Sustainability in Environment
ISSN 2470-637X (Print) ISSN 2470-6388 (Online)
Vol. 11, No. 1, 2026
www.scholink.org/ojs/index.php/se

Original Paper

Phenotype-specific Drought Strategies in the Invasive Weed *Avena fatua*

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Funding: 1. Doctoral Research Foundation of Henan University of Science and Technology [13480079]; 2. National Undergraduate Training Program for Innovation and Entrepreneurship of Henan University of Science and Technology [2025457]; 3. National Undergraduate Training Program for Innovation and Entrepreneurship of Henan Province [S202510464065].

Received: October 23, 2025 Accepted: November 22, 2025 Online Published: December 09, 2025
doi:10.22158/se.v11n1p30 URL: http://dx.doi.org/10.22158/se.v11n1p30

Abstract

Wild oat (Avena fatua L.) is a widespread invasive weed whose performance is strongly influenced by water availability. We compared two lemma-based phenotypes-W (hairy lemma) and B (glabrous lemma)-under four soil-water levels (80-85, 60-70, 50-60, 40-50% field capacity) in a completely randomized pot experiment. We determined organ dry masses and calculated allocation indices (root-to-shoot ratio, R/S; root and leaf mass fractions, RMF and LMF), leaf traits (total leaf area, leaf number, LAR), and growth metrics (RGR, NAR). Drought reduced aboveground biomass in both phenotypes. The W phenotype showed a prioritized allocation to roots under moderate stress, reflected by its R/S peaking at 0.508, while its LAR decreased by 40% under light stress. In contrast, the B phenotype exhibited a more dramatic fluctuation in leaf resource allocation, with its Leaf Mass Fraction (LMF) increasing by nearly 70% under light stress before plummeting under heavier stress. Growth analysis indicated that the Net Assimilation Rate (NAR) of W was relatively stable under light *stress, whereas B's NAR dropped sharply by 47%. These results show divergent but predictable allocation and growth adjustments to water limitation and provide a basis for phenotype-aware management of wild oat.*

Keywords

drought stress, Avena fatua, biomass allocation, phenotypic plasticity

1. Introduction

Globally, biological invasion has become a critical environmental issue, leading to significant economic losses and a decline in biodiversity (Grewell et al., 2016; Zheng et al., 2023). The increasing prevalence and damage caused by invasive plant species, driven by human activities and improper introductions, are being exacerbated annually (Fang et al., 2015). Wild oat (*Avena fatua* L.), a notorious example of such invaders, exhibits strong adaptability to environmental stress, often gaining a competitive advantage in natural ecosystems (Beckie et al., 2012). Studies have indicated that the competitive superiority of wild oat and other invasive gramineous species is primarily attributed to their potent reproductive and dispersal capabilities, high stress tolerance, and allelopathic effects (Hierro & Callaway, 2003). Therefore, investigating the underlying physiological and ecological mechanisms behind these advantages is crucial for understanding their invasion processes and developing effective control strategies.

In the context of plant adaptation, biomass, as the primary carrier of accumulated energy, and its allocation patterns among different organs serve as direct indicators of a plant's growth strategy and environmental fitness (Eziz et al., 2017). Concurrently, phenotypic plasticity-defined as the capacity of a single genotype to produce different phenotypes in response to varying environmental conditions (Nicotra et al., 2010), is another key adaptive mechanism. This capacity reflects an organism's responsiveness to environmental changes and is fundamental to adaptive evolution, allowing a species to exhibit diverse morphological and physiological traits that enhance its survival and reproductive success. Notably, the adjustment of biomass allocation patterns is a tangible manifestation of phenotypic plasticity (Eziz et al., 2017; Poorter et al., 2012). This plasticity enables organisms to optimize resource utilization, enhance competitiveness, or evade adverse conditions by modifying their physiological and morphological characteristics when facing environmental pressures such as drought, temperature fluctuations, or changes in light intensity (Nicotra et al., 2010).

