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Environmental heterogeneity and adaptive traits of *Panicum antidotale* under drought and salinity stress in Punjab, Pakistan

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Abstract

Panicum antidotale is a very tolerant C4 grass from the Indo-Pakistan region that can be used under harsh environmental conditions, especially when under drought and salinity stress. This review explores the morphological (phenological), anatomical, and physiological adaptations of *P. antidotale* in various ecological zones of Punjab, such as the Salt Range, wetland, desert, and mountain area. *P. antidotale* shows a suite of morphological adaptations, including a reduced leaf area, extensive leaf sclerification, and root changes for water retention and uptake. Anatomically, the species has thickly sclerified vascular bundles, wider metaxylem vessels, and salt excretion glands (food for osmotic adjustment). In addition, *P. antidotale* has a powerful biochemical defense system, which involves the accumulation of proline, increased antioxidant enzyme activity, and selective ion regulation to reduce the effect of reactive oxygen species (ROS) on the plant. These several-side nature of adaptations allows the species to be productive in unfavorable and degraded conditions. The review underscores the importance of the ecological role of *P. antidotale* and the need to better understand its adaptive mechanisms to facilitate breeding of stress-tolerant forage cultivars. Further studies are needed to understand the genetic and molecular mechanisms underlying this resilience, which should lead to the implementation of *P. antidotale* on a large scale in climate-smart agriculture and in the restoration of degraded rangelands.

Keywords: Environmental heterogeneity; *P. antidotale*; drought stress; Salinity stress; Punjab ecozones; Adaptive traits

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Introduction

Environmental Heterogeneity

One of the main mechanisms for understanding patterns of variety and species coexistence is environmental heterogeneity, which encompasses every aspect of spatial heterogeneity, complexity, diversity, structure, or variability in abiotic and biotic environmental circumstances. One important aspect of Pakistan is its

environmental variety, which includes a hot Arabian Sea coastline in the south and an excessively cold mountainous area in the north [2]. The northern highlands, the Indus River plain, the mountain ranges along the western border with Afghanistan, and the deserts south of the Sutlej River along the eastern border with India comprise Pakistan's diverse heterogeneity and wide range of landscapes. Parts of the Himalayas, the Karakoram Range, and the Hindu Kush are included in the northern highlands [3].

Environmental heterogeneity the variability in abiotic and biotic factors both in space and time is one of the most important factors in the evolutionary adaption of plants [4]. Selective pressures in a mosaic in the context of Pakistan are shown as a dramatic transition from dry southern coastal plains to the extreme coldness of the northern mountainous region. The complexity of the environment requires the emergence of special morpho-anatomical and physiological characteristics for the survival and co-existence of species [5].

In the southern deserts for example, the Cholistan and Thar regions, the excessive moisture deficits being experienced favor those plants which were selected to have a more efficient use of water, e.g., fewer leaves and deeper root systems [5]. On the other hand, the high elevation areas of the Himalayas, Karakoram and Hindu Kush create thermal stress, which benefits plants that are able to withstand it by altering their metabolism and membranes. Also, the salinity variations in the Indus River plains and in the Salt Range put a huge osmotic pressure, which leads to the development of specialized salt excretory glands and sequestration of ions [6]. It is this landscape scale heterogeneity that underpins the particular metabolic specialization of resilient species, such as *P. antidotale*, and its ability to sustain metabolic stability in a highly contrasting niche space, through an adaptive portfolio of traits including antioxidant defense systems and sclerification.

Introduction of *Panicum antidotale*

Panicum (panic grass) is a large genus of family Poaceae having over 500 species [7]. It is spread throughout tropical and subtropical regions of the world, but few species are reported in temperate regions Table 1. Various species of *Panicum,* viz., *P. antidotale Retz*. (Blue panic), *P. coloratum* L. (colored Guinea grass) and *P. maximum* Jacq. (Guinea grass) used as forage and cereal crops. These are also considered potential sources for livestock and wildlife in arid and semi-arid regions of the world [8]. *Panicum* species are more resistant and tolerant to harsh environmental conditions (drought and salinity) as compared to other grass species [9]. It has very distinct morpho-anatomical and physiological attributes, which assist them to grow in varied habitats [8, 9].

