of 3:3, indicating that *A. tauschii* had the strongest competitive ability when the number of *A. tauschii* and *T. aestivum* plants was equal. RCI of *A. tauschii* increased as diaspore/seed position increased indicating that competitive ability decreased. Potential ability of *A. tauschii* to colonize new environments increases as diaspore/seed positions increases. Thus, there is a colonization/competition trade-off, which is beneficial for species adaptation in diverse environments.

Introduction

Plants growing in the same microsite may compete with each other for the various resources needed for survival and growth. Competitive interaction among plants can affect plant survival, growth and reproduction (Johnson et al. 2008; Kula et al. 2020; Cao et al. 2025; Shen et al. 2026). Generally, plant survival and growth tend to be better in the absence of than in the presence of competition (Kula et al. 2020; Cao et al. 2025). However, Sheppard (2019) found that some alien species performed better with regard to some growth traits when they were exposed to a certain degree of competition, which is closely related to resource supply and distribution (Craine and Dybzinski 2013; Liu et al. 2016), plant size (Park et al. 2003), and seed production (Ferenc and Sheppard 2020). Many studies have shown that larger plants have an advantage in competition (Schwinning and Weiner 1998; Huang et al. 2017), which is conducive to their success in producing seeds. Also, seed size/mass is an important indicator of competitive ability in plants (Turnbull et al. 2004; Sheppard 2009; Graebner et al. 2014). Therefore, plant size and seed size/mass are important indicators that need to be considered in competition studies.

Intraspecific competition occurs among different individuals of the same plant species and interspecific competition among plants of different species that require the same or similar resources for survival or

growth (Begon et al. 2006; Cao et al. 2025; Guo et al. 2025; Shen et al. 2026). Studies suggest that the intensity of intraspecific competition is greater than that of interspecific competition because plants of the same species have the same resource demands (Goldberg and Barton 1992; Turnbull et al. 2004; Woo et al. 2020; Cao et al. 2025). However, the intensity of interspecific competition can be greater than that of intraspecific competition. For instance, Sheppard (2019) found that the intensity of interspecific competition among invasive plants was greater than that of intraspecific competition. However, native plants are showed more susceptible to interspecific competition (Golivets and Wallin 2018), while invasive plants experience relatively stronger intraspecific competition (Golivets and Wallin 2018; Cao et al. 2025). Also, invasive plants may be more affected when competing with other invasive species than when competing with native plants (Kuebbing and Nuñez 2016). Ferenc and Sheppard (2020) found that for most invasive plants the intensity of interspecific competition among them was greater than that of intraspecific competition. Therefore, the intensity of intraspecific and interspecific competition depends on the target plant species and the species it is grown with. However, in these studies, intraspecific and interspecific competition often are investigated separately. It remains unclear how the intensity of intraspecific and interspecific competition affects plants especially the invasive species, when both types of competition occur in the same experiment.

Aegilops tauschii Coss is an invasive annual grass (Poaceae) which is indigenous to Eastern Europe and Western Asia (Wang et al. 2021a). Wild populations of *A. tauschii* occur widely in arid and semi-arid environments across central Eurasia, extending from Turkey to western China (Zhou et al. 2021). Within China, the species has rapidly colonized the critical winter wheat-growing provinces of Shandong, Shanxi, Shaanxi, Henan, and Hebei (Wang et al. 2021a; He et al. 2026), and it is now recognized as one of the most challenging weeds to manage in wheat fields (Fang et al. 2012; He et al. 2026). Numerous studies have reported the effects of competition between the invasive *A. tauschii* and wheat. Fang et al (2014) found that as number of diaspores (spikelets) in *A. tauschii* increased, number of diaspores and yield of wheat decreased significantly. Wang et al (2018b) compared the morphology and biomass of *A. tauschii* and wheat grown alone and in a 1:1 mixture at different NH_4NO_3 concentrations, and they found that increase of NH_4NO_3 concentration enhanced competitive ability of *A. tauschii* against wheat. Under high nitrogen conditions, addition of phosphorus, increased soil nutrient heterogeneity, salt stress and waterlogging treatments enhanced the competitive effect of *A. tauschii* on wheat (Wang et al. 2018; Wang et al. 2021b; Wang et al. 2023a; Wang et al. 2023b). Moreover, under a 3:3 mixed culture of *A. tauschii* and wheat, plant height, number of tillers per plant and total biomass of plants of *A. tauschii* were significantly higher than that of wheat, and interspecific competition intensity between *A. tauschii* and wheat was less than the intraspecific competition intensity in *A. tauschii* (Wang et al. 2021a).

Our previous studies on seed ecology of *A. tauschii* showed significant seed position effects on life history traits (Wang et al. 2022; 2023; 2024); however, seeds of *A. tauschii* used in competition studies mentioned above were not classified according to their positions on mother plant. Thus, the effect of seed position on competition between *A. tauschii* and wheat are not known, and the influence of different culture ratios on competition between these two species has not been determined. Thus, in the present

study, seeds in different diaspore positions and seed positions on mother plants of *A. tauschii* were sown alone and mixed with seeds of wheat (*Triticum aestivum*) in different ratios (Since seeds of wheat almost in the same quality and size were always chosen in agricultural industry without considering their positions, seed position of wheat were not included in this study). Five culture ratios were set in the mixed treatment. Plant height, number of tillers per plant, number of seeds per plant and mass of seeds per plant of *A. tauschii* and wheat were determined. Differences among different diaspore and seed positions, between *A. tauschii* and wheat and among different treatments were compared. Also, relative competitive intensity (RCI) and relative performance in interspecific pairs and intraspecific pairs (LnRR□inter/intra) were determined.

Our aim was to test the effect of seed position on *A. tauschii* plants on competitive ability of offspring when grown with wheat. Specifically, we asked:

1. 1. What about the competitive ability of seeds in different positions of *A. tauschii*?
2. 2. What about the significance of seed position effects of *A. tauschii* in intraspecific and interspecific competition?
3. 3. What about differences in interspecific and intraspecific competitive ability between *A. tauschii* and wheat?

Materials and methods

Seed collection

The study was conducted in greenhouse at Henan University. Seeds were collected from about 3,000 individual plants each of *Aegilops tauschii* and of *Triticum aestivum* (wheat) growing at the study site on June 2–12, 2023, at which time seeds of both species were fully matured. Seeds from two positions of each of diaspores B and D and three positions of diaspore M4 in *A. tauschii* were isolated (Fig. 1a).

Competition experiment design

Germination was conducted at 22/12℃ (12h light/12h dark) which mimics the field temperature during the germination season. Germinated seeds with coleorhizae about 1cm long were transplanted into pots (36 cm-diameter and 42 cm-height) on the same day. The monoculture and mixed culture treatments of *A. tauschii* and *T. aestivum* were established, with the ratios of mixed culture being 1:5, 2:4, 3:3, 4:2 and 5:1. Each pot contained 6 plants. Each treatment had 6 replicates (Fig. 1b). During the study period, appropriate watering was provided to ensure normal growth of seedlings/plants. When plants were mature (1–8 June 2024), plant height, number of tillers per plant, number of seeds per plant and seed mass per plant were measured/counted for both species.

Relative competitive intensity (RCI) of each treatment was calculated according to the formula: RCI = (Pmono – Pmix) / Pmono (Weigelt and Jolliffe 2003). Pmono represents the performance of plants

under monoculture conditions, and Pmix performance of plants under mixed culture conditions. The higher the RCI value, the greater the competitive intensity and the weaker the competitive ability of the two species.

To compare intraspecies and interspecies competitive intensity of *A. tauschii* and *T. aestivum*, relative performance of interspecies and intraspecies pairs was calculated according to the formula: LnRR□inter/intra = $\log_{10}$ (performance of interspecies pair / performance of intraspecies pair) (Weigelt and Jolliffe 2003; Ferenc and Sheppard 2020). A positive result indicates a greater intraspecies competitive intensity and a negative result a greater interspecies competitive intensity. Monoculture represents the intraspecies pair, and when the culture ratio of *A. tauschii* and *T. aestivum* was 3: 3 it represented the interspecies pair of *A. tauschii* and *T. aestivum*.

Statistical analysis

Generalized linear model (GLM) was used to test effects of diaspore position in compound spike, of seed position in diaspore, species, culture ratios and their interactions on plant height, number of tillers per plant, number of seed per plant and seed mass, relative competitive intensity and relative performance of *A. tauschii* and *T. aestivum*.