Water availability is a primary limiting factor for plant growth, and a water deficit can have a more profound impact on plant development than the sum of other stresses, manifested in parameters such as plant height, root mass, leaf mass fraction, and root-to-shoot ratio (Chaves et al., 2002). Accordingly, water regime strongly modulates phenotypic plasticity and biomass allocation, and invasive plants often capitalize on high plasticity to maintain competitive performance across heterogeneous environments (Davidson et al., 2011). Therefore, studying the effects of different water conditions on the phenotypic plasticity and biomass allocation of invasive plants is instrumental in accurately understanding their control mechanisms, which in turn helps to protect local biodiversity and ensure agricultural production security.

Against this backdrop, we compared two wild-oat (*Avena fatua* L.) phenotypes-W (hairy lemma) and B (glabrous lemma)-across four soil-water gradients, using lemma traits as the diagnostic basis as recorded in Chinese floras/weed manuals (Flora of China Editorial Committee, 2006). We quantified differences in biomass allocation, leaf morphology, and growth characteristics to elucidate how soil water availability shapes phenotypic responses and to inform management of this invasive weed.

2. Method

2.1 Plant Materials and Pre-treatment

Seeds of two phenotypes of wild oat (*Avena fatua* L.) were collected in October 2022 from a winter wheat field in Luolong District, Luoyang City, Henan Province, China. The two phenotypes were distinguished by lemma traits: a typical, hairy-lemma phenotype (W) and a glabrous-lemma phenotype (B). After collection, the seeds were air-dried and stored at room temperature. In November of the same year (2022), the seeds were sown in seedling trays.

In March of the following year (2023), healthy seedlings of uniform size were carefully transplanted into plastic pots (25 cm in diameter) equipped with saucers. Each pot was filled with 5 kg of air-dried loam soil that had been passed through a 2 mm sieve. Following transplantation, the seedlings were acclimatized for one week under approximately 30% natural light intensity, provided by a neutral-density shade net. During this period, they were kept moist by watering the saucers. The water-stress treatments commenced after the acclimatization period.

2.2 Experimental Design and Water Control

Four soil water content gradients were established based on the percentage of field capacity (FC): a control group (CK, 80-85% FC), a light-stress group (LD, 60-70% FC), a moderate-stress group (MD, 50-60% FC), and a severe-stress group (SD, 40-50% FC). Prior to the experiment, the FC of the soil was determined using the cutting ring method (International Organization for Standardization, 2019; Ministry of Ecology and Environment of the People's Republic of China, 2011). A completely randomized design was used for each phenotype (Quinn & Keough, 2002). Each treatment consisted of four replicate pots, with five plants per pot.

To maintain the target water content, all pots were weighed daily at 18:00 using an electronic balance, and the water lost through evapotranspiration was replenished by adding deionized water (Gao et al., 2022). To minimize positional effects, the pots were randomly repositioned every three days. The stress treatment lasted for 45 days.

2.3 Measurement and Calculation of Indices

At the end of the treatment period, plants were harvested and separated into roots, stems, and leaves. Fully expanded leaves were scanned (600 dpi), and the leaf area (LA) was calculated using ImageJ software (Schindelin et al., 2012). The separated plant parts were oven-dried at 105°C for 30 minutes to deactivate enzymes, then dried to a constant weight (difference between two consecutive measurements < 0.2%) at 80°C to obtain the dry mass (Perez-Harguindeguy et al., 2016). The following indices were calculated:

Total Biomass (TB) = Leaf Dry Mass (LDM) + Stem Dry Mass (SDM) + Root Dry Mass (RDM)

Root to Shoot Ratio (R/S) = RDM / (LDM + SDM)

Leaf/Stem/Root Mass Fraction (LMF/SMF/RMF) = Dry mass of the respective organ / TB (Poorter et al., 2012)

Leaf Area Ratio (LAR) = LA / TB

Growth analysis indices, including Relative Growth Rate (RGR), Net Assimilation Rate (NAR), and the mean Leaf Area Ratio over the interval (LARm), were calculated according to classical growth analysis formulas (Poorter, 1999).