P. antidotale (Retz.) originated from Indo-Pakistan regions, locally called Murrot or Bansi grass [8]. It is also known as blue panic due to dark bluish-green leaves. It is the main source of forage and cereal crops with high nutritive and productivity values [10]. Its inflorescence is an open panicle bearing numerous spikelets, with each spikelet containing the individual florets (small flowers enclosed by modified, bract-like leaves). The outer covering of the floret is called the glume or bract, while the inner layer of the floret is known as the palea [11]. Non-reproductive parts or non-essential parts of the flower are absent while reproductive parts or essential parts are present. The Stem of blue Panic is hard, erect and smooth, the arrangement of leaves on the stem is alternate with parallel venation, and the base of the stem is swollen like a sugarcane stem [12]. Its roots are fibrous or adventitious type (develop from any part other than the radicle), and fibrous roots are hair-like roots forming clusters of hairs with strong speeding rhizomes.

Potential effects of *Panicum antidotale* on economy of Pakistan

In Pakistan's northern regions, blue panic reseeding boosts range production by a factor of 12. After Buffel grass, blue panic produces the second-highest volume of fodder in Kohistan ranges. Large-scale sowing of *P.*

antidotale is ideal for the Kohistan range, the Pothowar Plateau, and the foothills of Murree. *Amaranthus viridis, Rumex dentatus*, and *Chenopodium murale* are agricultural invaders linked to blue panic.

Table 1. Common Characteristics of *Panicum antidotale*

Characteristic	Description	Reference
Scientific Name	*Panicum antidotale* Retz.	[13]
Common Name	Blue Panic Grass	[13]
Family	*Poaceae* (*Gramineae*)	[14]
Growth Habit	Perennial, C4 grass, tufted	[15]
Native Range	South Asia, including Pakistan, India, and Afghanistan	[16]
Preferred Soil Type	Sandy to loamy soils, well-drained	[17]
Drought Tolerance	High; deep root system enables survival in arid conditions	[18]
Salinity Tolerance	Moderate to high; accumulates Na^+ in older leaves	[19]
Photosynthetic Pathway	C4 (Efficient in high-temperature environments)	[20]
Seed Germination	Optimal at 25–30°C; declines under extreme salinity	[21]
Ecological Role	Soil stabilization, forage grass, erosion control	[21]
Economic Importance	Used as livestock forage and for revegetation of degraded lands	[22]
Leaf Morphology	Long, narrow, bluish-green leaves with a prominent midrib	[13]
Root System	Deep, fibrous roots aiding in drought resistance	[23]
Tillering Ability	High tillering capacity, enhancing biomass production	[24]

Climate change impacts and response of grasses

Climate change will have a direct and indirect impact on grass primary production by altering the carbon and water cycles, mineral cycles, solar energy flow, and plant community composition [25]. Soil fertility, community types, dominating functional group types, soil water availability, and other factors may influence how sensitive the grassland ecosystem is to changes in the climate. *Andropogon gerardii* have the highest levels of water transport or storage as shown in Figure 1. Grasses with bigger xylem vessels had less bulliform area, which increased their capacity to transfer minerals and water. By using these tactics, populations of *A. gerardii* might be able to adapt to changes in rainfall and temperature during a growth season.

The grasses adjust the activation state of RuBisCO or the activity of RuBisCO activase as growth temperature changes and may shift nitrogen partitioning to the most limiting process (e.g., RuBP regeneration and RuBisCO carboxylation) to maximize photosynthesis at the new temperature [26]. C4 grasses, especially the major bioenergy grasses, are relatively freezing intolerant, although *Miscanthus*, upland switch grass, and prairie cord grass (*Spartina pectinata*) exhibit some cold tolerance.

From a leaf perspective, genotypes producing longer-lived, more expensive leaves (i.e., a conservative strategy) may have evolved a greater ability to adjust photosynthetic and respiratory capacity in response to changing temperatures than genotypes that produce shorter-lived, cheaper leaves (i.e., an acquisitive strategy). In switchgrass, for example, adaptation to a longer, more variable growing season in warm-origin genotypes could enable a greater capacity for temperature acclimation of leaf physiology [27].