One-way analysis of variance (ANOVA) was used to test the differences of each trait among different positions of diaspores, different positions of seeds and different culture ratios, and between different species. Before analysis, normality and homogeneity of variance tests were conducted on all data to meet the requirements of variance analyses. If data were normally distributed and homoscedastic, further analyses were carried out. If data did not meet the normal distribution and homoscedasticity requirements, they were $\log_{10}$ or square root transformed (untransformed data ± standard error are shown in all figures and tables).

All data analyses were performed using the R language software (R version 4.2.1). Tukey's HSD test was used to determine whether the differences among treatments were significant ($P < 0.05$).

Results

Plant height

In monoculture, position of diaspore on compound spike ($P < 0.001$) and the interaction of position of diaspore on compound spike and seed position in diaspore ($P < 0.001$) significantly affected plant height of *A. tauschii*, while seed position in diaspore did not ($P > 0.05$). Plant height of *A. tauschii* increased with an increase of diaspore position on compound spike and seed position in diaspore. That is, plants derived from distal diaspore / seeds were the tallest, while those from basal ones were the shortest; plants derived from middle diaspores / seeds were intermediate in height (Fig. 2a).

In mixed culture, diaspore position in compound spike ($P < 0.001$), seed position in diaspore ($P < 0.001$), culture ratio ($P < 0.001$) and interaction of diaspore position in compound spike and seed position in diaspore ($P < 0.05$) significantly affected plant height of *A. tauschii*, while other interactions did not ($P > 0.05$). Plant height of *A. tauschii* increased as diaspore / seed position increased. As culture ratio of *A. tauschii* and *T. aestivum* increased, plant height of *A. tauschii* increased and then decreased, and the highest and lowest values were in 3 : 3 and 1 : 5 culture ratios, respectively. (Fig. 3).

When cultured with *A. tauschii*, diaspore positions in compound spike of *A. tauschii* ($P < 0.001$) and culture ratio ($P < 0.001$) significantly affected plant height of *T. aestivum*, while seed position in diaspore and all other interactions did not. Plant height of *T. aestivum* decreased as diaspore position in compound spike and seed position in diaspore of *A. tauschii* increased. That is, plant height of *T. aestivum* was highest and lowest when plants of *T. aestivum* were grown with plants derived from basal and distal diaspores / seeds of *A. tauschii*, respectively. As culture ratio increased, plant height of *T. aestivum* significantly decreased. Plant height of *T. aestivum* was highest and lowest in culture ratios of 1 : 5 and 5 : 1, respectively (Fig. 3).

In monoculture, plant height of *T. aestivum* was significantly higher than that of *A. tauschii* ($P < 0.001$) (Fig. 2a), while it was the opposite in mixed culture ($P < 0.05$) (Fig. 3). For *A. tauschii*, plant height was significantly higher in mixed than in monoculture, while it was the opposite for *T. aestivum* (Fig. 2a, Fig. 3).

Number of tillers per plant

In monoculture, number of tillers per plant of *A. tauschii* was significantly affected by diaspore position in compound spike ($P < 0.001$) but not by seed position in diaspore ($P > 0.05$) or by the interaction of diaspore position in compound spike and seed position in diaspore ($P > 0.05$). As diaspore position in compound spike and seed position in diaspore increased, number of tillers per plant of *A. tauschii* significantly decreased. (Fig. 2b).

In mixed culture, diaspore position in compound spike ($P < 0.001$), seed position in diaspore ($P < 0.001$), culture ratio ($P < 0.001$) and interaction of diaspore position in compound spike and culture ratio ($P < 0.001$) significantly affected number of tillers per plant of *A. tauschii*, while other interactions did not. As diaspore position in compound spike and seed position in diaspore increased, number of tillers per plant of *A. tauschii* significantly decreased. As culture ratio increased, number of tillers per plant of *A. tauschii* significantly increased and then decreased. That is, number of tillers per plant was highest and lowest in mixed culture ratio 3 : 3 and 1 : 5, respectively (Fig. 4).

When cultured with *A. tauschii*, diaspore position in compound spike of *A. tauschii* ($P < 0.001$), seed position in diaspore of *A. tauschii* ($P = 0.002$), culture ratio ($P < 0.001$) and interaction of diaspore positions in compound spike of *A. tauschii* and culture ratio ($P < 0.001$) significantly affected the number of tillers per plant of *T. aestivum*, while other interactions did not. Number of tillers per plant of *T. aestivum* increased as diaspore positions in compound spike and seed position in diaspore of *A. tauschii*

increased. Number of tillers per plant of *T. aestivum* was highest and lowest when plants of *T. aestivum* were grown with plants derived from distal and basal diaspores / seeds of *A. tauschii*, respectively. As culture ratio increased, number of tillers per plant of *T. aestivum* significantly decreased, i.e., number of tillers per plant of *T. aestivum* was highest and lowest in culture ratios of 1 : 5 and 5 : 1, respectively (Fig. 4).

In both monoculture and mixed culture, number of tillers per plant of *A. tauschii* was significantly higher than that of *T. aestivum* ($P < 0.05$) (Fig. 2b). For *A. tauschii*, number of tillers per plant was significantly higher in mixed than in monoculture, while it was the opposite for *T. aestivum* (Fig. 2b, Fig. 4).

Number of seeds per plant

In monoculture, diaspore position in compound spike ($P < 0.001$), seed position in diaspore ($P < 0.001$) and their interaction ($P < 0.001$) significantly affected number of seeds per plant of *A. tauschii*. As diaspore position and seed position increased, number of seeds per plant of *A. tauschii* significantly decreased (Fig. 2c).

In mixed culture, diaspore position in compound spike ($P < 0.001$), seed position in diaspore ($P = 0.013$), culture ratio ($P < 0.001$) and their interactions ($P < 0.05$) significantly affected number of seeds per plant of *A. tauschii*. As diaspore position and seed position increased, number of seeds per plant of *A. tauschii* significantly decreased. As culture ratio increased, number of seeds per plant of *A. tauschii* decreased and then increased and was highest and lowest in culture ratios of 3 : 3 and 5 : 1, respectively (Fig. 5).

When cultured with *A. tauschii*, diaspore positions in compound spike of *A. tauschii* ($P < 0.001$), culture ratio ($P < 0.001$) and their interaction ($P < 0.05$) significantly affected number of seeds per plant of *T. aestivum*, while seed position in diaspore and interactions of seed position in diaspore or any other factor did not ($P > 0.05$). Number of seeds per plant of *T. aestivum* increased as diaspore positions in compound spike and seed position in diaspore of *A. tauschii* increased. Number of seeds per plant of *T. aestivum* was highest and lowest when plants of *T. aestivum* were grown with plants derived from distal and basal diaspores / seeds of *A. tauschii*, respectively. As culture ratio increased, number of seeds per plant of *T. aestivum* significantly decreased. That is, number of seeds per plant of *T. aestivum* was highest and lowest in culture ratios of 1 : 5 and 5 : 1, respectively (Fig. 5).

In both monoculture and mixed culture, number of seeds per plant of *A. tauschii* was significantly higher than that of *T. aestivum* ($P < 0.05$) (Fig. 2c, Fig. 5). For *A. tauschii*, number of seeds per plant was significantly higher in mixed than in monoculture, while it was the opposite for *T. aestivum* (Fig. 2c, Fig. 5).

Seed mass per plant

In monoculture, diaspore position in compound spike ($P < 0.001$) and interaction of diaspore position in compound spike and seed position in diaspore ($P < 0.001$) significantly affected seed mass per plant of *A. tauschii*. As diaspore position in compound spike and seed position in diaspore increased, seed mass per plant of *A. tauschii* decreased (Fig. 2d).

In mixed culture, diaspore position in compound spike ($P = 0.011$), seed position in diaspore ($P = 0.032$), culture ratio ($P < 0.001$) and their interactions ($P < 0.05$) significantly affected seed mass per plant of *A. tauschii*. As diaspore position in compound spike and seed position in diaspore increased, seed mass per plant of *A. tauschii* decreased. With an increase in culture ratio, seed mass per plant of *A. tauschii* increased and then decreased, and it was highest and lowest in culture ratios of 3 : 3 and 5 : 1, respectively (Fig. 6).

When cultured with *A. tauschii*, diaspore position in compound spike of *A. tauschii* ($P < 0.001$), culture ratio ($P < 0.001$) and their interaction ($P < 0.05$) significantly affected seed mass per plant of *T. aestivum*, while seed position in diaspore and interactions of seed position in diaspore and no other factor did so ($P > 0.05$). Seed mass per plant of *T. aestivum* increased as diaspore position in compound spike and seed position in diaspore of *A. tauschii* increased. Seed mass per plant of *T. aestivum* was highest and lowest when plants of *T. aestivum* were grown with plants derived from distal and basal diaspores / seeds of *A. tauschii*, respectively. As culture ratio increased, seed mass per plant of *T. aestivum* significantly decreased. Seed mass per plant of *T. aestivum* was highest and lowest in culture ratios of 1 : 5 and 5 : 1, respectively (Fig. 6).