The Phenotypic Plasticity Index (PPI) was calculated as PPI = (maximum value – minimum value) / maximum value, across the treatment gradients for each phenotype (Valladares et al., 2006).

For morphological and biomass measurements, five individual plants were randomly selected from each treatment (n=5).

2.4 Data and Statistical Analysis

Data were organized in Microsoft Excel 2019 and statistically analyzed using SPSS 20.0. For growth dynamics (plant height and leaf number), data were analyzed using ANOVA followed by Duncan's multiple range test ($P < 0.05$) to compare all treatment combinations. For biomass and morphological traits (Tables 1–6), one-way ANOVA was performed separately for each phenotype to assess the effect of water stress.

3 Result

3.1 Effects of Water Stress on Plant Height and Leaf Number

Under CK (control) conditions, the two oat phenotypes showed similar initial growth in plant height. After 15 days, however, the plant height of the W phenotype increased rapidly and was significantly greater than that of the B phenotype on days 20 and 25 (Fig. 1). Specifically, the plant height of the W phenotype increased by 90.1% from day 5 to day 25 under CK conditions, whereas the B phenotype's growth was only 57% over the same period, indicating a markedly higher growth rate for the W phenotype. A similar pattern was observed under other water conditions. Although there were no significant differences in early growth, the W phenotype consistently outperformed the B phenotype in the middle and late stages. Particularly under the more water-scarce MD and SD conditions, the plant height of W was significantly greater than that of B on days 20 and 25 ($P < 0.05$). Ultimately, the total height increases for the W phenotype under LD, MD, and SD conditions were 86.4%, 77.4%, and 68.6%, respectively, while for the B phenotype, the increases were merely 32.7%, 11.4%, and 5.0%.

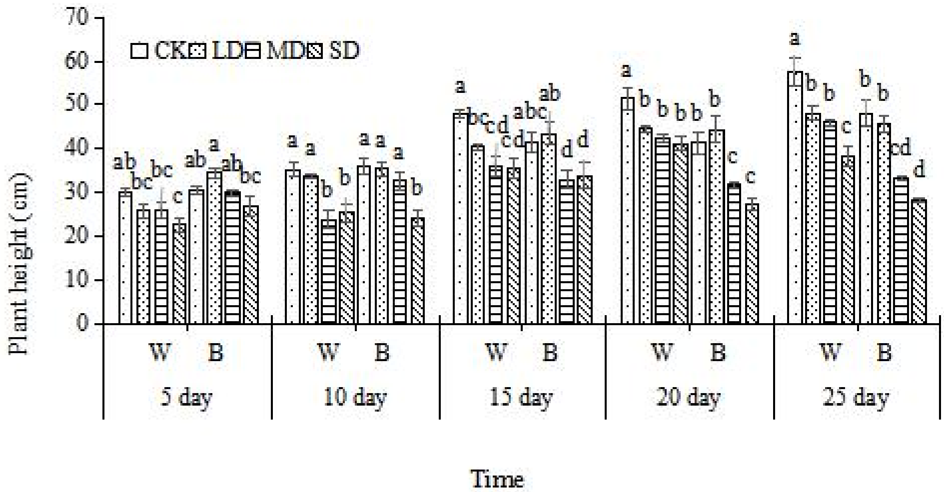

Figure 1. Temporal dynamics of plant height for hairy-lemma (W) and glabrous-lemma (B) *Avena fatua* phenotypes under four soil-water regimes. Data are mean ± SD (n = 5). Different lowercase letters indicate significant differences among all treatment combinations within each time point (Duncan's test, *P* < 0.05). Water levels: CK (80-85% FC), LD (60-70%), MD (50-60%), SD (40-50%)

The leaf number of both phenotypes was similar across all water treatments at the beginning of the experiment (day 5) (Fig. 2). Over time, the W phenotype showed a 1.4-fold increase in leaf number under CK conditions and a smaller increase under LD conditions. In contrast, the leaf number of the B phenotype did not increase notably under either CK or LD conditions. Under the more severe MD and SD conditions, the leaf number of both phenotypes decreased, with the B phenotype showing a dramatic 80% reduction in leaf number under SD conditions by day 25.