Anatomical and biochemical modifications may explain some of the observed physiological responses to climate change. For instance, elevated CO_2 reduced stomatal density and stomatal index [percentage derived from the stomatal density divided by stomatal density plus epidermal cells] in Guinea grass [28]. In the same study, warming reduced leaf thickness, which may explain the

lack of temperature effect on gas exchange physiology. In big bluestem, the increases in photosynthesis in response to both warming and elevated CO_2 independently may have resulted from increased Phosphoenolpyruvate carboxylase (PEPC). efficiency and electron transport rate [29]. Nonstructural carbohydrates may be involved in physiological temperature resistance, but they responded differently to warming in the two Guinea grass studies: In one study, sucrose, glucose, and fructose all declined with increasing temperature, but there was no difference in starch content, while in the other study, starch content declined with increasing temperature. Together, these studies suggest a complicated relationship between the effects of rise in CO_2 and warming on grass physiology.

P. antidotale has more plasticity in its anatomical and morphological characters that enables it to survive in different stress conditions. *P. antidotale* is dominant in arid regions with high tolerance characteristics in severe environmental conditions. With abiotic stress, the plant faces various problems like an increase in osmotic and ionic stress that leads to the formation of reactive oxygen species (ROS) [30]. High salt concentration reduces the water uptake, photosynthesis, nitrogen assimilation and mineral nutrient uptake, which adversely affects the growth, development and yield of *P. antidotale* [31]. These involve very specific structural modifications such as cuticle and epidermal thickness, widened metaxylem vessels, intensive sclerifications, and formation of storage parenchyma tissues, palisade and spongy mesophyll tissues [32].

Significance of the Study

In dry and semi-arid regions, *P. antidotale* (blue panic grass) is a highly resilient C_4 species essential for rangeland rehabilitation, erosion control, and forage production. While previous studies have examined the general physiological responses of *P. antidotale* to individual stressors, this review distinguishes itself by integrating morpho-anatomical, physiological, and biochemical data specifically across the heterogeneous ecological zones of Punjab, Pakistan. Unlike earlier syntheses that may focus on isolated mechanisms, this study provides a holistic assessment of how environmental heterogeneity in Pakistan ranging from saline plains to arid deserts drives adaptive plasticity in this species. The practical applications of this research are multifaceted: identifying the most effective morpho-anatomical traits provides a blueprint for plant breeders to develop stress-resistant forage cultivars tailored for high-salinity and drought-prone regions; characterizing *P. antidotale* across diverse landscapes offers actionable data for the restoration of degraded rangelands, enabling more sustainable land-use optimization in climate-vulnerable zones; and providing a strategic resource for policymakers and agricultural extension services to mitigate the impacts of climate change on forage security. Ultimately, by deciphering these adaptive strategies, this study bridges the gap between fundamental plant science and field-level agricultural resilience, offering practical solutions for farmers and land managers operating in increasingly harsh environments.

Ecozones of Punjab

Salt Ranges

The Salt Range exhibited numerous geographical significance with distinctive components of soil and biodiversity facing abiotic stress for example drought and salinity (Figure 2) [33]. Salt Range is located at 70^0 31 E in longitude and 33º24-32˚ N in latitude. It has a very unique range extending from the northern (Potohar plateau) to the western region (Thal desert). It is bestowed of biodiversity for vegetation studies and evolutionary perspectives. It is the key source for paleontologists to uncover fossil records due to its long evolutionary history, as it originated in the Cambrian era [34]. The high salinity levels prevalent in this region necessitate advanced osmotic adjustment, compelling the species to develop sophisticated strategies for maintaining cellular homeostasis under extreme stress. To manage these saline conditions, *P. antidotale* has evolved specialized glands that facilitate