Seed mass per plant of *A. tauschii* was significantly lower in monoculture ($P < 0.001$) and in mixed culture ratios of 3 : 3, 2 : 4 and 1 : 5 ($P < 0.05$) than that of *T. aestivum* (Fig. 2d, Fig. 6). For *A. tauschii*, seed mass per plant was significantly higher in mixed than in monoculture, while it was the opposite for *T. aestivum* (Fig. 2d, Fig. 6).

Relative competitive intensity and relative performance of interspecies and intraspecies pairs

Diaspore position in compound spike ($P < 0.001$) and culture ratio ($P < 0.001$) significantly affected relative competition index (RCI) represented by any growth trait of *A. tauschii*, while seed position in diaspore ($P > 0.05$) and all interactions ($P > 0.05$) did not. RCI of all growth traits in *A. tauschii* increased as diaspore position and seed position increased in most mixed culture ratios. When compared with *T. aestivum*, height, number of tillers per plant, number of seeds per plant and seed mass per plant were of more advantage to plants derived from basal diaspores / seeds than distal ones of *A. tauschii*. As mixed culture ratio increased, RCI of all growth traits of *A. tauschii* decreased and then increased, which was the highest and lowest in mixed culture ratio 1 : 5 and 3 : 3, respectively (except in a few cases). Competitive ability of *A. tauschii* was highest and lowest in mixed culture ratio 3 : 3 and 1 : 5, respectively (Table 1).

Table 1
Relative competition index of *Aegilops tauschii* grown with *Triticum aestivum*

Culture ratio	P1	P2	Height	No. of tillers per plant	No. of seeds per plant	Mass of seeds per plant
1 : 5	B	1	-0.46 ± 0.06 Aa	-0.05 ± 0.04 Aa	-0.19 ± 0.05 Bb	-0.16 ± 0.08 Ab
		2	-0.48 ± 0.13 Aa	-0.05 ± 0.04 Aa	-0.12 ± 0.07 Ba	-0.08 ± 0.06 Aa
	M4	1	-0.31 ± 0.04 Aa	-0.05 ± 0.06 Aa	-0.11 ± 0.08 ABa	-0.04 ± 0.04 Aa
		2	-0.34 ± 0.05 Aa	-0.05 ± 0.04 Aa	-0.10 ± 0.04 ABa	-0.02 ± 0.03 Aa
		3	-0.33 ± 0.05 Aa	-0.04 ± 0.03 Aa	-0.09 ± 0.07 ABa	-0.01 ± 0.06 Aa
	D	1	-0.35 ± 0.04 Aa	-0.03 ± 0.03 Aa	-0.07 ± 0.06 Aa	0.02 ± 0.06 Aa
		2	-0.33 ± 0.03 Aa	-0.03 ± 0.05 Aa	-0.07 ± 0.08 Aa	0.04 ± 0.06 Aa
2 : 4	B	1	-1.01 ± 0.04 Ba	-0.21 ± 0.08 Ab	-0.82 ± 0.17 Bb	-0.79 ± 0.11 Bb
		2	-1.00 ± 0.14 Ba	-0.17 ± 0.05 Aa	-0.66 ± 0.12 Ba	-0.69 ± 0.22 Ba
	M4	1	-0.60 ± 0.07 Aa	-0.17 ± 0.06 Ab	-0.55 ± 0.05 ABb	-0.49 ± 0.11 Ac
		2	-0.60 ± 0.06 Aa	-0.15 ± 0.03 Aab	-0.50 ± 0.06 ABab	-0.38 ± 0.07 Ab
		3	-0.60 ± 0.08 Aa	-0.14 ± 0.06 Aa	-0.46 ± 0.04 ABa	-0.28 ± 0.07 Aa
	D	1	-0.49 ± 0.08 Aa	-0.11 ± 0.03 Aa	-0.39 ± 0.08 Aa	-0.23 ± 0.10 Aa
		2	-0.44 ± 0.07 Aa	-0.08 ± 0.03 Aa	-0.30 ± 0.06 Aa	-0.14 ± 0.12 Aa
3 : 3	B	1	-1.36 ± 0.06 Ba	-0.42 ± 0.08 Aa	-1.74 ± 0.16 Ba	-1.71 ± 0.16 Aa
		2	-1.32 ± 0.17 Ba	-0.43 ± 0.05 Aa	-1.64 ± 0.06 Ba	-1.61 ± 0.18 Aa
	M4	1	-0.93 ± 0.13 Aa	-0.42 ± 0.06 Aa	-1.49 ± 0.06 ABa	-1.36 ± 0.11 Ab

Culture ratio	P1	P2	Height	No. of tillers per plant	No. of seeds per plant	Mass of seeds per plant
		2	-0.87 ± 0.04 Aa	-0.42 ± 0.06 Aa	-1.38 ± 0.06 ABa	-1.24 ± 0.22 Aa
		3	-0.90 ± 0.11 Aa	-0.40 ± 0.04 Aa	-1.44 ± 0.15 ABa	-1.21 ± 0.09 Aa
	D	1	-0.75 ± 0.09 Aa	-0.40 ± 0.02 Aa	-1.33 ± 0.14 Ab	-1.10 ± 0.13 Aa
		2	-0.74 ± 0.07 Aa	-0.37 ± 0.08 Aa	-1.23 ± 0.22 Aa	-1.05 ± 0.27 Aa
4 : 2	B	1	-1.33 ± 0.07 Ba	-0.35 ± 0.08 Aa	-0.94 ± 0.18 Ba	-0.81 ± 0.18 Bb
		2	-1.25 ± 0.18 Ba	-0.35 ± 0.04 Aa	-0.88 ± 0.10 Ba	-0.67 ± 0.06 Ba
	M4	1	-0.93 ± 0.14 Ab	-0.31 ± 0.06 Aa	-0.77 ± 0.05 ABa	-0.51 ± 0.07 Bb
		2	-0.79 ± 0.06 Aa	-0.27 ± 0.04 Aa	-0.68 ± 0.08 ABa	-0.44 ± 0.08 Bab
		3	-0.80 ± 0.15 Aa	-0.27 ± 0.07 Aa	-0.71 ± 0.14 ABa	-0.41 ± 0.09 Ba
	D	1	-0.72 ± 0.09 Aa	-0.26 ± 0.06 Aa	-0.68 ± 0.11 Ab	-0.39 ± 0.08 Ab
		2	-0.70 ± 0.06 Aa	-0.22 ± 0.04 Aa	-0.55 ± 0.06 Aa	-0.24 ± 0.10 Aa
5 : 1	B	1	-1.18 ± 0.06 Ba	-0.19 ± 0.02 Aa	-0.48 ± 0.09 Aa	-0.15 ± 0.10 Ba
		2	-1.14 ± 0.13 Ba	-0.18 ± 0.08 Aa	-0.45 ± 0.09 Aa	-0.09 ± 0.07 Ba
	M4	1	-0.80 ± 0.15 Aab	-0.14 ± 0.04 Aa	-0.36 ± 0.13 Aa	-0.04 ± 0.10 ABb
		2	-0.84 ± 0.03 Ab	-0.10 ± 0.03 Aa	-0.30 ± 0.07 Aa	0.05 ± 0.02 ABab
		3	-0.72 ± 0.12 Aa	-0.13 ± 0.04 Aa	-0.34 ± 0.05 Aa	0.12 ± 0.05 ABa
	D	1	-0.69 ± 0.10 Aa	-0.11 ± 0.05 Aa	-0.29 ± 0.06 Aa	0.14 ± 0.05 Aa
		2	-0.60 ± 0.08 Aa	-0.10 ± 0.06 Aa	-0.25 ± 0.07 Aa	0.26 ± 0.10 Aa

In mixed culture with *A. tauschii*, diaspore position in compound spike ($P < 0.001$) and culture ratio ($P < 0.001$) significantly affected RCI represented by each growth trait of *T. aestivum*. Seed position in diaspore significantly ($P < 0.05$) only affected number of tillers and interaction of diaspore position in compound spike and culture ratio significantly affected number of tillers ($P < 0.001$) and mass per plant ($P < 0.05$).