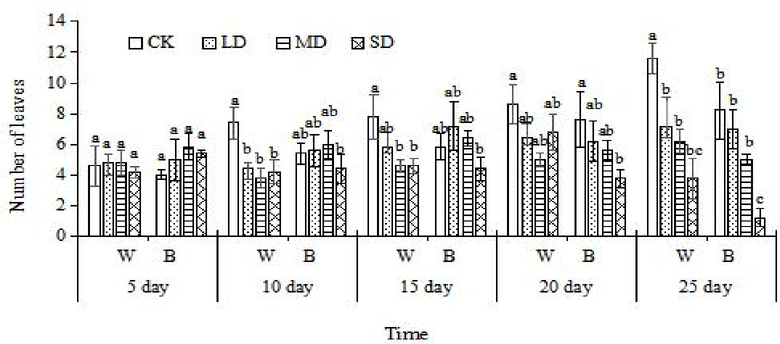

Figure 2. Temporal dynamics of leaf number for hairy-lemma (W) and glabrous-lemma (B) *Avena fatua* phenotypes under four soil-water regimes. Data are mean ± SD (n = 5). Different lowercase letters indicate significant differences among all treatment combinations within each time point (Duncan's test, *P* < 0.05). Water levels: CK (80-85% FC), LD (60-70%), MD (50-60%), SD (40-50%)

3.2 Effects of Water Stress on Biomass Accumulation and Allocation

3.2.1 Absolute Biomass

Water stress significantly affected the dry matter accumulation in various organs of both phenotypes (Table 1, 2). For the B phenotype, the dry mass of stems, leaves, panicles, and the entire above-ground part decreased significantly as water supply diminished, with most organs showing a significant reduction starting from the light-stress (LD) condition. The W phenotype exhibited a similar trend for its above-ground organs; however, its root dry mass showed no significant difference from the control under light and moderate stress, only decreasing significantly under severe stress.

Table 1. Biomass allocation of the glabrous-lemma phenotype (B) of wild oat under different water gradients (n=5).

Index	Root dry mass (g)	Stem dry mass (g)	Leaf dry mass (g)	Panicle dry mass (g)	Aboveground dry mass (g)
CK	0.083±0.012a	0.138±0.023a	0.082±0.019a	0.091±0.009a	0.311±0.055a
LD	0.041±0.002b	0.093±0.010b	0.092±0.015a	0.037±0.010c	0.222±0.019b
MD	0.066±0.007ab	0.076±0.010b	0.035±0.005b	0.064±0.007b	0.174±0.025b
SD	0.040±0.007b	0.042±0.004c	0.011±0.003b	0.039±0.002c	0.093±0.011c

Note. Values are mean ± standard deviation. Different lowercase letters within a column indicate significant differences among water treatments for a given trait (Duncan's multiple range test, $P < 0.05$). The same notation and abbreviations are used in subsequent tables unless otherwise stated.

Table 2. Biomass allocation of the typical phenotype (W) of wild oat under different water gradients (n=5).