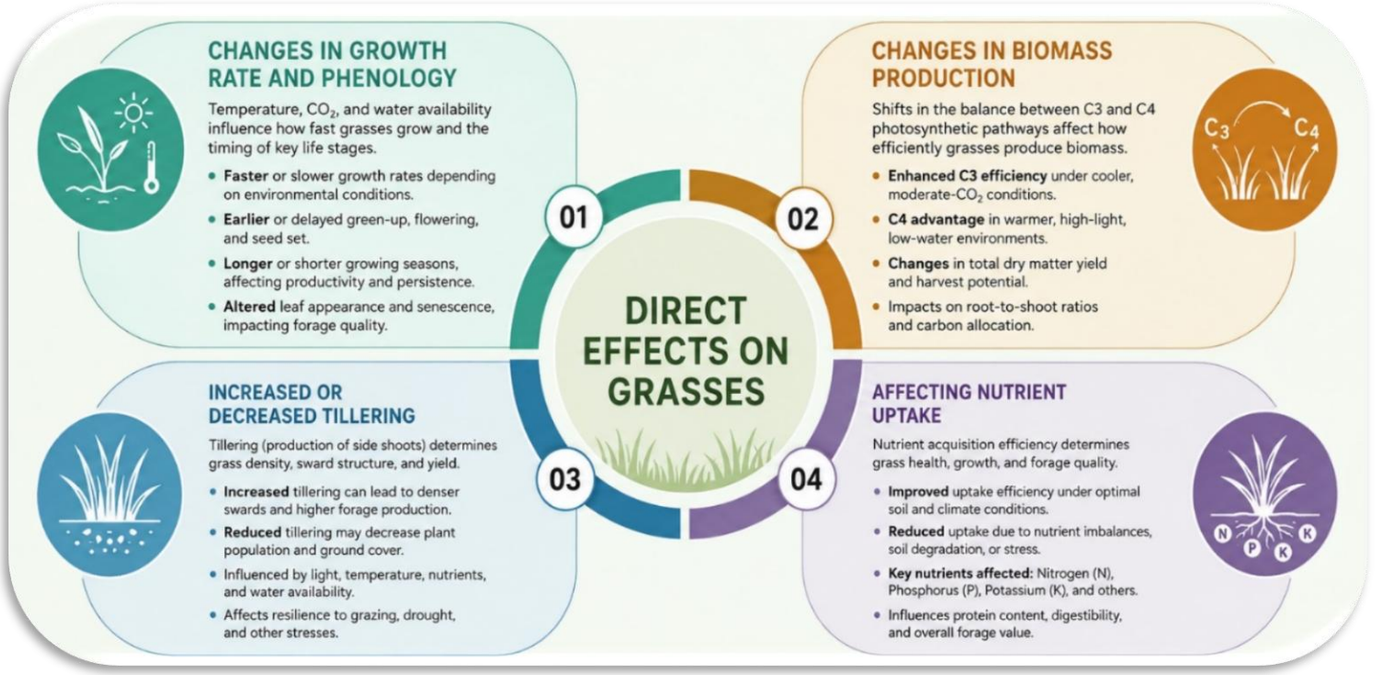

Figure 1. Direct effects on grasses under changing environmental conditions. The schematic illustration summarizes the major direct responses of grasses to environmental and climatic variations. These responses include: (1) changes in growth rate and phenology, characterized by alterations in germination, vegetative growth, flowering time, and seasonal development patterns; (2) changes in biomass production, resulting from variations in photosynthetic efficiency and carbon assimilation pathways, particularly the differential responses of C_3 and C_4 grasses; (3) increased or decreased tillering, affecting plant architecture, population density, forage yield, and overall productivity; and (4) modifications in nutrient uptake efficiency, influencing the acquisition and utilization of essential macro- and micronutrients, thereby impacting plant growth, physiological performance, and ecosystem functioning. Collectively, these direct effects determine grassland productivity, resilience, species composition, and adaptation to environmental stressors.

the active excretion of excess salts, thereby preventing toxic accumulations within its tissues. Furthermore, the environment has shaped the anatomical structure of the grass, leading to modifications such as heavily sclerified vascular bundles and broadened metaxylem vessels which ensure efficient water transport despite high osmotic potential.

Soon Valley

Soon valley will be the main habitat for flora and fauna diversity in the Salt Range. Different types of grasses and leguminous species dominate in this valley on which various wild grazing animals feed [35]. These species are rich sources of carbohydrates, soluble sugar and starch contents. Regions situated near the Chenab, Indus and Jhelum Rivers are frequently subjected to seasonal floods, as result vast areas of these regions have been transformed into swamps or seasonal inundation, riverians, or bela forests. The dominant species of this valley are used as forage and are considered as a significant role in grazing point of view [36].