RCI represented by plant height of *T. aestivum* increased as diaspore position in compound spike and seed position in diaspore of *A. tauschii* increased. Specifically, RCI represented by plant height of *T. aestivum* was highest and lowest when mixed cultured with plants derived from seeds in distal and basal diaspore / seed positions of *A. tauschii*, respectively. Competitive ability of *T. aestivum* represented by plant height was lowest and highest when mixed cultured with plants derived from seeds in distal and basal diaspore / seed positions of *A. tauschii*, respectively (Table 2).

Table 2
Relative competition index of *Triticum aestivum* grown with *Aegilops tauschii*

Culture ratio	Positions of seeds of A. *tauschii* planted with seeds of *T. aestivum*		Height	No. of tillers per plant	No. of seeds per plant	Mass of seeds per plant
	P1	P2				
1 : 5	B	1	0.05 ± 0.02 Aa	0.08 ± 0.05 Aa	0.35 ± 0.04 ABa	0.42 ± 0.02 Aa
		2	0.06 ± 0.02 Aa	0.08 ± 0.03 Aa	0.34 ± 0.04 ABa	0.42 ± 0.03 Aa
	M4	1	0.07 ± 0.02 Aa	0.05 ± 0.04 Aa	0.30 ± 0.05 Ba	0.39 ± 0.04 Aa
		2	0.07 ± 0.02 Aa	0.03 ± 0.02 Aa	0.32 ± 0.05 Ba	0.39 ± 0.05 Aa
		3	0.08 ± 0.02 Aa	0.03 ± 0.04 Aa	0.33 ± 0.06 Ba	0.39 ± 0.04 Aa
	D	1	0.09 ± 0.02 Aa	0.02 ± 0.02 Aa	0.35 ± 0.06 Aa	0.39 ± 0.07 Aa
		2	0.10 ± 0.03 Aa	0.02 ± 0.01 Aa	0.38 ± 0.08 Aa	0.40 ± 0.09 Aa
2 : 4	B	1	0.23 ± 0.02 Ba	0.15 ± 0.03 Aa	0.56 ± 0.03 Aa	0.66 ± 0.01 Aa
		2	0.23 ± 0.02 Ba	0.12 ± 0.02 Aa	0.53 ± 0.01 Aa	0.63 ± 0.02 Aa
	M4	1	0.24 ± 0.02 ABa	0.09 ± 0.02 ABa	0.48 ± 0.02 ABa	0.58 ± 0.01 ABa
		2	0.26 ± 0.02 ABa	0.06 ± 0.03 ABa	0.42 ± 0.04 ABa	0.51 ± 0.05 ABa
		3	0.27 ± 0.02 ABa	0.05 ± 0.02 ABa	0.42 ± 0.03 ABa	0.51 ± 0.03 ABa
	D	1	0.28 ± 0.02 Aa	0.05 ± 0.02 Ba	0.43 ± 0.04 Ba	0.49 ± 0.04 Ba
		2	0.30 ± 0.02 Aa	0.03 ± 0.03 Ba	0.44 ± 0.02 Ba	0.48 ± 0.03 Ba
3 : 3	B	1	0.30 ± 0.02 Aa	0.32 ± 0.04 Aa	0.71 ± 0.02 Aa	0.80 ± 0.01 Aa
		2	0.32 ± 0.02 Aa	0.30 ± 0.05 Aa	0.69 ± 0.03 Aa	0.77 ± 0.01 Aa

	M4	1	0.33 ± 0.02 Aa	0.27 ± 0.04 Ba	0.69 ± 0.01 Aa	0.75 ± 0.01 ABa
		2	0.34 ± 0.02 Aa	0.23 ± 0.02 Bab	0.67 ± 0.03 Aa	0.73 ± 0.02 ABa
		3	0.35 ± 0.02 Aa	0.18 ± 0.03 Bb	0.66 ± 0.03 Aa	0.72 ± 0.03 ABa
	D	1	0.36 ± 0.03 Aa	0.15 ± 0.03 Ca	0.65 ± 0.04 Aa	0.70 ± 0.03 Ba
		2	0.38 ± 0.03 Aa	0.10 ± 0.03 Ca	0.65 ± 0.03 Aa	0.69 ± 0.01 Ba
4 : 2	B	1	0.36 ± 0.02 Ba	0.41 ± 0.04 Aa	0.82 ± 0.03 Aa	0.90 ± 0.01 Aa
		2	0.38 ± 0.02 Ba	0.34 ± 0.03 Aa	0.81 ± 0.01 Aa	0.88 ± 0.01 Aa
	M4	1	0.39 ± 0.02 ABa	0.26 ± 0.01 Ba	0.80 ± 0.02 Aa	0.87 ± 0.01 Aa
		2	0.41 ± 0.02 ABa	0.20 ± 0.02 Ba	0.81 ± 0.01 Aa	0.87 ± 0.01 Aa
		3	0.41 ± 0.02 ABa	0.19 ± 0.03 Ba	0.82 ± 0.03 Aa	0.87 ± 0.01 Aa
	D	1	0.42 ± 0.02 Aa	0.10 ± 0.03 Ca	0.83 ± 0.02 Aa	0.88 ± 0.01 Aa
		2	0.43 ± 0.02 Aa	0.06 ± 0.01 Ca	0.84 ± 0.01 Aa	0.88 ± 0.00 Aa
5 : 1	B	1	0.43 ± 0.00 Ba	0.57 ± 0.04 Aa	0.93 ± 0.01 Aa	0.97 ± 0.00 Aa
		2	0.44 ± 0.00 Ba	0.53 ± 0.02 Aa	0.92 ± 0.01 Aa	0.96 ± 0.00 Aa
	M4	1	0.45 ± 0.01 ABa	0.50 ± 0.01 Ba	0.92 ± 0.01 Aa	0.95 ± 0.00 ABa
		2	0.46 ± 0.00 ABa	0.44 ± 0.05 Bab	0.92 ± 0.01 Aa	0.95 ± 0.00 ABa
		3	0.47 ± 0.00 ABa	0.39 ± 0.02 Bb	0.92 ± 0.01 Aa	0.95 ± 0.00 ABa
	D	1	0.49 ± 0.01 Aa	0.35 ± 0.05 Ca	0.92 ± 0.01 Aa	0.95 ± 0.00 Ba
		2	0.50 ± 0.01 Aa	0.28 ± 0.02 Ca	0.91 ± 0.01 Aa	0.94 ± 0.01 Ba

RCI represented by number of tillers per plant, number of seeds per plant and seed mass per plant of *T. aestivum* decreased as diaspore position in compound spike and seed position in diaspore of *A. tauschii* increased. Specifically, RCI represented by number of tillers per plant, number of seeds per plant and seed mass per plant of *T. aestivum* was highest and lowest when mixed cultured with plants derived from seeds in basal and distal diaspore / seed positions of *A. tauschii*, respectively. Competitive ability of *T. aestivum* was highest and lowest when mixed cultured with plants derived from seeds in distal and basal diaspore / seed positions of *A. tauschii*, respectively.

RCI of *T. aestivum* represented by each growth trait increased as mixed culture ratio increased (except in a few cases). Specifically, RCI of *T. aestivum* was lowest and highest in mixed culture ratio 1 : 5 and 5 : 1, respectively (Table 2).

LnRR inter/intra of *A. tauschii* was positive (Table 3), while that of *T. aestivum* was negative (Table 4), i.e, intraspecific competition intensity was higher than interspecific competition intensity in *A. tauschii* and the opposite in *T. aestivum*.

Table 3
Relative performance in interspecific pairs and intraspecific pairs of *Aegilops tauschii* (LnRR inter/intra)

P1	P2	Height	No. of tillers per plant	No. of seeds per plant	Mass of seeds per plant
B	1	0.37 ± 0.01	0.15 ± 0.02	0.43 ± 0.03	0.41 ± 0.07
	2	0.36 ± 0.03	0.15 ± 0.02	0.42 ± 0.01	0.41 ± 0.04
M4	1	0.28 ± 0.03	0.15 ± 0.02	0.4 ± 0.01	0.37 ± 0.03
	2	0.27 ± 0.01	0.15 ± 0.02	0.38 ± 0.01	0.34 ± 0.04
	3	0.28 ± 0.03	0.14 ± 0.01	0.38 ± 0.03	0.34 ± 0.02
D	1	0.24 ± 0.02	0.15 ± 0.01	0.36 ± 0.03	0.32 ± 0.04
	2	0.24 ± 0.02	0.14 ± 0.02	0.34 ± 0.04	0.29 ± 0.06

Table 4
Relative performance in interspecific pairs and intraspecific pairs of *Triticum aestivum* (LnRR□inter/intra)