Index	Root dry mass (g)	Stem dry mass (g)	Leaf dry mass (g)	Panicle dry mass (g)	Aboveground dry mass (g)
CK	0.121±0.030a	0.185±0.036a	0.171±0.027a	0.086±0.020a	0.496±0.024a
LD	0.085±0.010a	0.113±0.01b	0.095±0.013b	0.045±0.01b	0.306±0.026b
MD	0.079±0.011a	0.067±0.007b	0.065±0.013b	0.024±0.003b	0.276±0.046b
SD	0.029±0.006b	0.056±0.014b	0.038±0.016b	0.040±0.010b	0.154±0.018c

3.2.2 Biomass Allocation Ratios

The two phenotypes displayed divergent allocation strategies in response to water stress (Table 3 and 4). For the W phenotype, the root-to-shoot ratio (R/S) significantly increased from 0.323 under control (CK) to a peak of 0.508 under moderate stress (MD), an increase of 57%. In contrast, the B phenotype showed a dramatic fluctuation in leaf allocation. Its Leaf Mass Fraction (LMF) sharply increased by 69.9% from 0.213 (CK) to 0.362 (LD), before plummeting to 0.049 under severe stress (SD).

Correspondingly, its R/S first decreased by 25.7% from CK to LD, and then progressively increased to a maximum of 0.445 under SD.

Table 3. Effects of different water gradients on biomass-related ratios of the glabrous-lemma phenotype (B) of wild oat (n=5).

Index	Root mass fraction (RMF)	Leaf mass fraction (LMF)	Panicle mass fraction (PMF)	Root-to-shoot ratio (R/S)
CK	0.205 ± 0.042 c	0.213 ± 0.052 b	0.222 ± 0.044 ab	0.261 ± 0.071 d
LD	0.162 ± 0.019 d	0.362 ± 0.103 a	0.115 ± 0.068 b	0.194 ± 0.027 c
MD	0.274 ± 0.022 b	0.150 ± 0.009 c	0.258 ± 0.032 a	0.378 ± 0.039 b
SD	0.299 ± 0.066 a	0.049 ± 0.050 d	0.312 ± 0.069 a	0.445 ± 0.133 a

Table 4. Effects of different water gradients on biomass-related ratios of the typical phenotype (W) of wild oat (n=5).

Index	Root mass fraction (RMF)	Leaf mass fraction (LMF)	Panicle mass fraction (PMF)	Root-to-shoot ratio (R/S)
CK	0.237 ± 0.084 b	0.370 ± 0.083 a	0.084 ± 0.072 b	0.323 ± 0.142 b
LD	0.274 ± 0.045 ab	0.273 ± 0.050 b	0.112 ± 0.071 ab	0.389 ± 0.097 ab
MD	0.336 ± 0.014 a	0.286 ± 0.049 b	0.082 ± 0.063 b	0.508 ± 0.030 a
SD	0.214 ± 0.088 b	0.296 ± 0.163 b	0.117 ± 0.152 a	0.277 ± 0.152 b

3.3 Effects of Water Stress on Leaf Morphology

Soil water content had different effects on the leaf morphology of the two phenotypes (Table 5). For the W phenotype, both total leaf area and leaf number decreased significantly with increasing drought stress. However, the mean leaf area (MLA) remained stable and showed no significant difference among the treatments. The leaf area ratio (LAR) of W decreased significantly from CK (192.52 $cm^2\ g^{-1}$) to LD (116.40 $cm^2\ g^{-1}$), but then gradually recovered under MD and SD conditions.

In contrast, the B phenotype maintained its leaf growth under light stress. There were no significant differences in total leaf area, leaf number, or LAR between the CK and LD treatments. However, as stress intensified (MD and SD), these values dropped sharply. Notably, the MLA of the B phenotype decreased significantly under severe stress, differing from the stable response of the W phenotype. Consequently, the LAR of B peaked at LD but then decreased by roughly 70% to a minimum of 27.61 $cm^2\ g^{-1}$ under SD.

Table 5. Effects of soil moisture on the leaf morphology of the glabrous-lemma (B) and typical (W) phenotypes of wild oat.