Among the more than 60 palatable grass species found in this region, *Cgrysopogon serrulatus, Heteropogon contortus, Dichanthium foveolatum, Cynodon dactylon,* and *P. antidotale* are the most common [37]. On one end of the Salt Range, which runs southwest along the River

Jhelum, are the ridges of Bakrala and Jogi Tilla, which are located east of Jhelum. The Salt Range area is dominated by grass flora, with several writers reporting a great deal of variety in the Poaceae family. Irshad and Hameed [38] observed 62 species from the Salt Range. *P. antidotale* and other related species, including *Cymbopogon jwarancusa, Senegalia modesta,* and *Maytenus royleanus*, colonized Jhallar Lake, a saltwater lake in the southern Salt Range. The majority of the related species, including *Dipterygium glaucum, Calligonum polygonoides,* and *Lasiurus scindicus*, as well as *P. antidotale*, are found in Lilah (District Jhelum), which is a strongly salt-affected area.

Wetlands

Pakistan is bestowed with numerous wetlands that are very important from an ecological and biodiversity point of view. Uchalli complex is part of the Salt Range (located in district Khushab) comprising three most important wetlands Jhallar, Uchalli and Khabeki Lakes [39, 40].

Deserts

Cholistan Desert

The Cholistan Desert (locally known as Rohi) situated in southern Punjab extending from latitudes 26°45 and 28°42 North and longitude 68°53 and 74°26 East covers approximately 2.7 million hectares. Based on the soil type, structure, texture and topography. The Greater Cholistan contains great dunes with smooth interdunal regions and the Lesser Cholistan contains fewer dunes [41].

The Cholistan Desert is considered as the seventh largest desert with greater and lesser deserts, the greater desert extends along the southern border, while the lesser desert is spread in the northern region of Punjab province [42]. Its soil is very poor due to a deficiency of organic matter and the unavailability of water. Dominant species of Cholistan desert are *P. antidotale, Capparis decidua, Calatropis procera, Prosopis cineraria, Salsola imbricata* and *Suaeda vera*.

Thal Desert

Thal desert is located between the Jhelum and Chenab rivers in northwest Punjab [43]. The Thal desert extends from 30°10 N to 70°31 E in the Punjab province of Pakistan and covers 195 miles from north to east. It exhibits a resemblance to Cholistan and Thar Desert in geographical features. There are 250 species, 169 genera and 39 families reported, out of which 52 species belong to the grass family, 17 *Asteraceae,* and remaining to *Amaranthaceae*.

That is abundant in sedges and grasses, according to earlier research. With 52 species (21.49%), the Poaceae family was the most dominant, followed by the Fabaceae (34 species, 13.05%) and *Amaranthaceae* & *Asteraceae* (17 species, 7.02% each) [44]. Six species of Euphorbia, five species each of *Cyperus, Eragrostis*, and *Solanum*, four species each of *Mollugo, Heliotropium, Panicum*, and *Cenchrus, Acacia, Prosopis, Tephrosia, Boerhavia, Ziziphus*, and *Corchorus* (three species each) [45].

Mountains

Sulaiman mountain range

The Sulaiman Mountains or Koh-e Sulayman" comprise the eastern border of the northeast border of the Balochistan Plateau and the Iranian plateau. They are found in Afghanistan's Kandahar, Loya Paktia, and Zabul provinces, as well as areas of Pakistan's "Balochistan" province and southwest Khyber Pakhtunkhwa as well as Punjab [46]. The project area's climate is prone to slight changes. It has pronounced seasonality in both temperature and precipitation. Summer temperatures can reach 35 degrees Celsius. Winters are chilly, with temperatures as low as -15oC at times, and there is a significant difference between day and night temperatures [47]. Grass dominates the Suliman mountain range. *Dactyloctenium scindicum, P. antidotale*, and *Cenchrus ciliaris* are the most widespread.

Kala Chitta Range

The Kala Chitta Mountains are located in the Attock District of Punjab, Pakistan [48]. The words kala-chitta are derived from the Punjabi language means black and white respectively. The mountain range moves eastward through the Potohar plateau towards Rawalpindi. The region is made up of terrain and plains, and its temperatures fluctuate between 17.92°C in January to 41°C in June. It receives only 650 mm of rainfall per year, and it is covered by dry temperate forest with vegetation, having dominant species like *Acacia*, *Dalbergia sissoo*, *Justicia adhatoda*, *Dodonaea viscosa*, and *Olea europaea subsp. Cuspidate* [49].