Positions of seeds of *A. tauschii* planted with seeds of *T. aestivum*		Height	No. of tillers per plant	No. of seeds per plant	Mass of seeds per plant
P1	P2				
B	1	-0.16 ± 0.02	-0.19 ± 0.07	-0.54 ± 0.03	-0.70 ± 0.02
	2	-0.17 ± 0.02	-0.17 ± 0.04	-0.52 ± 0.05	-0.64 ± 0.03
M4	1	-0.17 ± 0.01	-0.14 ± 0.03	-0.51 ± 0.01	-0.61 ± 0.02
	2	-0.18 ± 0.02	-0.10 ± 0.01	-0.49 ± 0.04	-0.58 ± 0.04
	3	-0.19 ± 0.02	-0.06 ± 0.02	-0.48 ± 0.05	-0.56 ± 0.05
D	1	-0.20 ± 0.02	-0.04 ± 0.02	-0.47 ± 0.05	-0.53 ± 0.05
	2	-0.21 ± 0.02	-0.04 ± 0.03	-0.46 ± 0.03	-0.51 ± 0.02

Discussion

Effect of seed position on competitive ability

Plants derived from distal diaspores/seeds of *A. tauschii* were taller but had lower numbers of tillers and seeds and lower mass of seeds per plant compared to plants derived from basal diaspores/seeds under all treatments. Plants derived from basal diaspores/seeds had lower relatively competitive intensity (RCI), while those derived from distal diaspores/seeds had a higher relatively competitive intensity. Thus, plants derived from basal diaspores/seeds had the greatest competitive ability, while those derived from distal diaspores/seeds had the lowest competitive ability; plants derived from middle diaspores were intermediate.

According to the competition / colonization trade - off model (Turnbull et al. 2004), allocating resources to individuals with higher colonization ability naturally leads to allocating less resources to competition. Distal diaspores/seeds of *A. tauschii* had the highest dispersal ability (Wang et al. 2003), greatest dispersal distance and are more likely to colonize new habitats than basal diaspores/seeds. For distal diaspores/seeds, more resources were allocated to "colonization" and relatively less to "competition". Therefore, competitive abilities of plants derived from distal diaspores/seeds with greater dispersal ability were not as high as those formed by the basal diaspore/seeds with lower dispersal ability.

For *A. tauschii*, different performances of plants from seeds at different positions on the same plant in competition with wheat reflects its adaptation to diverse environmental conditions. As position of diaspores/seeds increased, colonization ability increased, while competitive ability decreased. The competition/colonization trade-off on compound spikes enables the species to adapt to a diversity of environments and thus expand its population. In addition, the competitive ability of *T. aestivum* plants was highest and lowest against plants formed from distal and basal diaspores/seeds of *A. tauschi*.

Effect of culture ratio on competitive ability

In most cases for *A. tauschii*, growth indicators were highest, while relative competitive intensity was lowest under the mixed culture ratio of 3:3, indicating that *A. tauschii* had the strongest competitive ability when numbers of plants in *A. tauschii* and *T. aestivum* were equal. However, *A. tauschii* had the lowest growth indicators under monoculture, and intra-specific competitive intensity was greater than inter-specific competitive intensity. That is, *A. tauschii* planted alone faced greater competitive pressure than when it was planted mixed with *T. aestivum*. Therefore, *A. tauschii* had a relatively lower competitive ability under monoculture. Similarly, Wang et al. (2021b) found that intra-specific competitive intensity of *A. tauschii* was greater than inter-specific competitive intensity when it was mixed with *T. aestivum*. That is, resource demands of intra-specific individuals are the same (e.g., Goldberg and Barton 1992; Turnbull et al. 2004; Woo et al. 2020), which results in increased competition. However, *T. aestivum* exhibited an increasing set of growth indicators as the culture ratio of *A. tauschii* and *T. aestivum* decreased, and they were the highest in monoculture conditions. The intra-specific competitive intensity of *T. aestivum* decreased as the culture ratio decreased, and relative performance results also showed that the inter-specific competitive intensity of *T. aestivum* was less than that in mixture with *A. tauschii*.

Golivets and Wallin (2018) analyzed data for 192 peer-reviewed studies on pairwise plant competition within a Bayesian multilevel meta-analytic framework and found that compared to native plants the intra-specific competitive intensity of non-native plants was higher. Thus, introduced plants are more likely to occupy new habitats, and the relatively lower inter-specific competitive intensity means a stronger inter-specific competitive ability, enabling plants to survive in new habitats surrounded by other species of competitors. Native plants in their natural habitats growing with individuals of the same species would have lower intra-specific competitive intensity, which is conducive to coexistence within the same species. *T. aestivum* is not a native species, but as a cultivated plant it benefits from an agricultural cultivation management system, including weeding, allowing it to obtain relatively "favorable" growth conditions and not needing to allocate more resources to inter-specific competition. Therefore, in mixture with *A. tauschii*, the inter-specific competitive intensity for *T. aestivum* was high, which inhibited its growth. However, the intra-specific competitive intensity of *T. aestivum* was low, which was beneficial for its large-scale cultivation.

Comparison of competitive ability of A. tauschii and T. aestivum

Under monoculture, plant height and seed mass per plant for *A. tauschii* were lower, while numbers of tillers and seeds per plant of were significantly higher than those of *T. aestivum*. When grown in mixed

culture, plant height and numbers of tillers and seeds per plant of *A. tauschii* were significantly higher than those of *T. aestivum* regardless of culture ratio. The results indicated that when competed with *T. aestivum*, plant height of *A. tauschii* was increased, which allowed plants to obtain more sunlight, promoting photosynthesis and growth (Wang 2020; Ferenc and Sheppard 2020), thereby producing more tillers and seeds per plant than when grown alone.

The high number of seeds and thus high number of offspring formed by the invasive *A. tauschii* is an advantage for survival and population expansion of the species (Zhao 2021). Seed mass per plant of *A. tauschii* was lower than that of *T. aestivum* whether under monoculture condition or under lower ratio (1 : 5) of mixed culture conditions, which might be caused by different seed characteristics of *T. aestivum* and *A. tauschii*; *T. aestivum* seeds are larger and heavier than those of *A. tauschii* (Fang 2012; Fang et al. 2014). However, seed mass is not correlated with seed dormancy/germination, seedling/plant survival and growth in *A. tauschii* (Wang et al. 2022; Wang et al 2023). Therefore, seed mass of *A. tauschii* does not seem to be an indicator of its competitive ability against *T. aestivum*. Additionally, relative competitive intensity of *A. tauschii* was lower than that of *T. aestivum*, thus *A. tauschii* had stronger competitive ability when competing with *T. aestivum*.

Conclusions

For *A. tauschii*, all growth indicators of plants derived from distal diaspores/seeds compared to those from the basal ones were lower. and the relative competitive intensity of plants formed by distal diaspores/seeds was higher. Thus, competitive ability of plants formed by distal diaspores/seeds was lower than that of plants formed from basal diaspores/seeds. In *A. tauschii*, colonization ability increased while competitive ability decreased as position of diaspores/seeds increased, indicating that there might be a colonization/competition trade-off, which is beneficial for species adaptation and growth in diverse environments (Fig. 7). Although there were differences in competitive abilities among diaspores/seeds at different positions, all plants formed from seeds of *A. tauschii* had a stronger interspecific competitive ability than those of *T. aestivum* (Table 3 and Table 4). The stronger interspecific competitive ability allows *A. tauschii* to out-compete *T. aestivum* and thus invade and survive in wheat fields. In contrast, *T. aestivum* had a higher intraspecific competitive intensity than interspecific competitive intensity, indicating that if *A. tauschii* invaded wheat fields growth of *T. aestivum* would be inhibited. However, *T. aestivum* had lower intraspecific than interspecific competitive intensity, which was conducive to coexistence of individuals of the same species and for large-scale cultivation.

Declarations

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Author contributions Ai Bo Wang designed and performed the experiments, analyzed and interpreted the data, and wrote the initial draft of the manuscript. Carol C. Baskin and Jerry M. Baskin wrote and revised several drafts of the manuscript. Lin Tang, Jingyi Huang, Yonghong He, Shuai Peng wrote the initial draft of the manuscript. All authors reviewed the manuscript.

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Data availability Data analysed during the current study are available from the corresponding author upon reasonable request.

Conflict of interest The authors have no relevant financial or non-financial interests to disclose.