Phenotype	Treatment	Total leaf area (cm^2)	Leaf number	Mean leaf area (cm^2)	Leaf area ratio, LAR ($cm^2\ g^{-1}$)
W	CK	56.737±16.899a	11.6±1.03a	4.664±1.116a	192.52±11.07a
	LD	36.071±6.035ab	7.2±1.828b	5.524±0.728a	116.40±13.18b
	MD	32.142±3.375ab	6.2±0.735b	5.304±0.611a	132.36±9.26b
	SD	17.647±5.722b	3.8±0.878b	4.787±1.448a	164.01±5.42ab
B	CK	32.283±8.597a	7.2±1.881a	4.883±1.112a	83.84±14.37a
	LD	33.568±10.545a	7.0±1.265a	4.705±0.879a	93.53±12.04a
	MD	14.628±1.947b	5.0±0.316a	2.993±0.494ab	59.92±3.73ab
	SD	2.406±1.209b	1.2±0.583b	1.165±0.483b	27.61±8.04b

Note: Letters are assigned separately for each phenotype; see Table 1 for other notation and abbreviations.

3.4 Effects of Water Stress on Plant Growth Characteristics

Soil water content significantly influenced the growth characteristics of both phenotypes, but the W phenotype demonstrated greater physiological stability than the B phenotype (Table 6).

Regarding the relative growth rate (RGR), both phenotypes showed a continuous and significant decrease as stress intensified, starting from the LD condition. However, the total reduction in RGR from CK to SD was much larger for the B phenotype (80.0%) than for the W phenotype (69.4%).

This difference was more pronounced in the net assimilation rate (NAR). The NAR of the W phenotype remained at a level comparable to CK under the LD condition ($P > 0.05$) and only began to decrease significantly under the MD condition. In contrast, the NAR of the B phenotype was already significantly lower than its CK level under the LD condition.

The two phenotypes also exhibited different morphological adjustment patterns in their mean leaf area ratio (LARm). The LARm of the B phenotype remained unchanged from CK to MD, only decreasing significantly under the SD condition. In contrast, the LARm of the W phenotype decreased significantly under LD and then partially recovered under MD and SD, although it remained significantly below the control level.

Table 6. Effects of soil moisture on the growth characteristics of two wild oat phenotypes.

Phenotype	Treatment	RGR($g\ g^{-1}\ d^{-1}$)	NAR($g\ m^{-2}\ d^{-1}$)	LARm($m^2\ kg^{-1}$)
W	CK	0.062 ± 0.001 a	3.568 ± 0.221 a	17.411 ± 0.670 a
	LD	0.044 ± 0.003 b	3.531 ± 0.301 a	12.646 ± 0.842 c
	MD	0.035 ± 0.003 b	2.519 ± 0.197 b	13.718 ± 0.548 b
	SD	0.019 ± 0.005 c	1.287 ± 0.304 c	14.008 ± 1.494 b
B	CK	0.045 ± 0.004 a	4.530 ± 0.370 a	10.053 ± 0.949 a

LD	0.029 ± 0.004 b	2.385 ± 0.315 bc	10.867 ± 0.773 a
MD	0.026 ± 0.004 b	2.247 ± 0.430 b	8.686 ± 0.226 a
SD	0.009 ± 0.002 c	1.476 ± 0.286 c	6.343 ± 0.796 b

Note: Letters are assigned separately for each phenotype; see Table 1 for other notation and abbreviations.

3.5 Effects of Water Stress on Phenotypic Plasticity Index (PPI)

The two phenotypes showed different priorities in the plasticity of their traits (Table 7). The W phenotype exhibited higher plasticity in root-related traits, such as root mass fraction (RMF, PPI=0.72) and leaf-to-root ratio, as well as in net assimilation rate (NAR, PPI=0.60). In contrast, the B phenotype displayed greater plasticity in growth- and leaf-related traits, including relative growth rate (RGR, PPI=0.92), mean leaf area (MLA, PPI=0.76), leaf area ratio (LAR), and leaf mass fraction (LMF, PPI=0.72). Data indicate that W phenotype's root plasticity and photosynthetic efficiency adjustment are more prominent, while B phenotype's leaf resource allocation and growth rate responses are more flexible.