Abiotic stresses like water deficiency, excessive salts and high temperatures are significant threats to crops and wild plant communities, as these continuously deteriorate the natural environment and cause low productivity of crops. Numerous stresses can further suppress crop production when it occurs at a critical stage [50]. For instance, low water availability to plants might be a reflection of high temperature and photon irradiance. Moreover, a high level of salt in the soil delimits the low water availability by lowering soil water potential, which has a detrimental effect on the growth of plants. Plants that are subjected to one kind of abiotic stress may become less tolerant when subjected to other kinds of stress [51]. For instance, plants with fewer water supplies are more vulnerable to the negative impacts of high irradiance because their ability to recycle NADPH (Nicotinamide Adenine Dinucleotide Phosphate) is limited and the surplus energy provided to the photosynthetic system is wasted.

Morphological adaptations of *Panicum antidotale*

Elevation-driven morphological changes

High-elevation-inhabiting *P. antidotale* plants have a variety of morphological traits, including small, thick branches that grow near the ground. Their stomata are frequently grooved and protected within tiny chambers, and their leaves are usually small yet thick, covered in dense hair-like filaments. *Panicum* can store water and avoid water loss due to this modification.

Panicum inhabiting higher elevations have short height and reduced root length and leaf [52]. It shows varying changes in its height and stem length at different elevations for example the plant height is reduced at moderate elevation of about 600 meters but there is a significant reduction in its height at 800 meters and plants found at 1000 meters heights are the shortest. This reduced plant height and root, stem length helps *Panicum* to conserve more energy and helps to mitigate low oxygen stress [53]. There is a negative relation between *Panicum* root length and height i.e., as heights increased root length decreased proportionally. But the surface area of the root increased. These changes in the root structure of *Panicum* are important for increased water and nutrient absorption and increased transport from roots to the stem area in extremely harsh environments at different elevation gradients.

Alternately the number of leaves increased at higher elevations i.e., 1000 meters. This adaptation helps *Panicum* absorb more sunlight to increase photosynthesis and more energy production to survive in harsh environments [54]. As the elevation gradient increases gradually the overall leaf area per plant decreases proportionally. This reduction in leaf area is an important adaptation of *Panicum* to prevent water loss through leaf surfaces but it also helps it to increase nutrient storage.

Salinity-driven morphological changes

In arid areas affected by salt stress, salinity is the major limiting factor in crop yield and growth [55]. Salt stress is a global problem responsible for the degradation of land [56]. In deserts increased evaporation, temperature and low rainfall is responsible for salt stress. It causes late germination, decreased growth and yield in desert [57]. Plant development and physiology are adversely affected by salinity, mostly as a result of oxidative stress and ionic imbalance. Plant species' development and biomass output are directly impacted by salt stress.

Panicum develops longer roots during salt stress to absorb more water from deeper soil layers. Its roots absorb important nutrients from soil like potassium and magnesium while excreting harmful nutrients responsible for salinity stress like sodium and chloride through special pores in roots [58]. Specialized salt glands are formed on the root, shoots and leaves of grasses for salt exclusion. Stem growth decreases to save water and metabolic energy [59]. Leaves are thicker, succulent, short, and small and have waxy cuticle deposition to reduce water loss and conserve more water.