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Figures

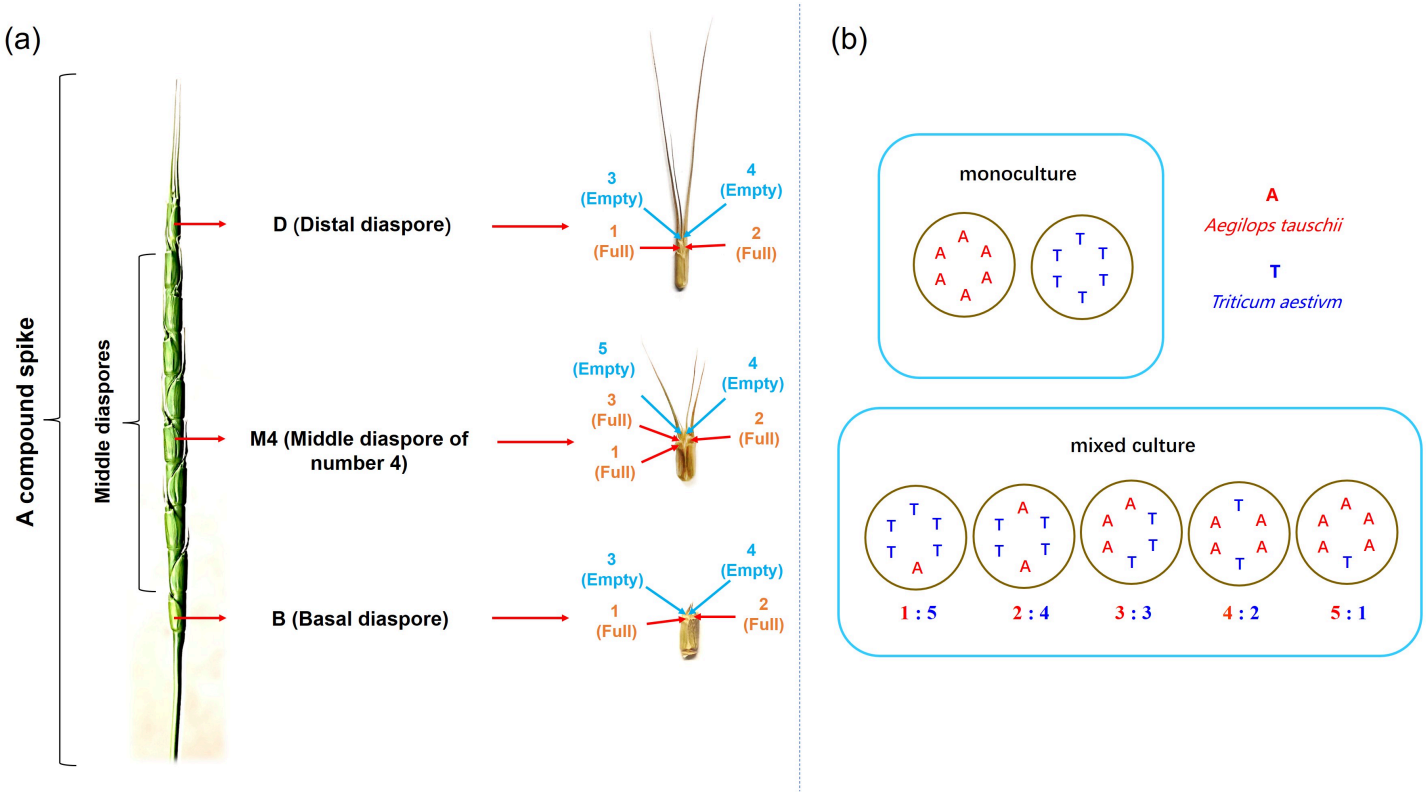


Figure 1

Diaspore and seed positions of *Aegilops tauschii* (a) and planting ratios of *A. tauschii* and *Triticum aestivum* (b).

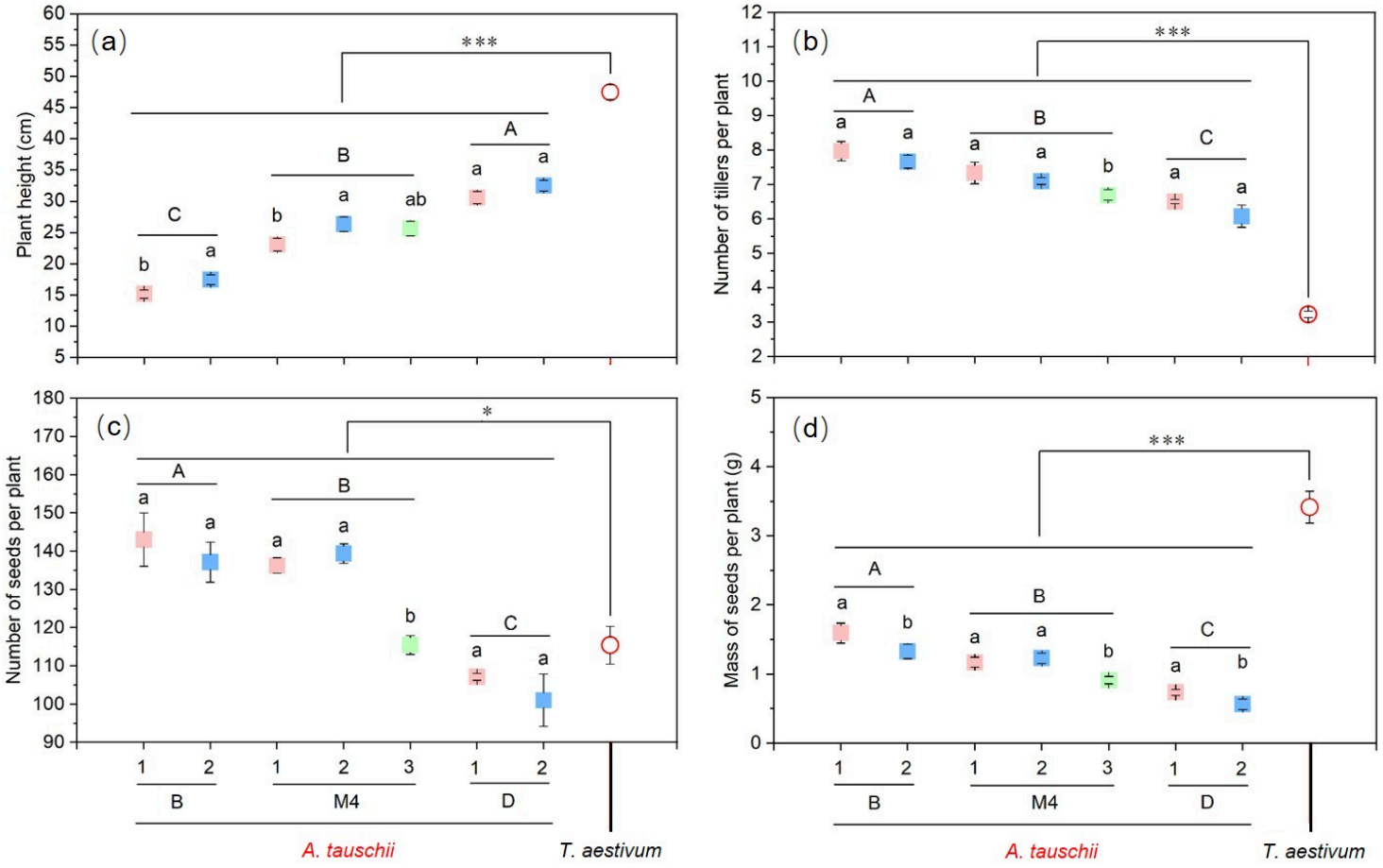


Figure 2

Height (a), numbers of tillers per plant (b), numbers of seeds per plant (c) and mass of seeds per plant (d) of *Aegilops tauschii* and *Triticum aestivum* under monoculture. B, basal diaspore, M4, middle diaspore, D, distal diaspore, numbers 1, 2 and 3 following B, M4 and D indicate different seed positions in diaspores; Different uppercase letters indicate significant differences among different diaspore positions and different lowercase letters indicate significant differences among/between different seed positions in diaspores; ** $P < 0.01$, *** $P < 0.001$.