Table 7. Effects of water stress on the phenotypic plasticity index (PPI) of wild oat.

Trait	W phenotype	B phenotype
Root mass fraction (RMF)	0.72	0.44
Leaf/root ratio (L/R)	0.74	0.57
Root-to-shoot ratio (R/S)	0.47	0.33
Leaf mass fraction (LMF)	0.23	0.72
Leaf area ratio (LAR)	0.14	0.74
Mean leaf area (MLA)	0.16	0.76
Relative growth rate (RGR)	0.63	0.92
Net assimilation rate (NAR)	0.6	0.54
Mean leaf area ratio (LARm)	0.97	0.99

4. Conclusion

4.1 Divergence in Survival Strategies

Phenotypic plasticity is a core mechanism for plant adaptation to environmental heterogeneity (Bradshaw, 1965), influenced by both genetic regulation and epigenetic modifications such as DNA methylation (Gallego-Bartolomé, 2020). Under drought, plants are expected to adjust biomass allocation to optimize resource acquisition, adhering to the Optimal Partitioning Theory (Bloom et al., 1985). Our study reveals that while both wild oat phenotypes exhibit plasticity, their strategies for coping with water deficits appear to be fundamentally different.

The W phenotype adopted a strategy of proactive adjustment and physiological resilience. A key observation was its prioritized investment in roots under moderate stress (MD), as indicated by the peak in its root-to-shoot ratio (R/S).

This response is a classic example of partitioning resources to the organ acquiring the most limiting resource (Poorter et al., 2012; Bloom et al., 1985) and may be linked to hormone-signaling pathways that regulate root development (Chen et al., 2020). Consistent with this view, studies in cereals indicate that soil- water deficit can trigger an ABA surge accompanied by declines in cytokinins and nitric oxide, coordinating stomatal control and a shift in carbon allocation that restrains leaf expansion while promoting root investment (Ji et al., 2023). This active belowground adjustment was complemented by a robust physiological performance; its net assimilation rate (NAR) remained stable under light stress. This "morphology-first" response, where growth reduction is initially driven by morphological trade-offs (i.e., a lower LAR) rather than physiological failure, is consistent with a stress-tolerant strategy aimed at maintaining long-term growth (Grime, 1977).

In contrast, the B phenotype’s response was more reactive and seemingly higher- risk, aligning with a “stress- avoidance” strategy. The early increase in Leaf Mass Fraction (LMF) under light stress occurred alongside a 47% drop in NAR, suggesting stomatal and/or biochemical down- regulation under drought- induced signaling (Chaves et al., 2002; Chen et al., 2020). As water deficit intensified, B sharply curtailed leaf investment to limit transpirational demand, a pattern consistent with avoidance behavior observed in xeric species (Huang et al., 2008) and indicative of a growth–survival trade- off (Zhang et al., 2020). Such shifts in leaf development and photosynthetic regulation have been associated with small RNA (miRNA)–hormone regulatory networks in other species (Zhakypbek et al., 2025).

4.2 Implications for Control and Conclusion

The divergent strategies observed have potential management implications. For the W phenotype, its root-centric strategy under moderate drought could be a target. For the B phenotype, its physiological sensitivity to even light stress presents a key vulnerability. These findings underscore the importance of considering intraspecific variation for developing more effective, phenotype-aware management (Zheng et al., 2023).

It is important to acknowledge the limitations of this pot experiment, as field conditions may elicit more complex responses. In conclusion, the W and B phenotypes of wild oat exhibit distinct adaptive pathways under drought. The W phenotype shows a resilient, morphology-first adjustment, while the B phenotype displays a reactive response limited by physiological instability. This highlights that a deeper understanding of such intraspecific strategies is crucial for predicting and managing plant invasions.

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