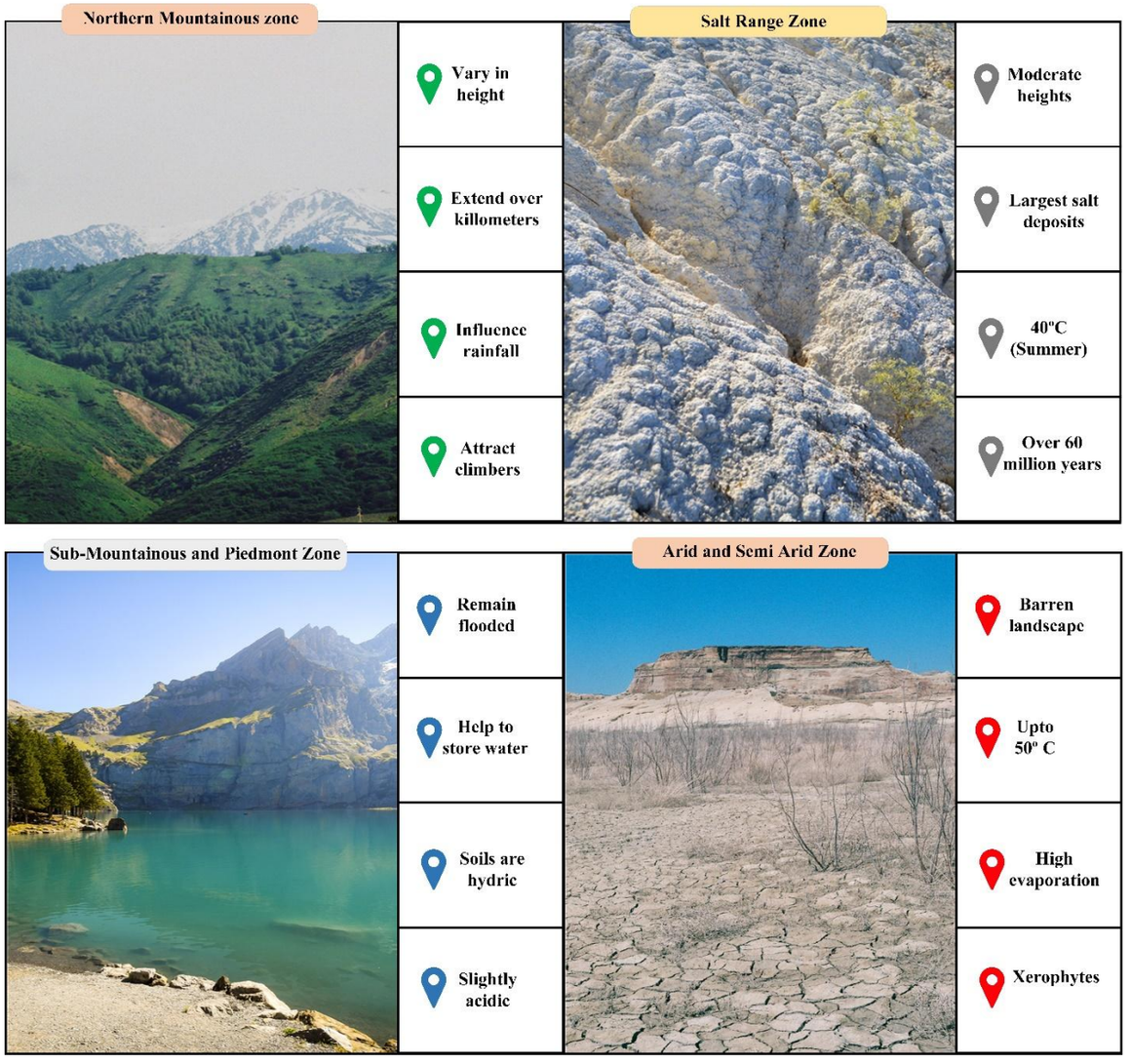

Figure 2. Ecological zones of Punjab, showing the major environmental features, topographical characteristics, and climatic conditions of the Northern Mountainous Zone, Salt Range Zone, Sub-Montane and Piedmont Zone, and Arid and Semi-Arid Zone. The figure is an original illustration prepared by the authors using photographs obtained from Pexels under the Pexels License (https://www.pexels.com/license/).

Drought-driven morphological changes

In the drought avoidance mechanism, plants exhibit small or reduced stomata may lead to slow growth of plants resulting in reduced cell metabolism and photosynthesis [60]. During such serious conditions, plants adapt succulent strategy to increase water storage and minimize water loss through leaves, this enables the plants to cope

with altered environmental conditions. In general, plants adapted to drought stress by using both drought avoidance and drought escape mechanisms. Most plants' ability to withstand drought is directly related to structural modifications such as increased leaf thickness [61]. Succulence in terms of leaf thickness, which is primarily due to mesophyll and cortical cells, is a rare phenomenon in monocots, especially in grasses [62]. However, there are a few reports of increased leaf thickness under drought stress due to parenchymatous cells, which are the primary storing cells of the leaf and are therefore very important when moisture availability is limited.