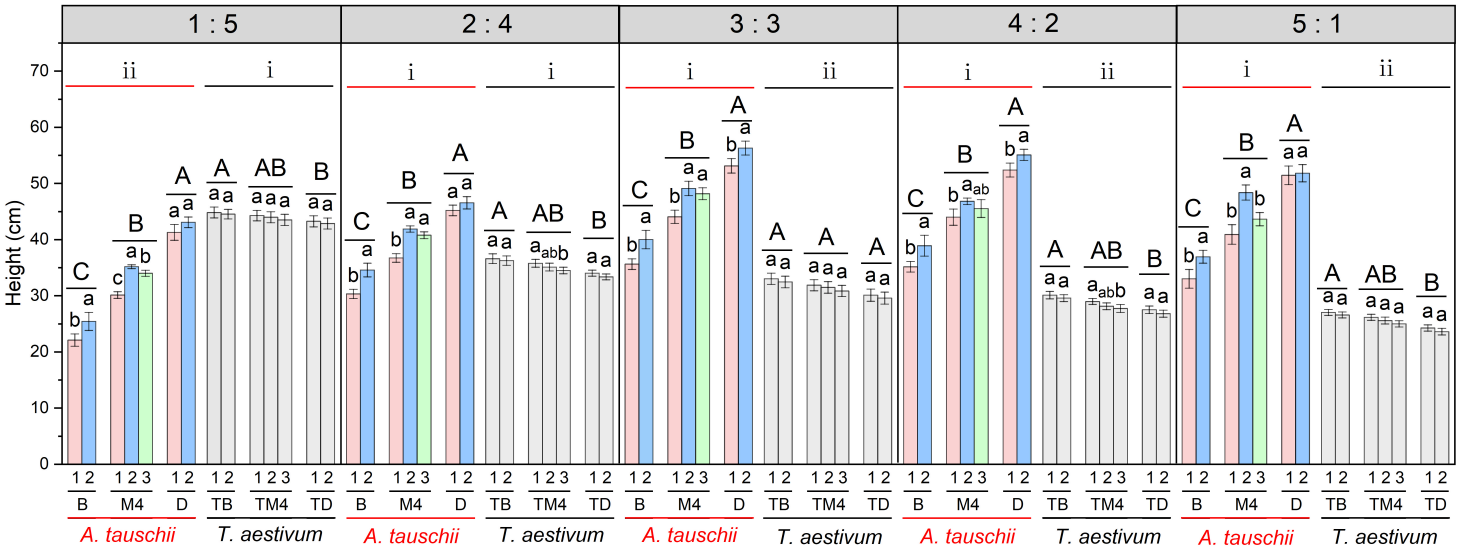


Figure 3

Plant height of *Aegilops tauschii* and *Triticum aestivum* when grown together at ratios of 5 : 1, 4 : 2, 3 : 3, 2 : 4 and 1 : 5. B, M4 and D indicate height of plants derived from basal, middle and distal diaspores in *Agelops tauschii* respectively; numbers 1, 2 and 3 above B, M4 and D different seed positions in diaspores in *A. tauschii*; TB, TM4 and TD height of plants derived from seeds in *Triticum aestivum* planted with seeds of basal, middle and distal diaspores in *A. tauschii* respectively; and 1, 2 and 3 above TB, TM4 and TD indicate different seed positions in diaspores in *A. tauschii*. Different lowercase Roman numerals indicate significant differences among invasive and native species, and different uppercase letters and lowercase letters indicate significant differences among different diaspore positions and among/between different seed positions in diaspores ($P < 0.05$).

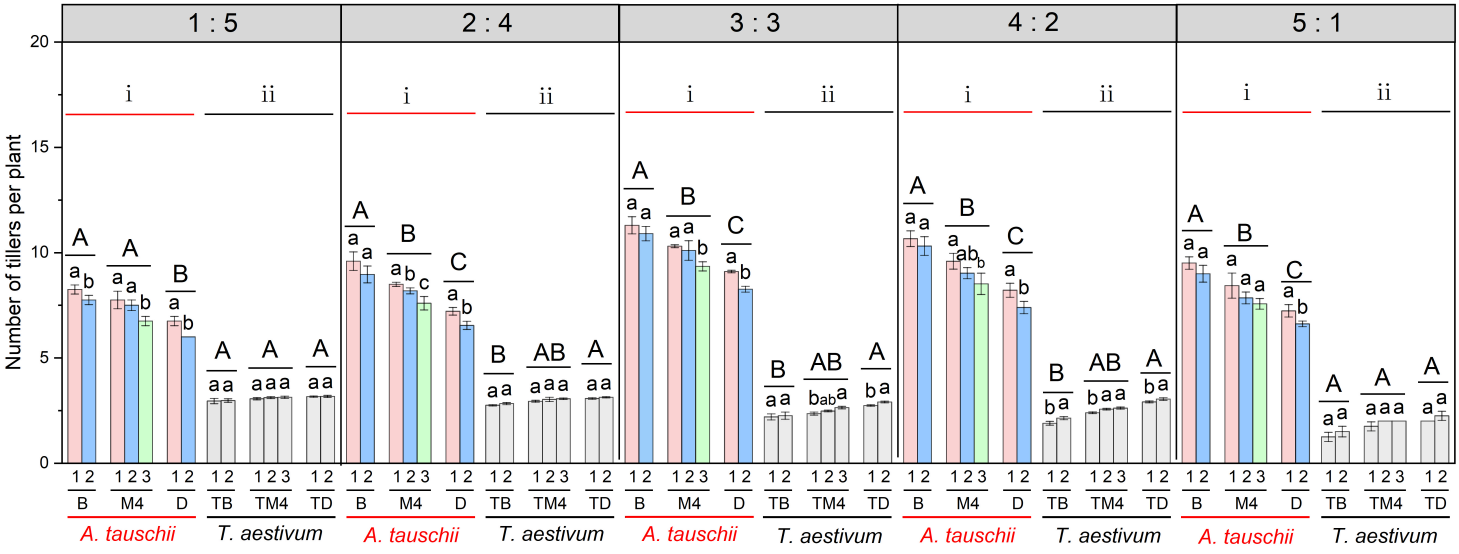


Figure 4

Numbers of tillers per plant of *Aegilops tauschii* and *Triticum aestivum* planted together at ratios of 5 : 1, 4 : 2, 3 : 3, 2 : 4 and 1 : 5. B, M4 and D indicate number of tillers per plants of plants derived from basal,

middle and distal diaspores in *Agelops tauschii,* respectively; numbers 1, 2 and 3 above B, M4 and D indicate different seed positions in diaspores in *A. tauschii*; TB, TM4 and TD number of tillers per plant of plants derived from seeds in *Triticum aestivum* planted with seeds of basal, middle and distal diaspores in *A. tauschii,* respectively; and, 1, 2 and 3 above TB, TM4 and TD different seed positions in diaspores in *A. tauschii*. Different lowercase Roman numerals indicate significant differences among invasive and native species and different uppercase letters and lowercase letters significant differences among different diaspore positions and among/between different seed positions in diaspores ($P < 0.05$).

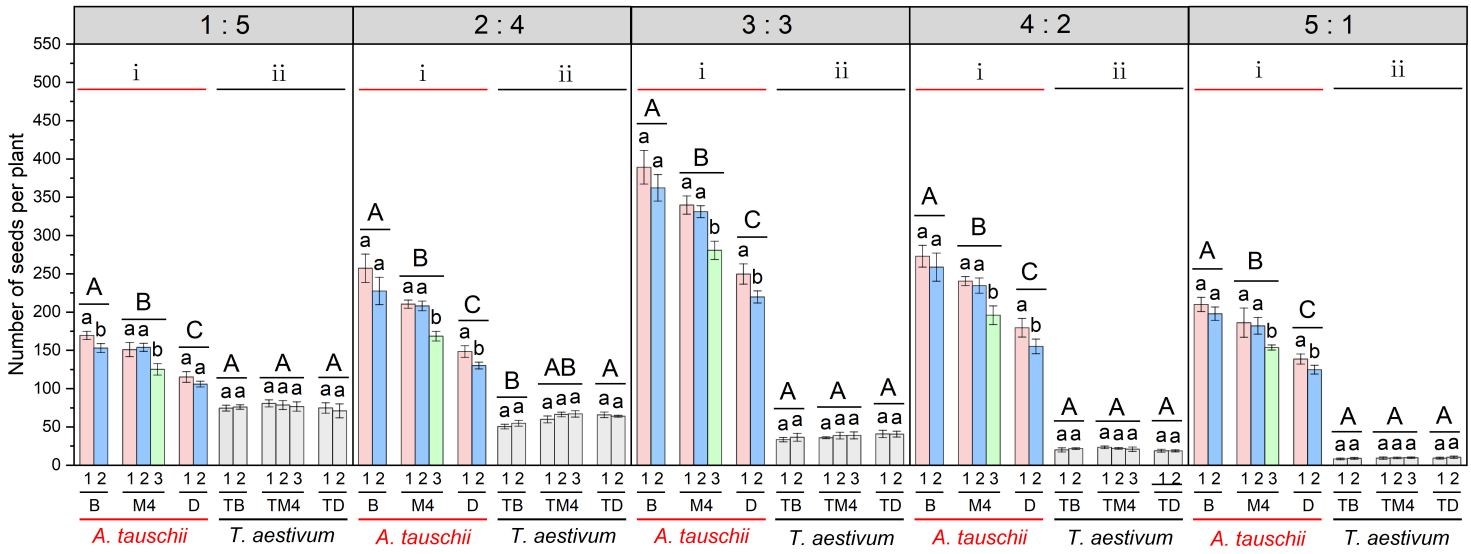


Figure 5

Numbers of seeds per plant of *Aegilops tauschii* and *Triticum aestivum* grown at ratios of 5 : 1, 4 : 2, 3 : 3, 2 : 4 and 1 : 5. B, M4 and D indicate number of seeds per plant of plants derived from basal, middle and distal diaspores in *Agelops tauschii,* respectively; numbers 1, 2 and 3 above B, M4 and D different seed positions in diaspores in *A. tauschii*; TB, TM4 and TD number of seeds per plant of plants derived from seeds in *Triticum aestivum* planted with seeds of basal, middle and distal diaspores in *A. tauschii,* respectively, 1, 2 and 3 above TB, TM4 and TD different seed positions in diaspores in *A. tauschii*. Different lowercase Roman numerals indicate significant differences among invasive and native species and different uppercase letters and lowercase letters significant differences among different diaspore positions and among/between different seed positions in diaspores ($P < 0.05$).

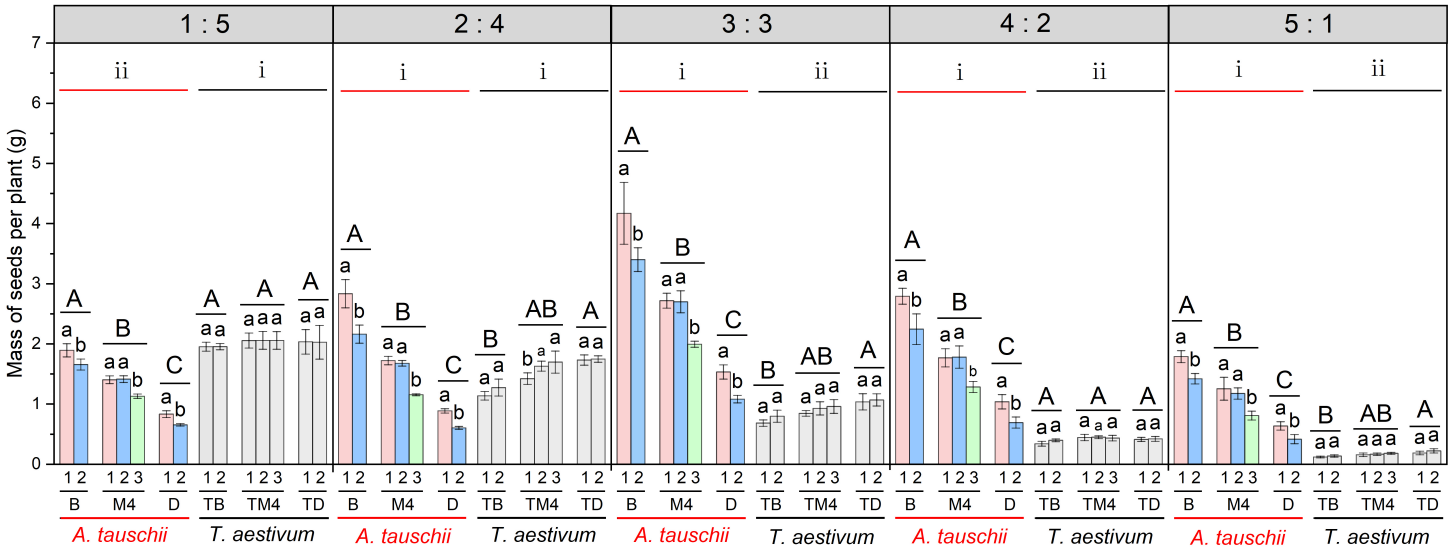


Figure 6

Mass of seeds per plant of *Aegilops tauschii*and *Triticum aestivum* grown together in ratios of 5 : 1, 4 : 2, 3 : 3, 2 : 4 and 1 : 5. B, M4 and D indicate mass of seeds of plants derived from basal, middle and distal diaspores in *Agelops tauschii,*respectively; numbers 1, 2 and 3 above B, M4 and D different seed positions in diaspores in *A. tauschii*; TB, TM4 and TD mass of seeds of plants derived from seeds in *Triticum aestivum* planted with seeds of basal, middle and distal diaspores in *A. tauschii* respectively; and 1, 2 and 3 above TB, TM4 and TD different seed positions in diaspores in *A. tauschii*. Different lowercase Roman numerals indicate significant differences among invasive and native species and different uppercase letters and lowercase letters significant differences among different diaspore positions and among/between different seed positions in diaspores ($P < 0.05$).

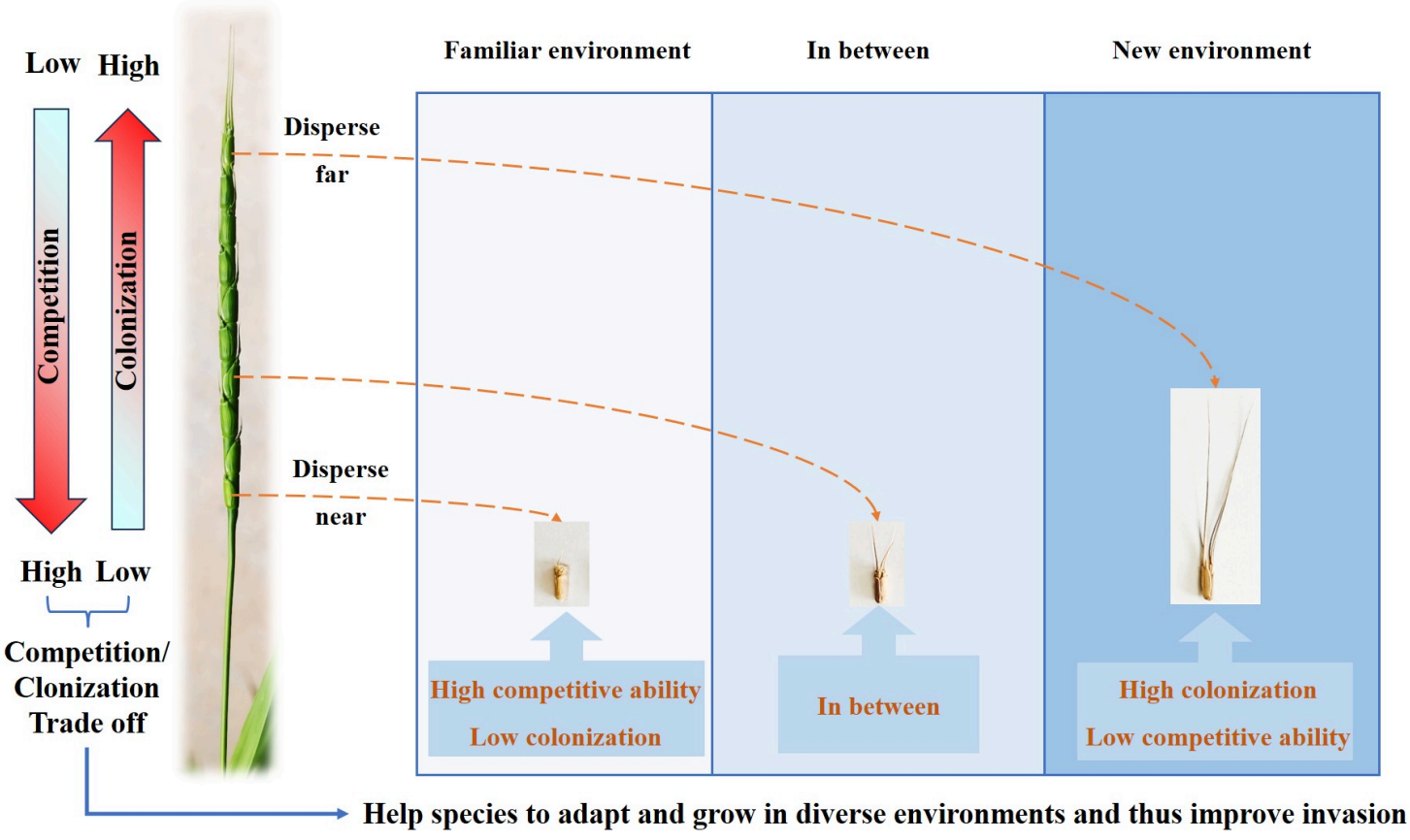


Figure 7

Summary diagram of the trade-off between competition and colonization of the invasive annal grass *Aegilops tauschii* in relation to position on maternal plant where seeds developed.