Since *P. antidotale* uses more energy on survival and other metabolic functions than on growth and development, stunted growth may be a crucial survival strategy in habitats with low moisture [63]. Since this grass is directly impacted by environmental stressors, the leaves and total leaf area per plant are the primary growth factors that contribute to plant survival and growth [64]. In times of stress, this ecotype primarily depended on thicker leaves. This ecotype's ability to store water may be enhanced by this leaf trait, which is crucial for its resistance to desiccation in environments with low moisture levels.

Panicum's primary response to severe osmotic stress was significantly thinner leaves, or fibrous leaves, which may effectively roll to shield the adaxial leaf surface and are hence a crucial adaptation for drought tolerance [65]. This ecotype's reduced diameter metaxylem represents a significant adaption to dry conditions. Better conduction can occur in smaller vessels [66]. The presence of bulliform or motor cells is also an important morphological adaptation to protect the leaf from direct sunlight to reduce water loss.

Table 2. Effects of drought and salinity stress on selected physiological and growth parameters

Meter	Control	Drought	Salinity (100 Mm NaCl)	Combined	Source
Plant Height (cm)	62.6 ± 0.93	33.4 ± 1.81	21.0 ± 1.00	26.8 ± 0.97	[67]
Relative Water Content (%)	85 ± 2.5	60 ± 3.0	75 ± 2.0	70 ± 2.5	[68]
Chlorophyll Content (SPAD)	45.0 ± 1.2	30.5 ± 1.5	40.0 ± 1.0	35.0 ± 1.3	[68]
Proline Content (µmol g^{-1} FW)	2.5 ± 0.2	5.0 ± 0.3	4.0 ± 0.2	4.5 ± 0.3	[38]
Na^+/K^+ Ratio	0.5 ± 0.05	0.8 ± 0.07	1.5 ± 0.10	1.2 ± 0.08	[10]

Anatomical adaptations of *P. antidotale*

Elevation-driven anatomical changes

Panicum has different elevation-driven anatomical adaptations such as reduced root diameter and root epidermal thickness, small cortical and epidermal cells, reduced stomata, and narrow xylem and phloem vessels, which are among the elevation-driven changes in *P. antidotale*. [69].

At higher elevations, *P. antidotale* enhances its survival through specific anatomical modifications that address the unique challenges of extreme temperature fluctuations and reduced water availability [70]. The development of broadened metaxylem vessels optimizes water conduction, which is vital for maintaining hydration against the high transpiration demands characteristic of high-altitude environments.

Plant root system anatomical features are very sensitive to environmental changes in a variety of ecological

situations [71]. To avoid excessive salt absorption and its subsequent transfer to upper plant parts, the root radius tends to reduce as elevation gradients rise. Furthermore, at higher elevations, grasses typically show a decrease in root surface area. By limiting radial water flow from the vascular bundles, an increase in root endodermal thickness is seen at moderate altitudes, which helps with water conservation [72].

There are interesting changes in stem morphology: the stem radius first increases at low altitudes (600 m), but then decreases as elevations increase. This variation is an adaptive reaction to stresses brought on by altitude. At the same time, changes in the root radius caused by a reduction in store parenchyma limit the movement of toxic nutrients to the higher foliar areas. Fatima, et al. [73] research indicates that this protective mechanism is especially effective at higher elevations.

Salinity-driven anatomical changes

Salinity has become a major constraint that reduces plant growth and development all over the world [55]. Salinization of cropland due to repeated irrigation in arid regions is a major drawback of low crop production [74]. The plant response to salinity is based on the prevailing stress condition and the duration to which plants respond at various developmental stages [75]. There are some prominent problems i.e., osmotic effect, nutritional imbalance, and ion toxicity that plants have faced during prolonged saline stress. All of these reduce the yield, growth, and development of plants [9].

Different mechanisms and adaptations allow plants to withstand salt stress. Because of root adaptations such as larger inner tangential walls of the endodermis, lignified cortical parenchyma, and thicker epidermis, toxic ions were originally confined at the root level [76]. Panicum has many extensions on its body like micro hairs, salt-excreting glands and salt hairs that help it to excrete excessive salt from its body. Other cellular entities like vacuoles or old leaves can also serve as salt dumps.

In salt-affected areas, the epidermis acts as a barrier that prevents the entry of excessive salts in the plant body. It is an important feature of plants inhibiting salt-affected areas [77]. The presence of thick epidermis in arid areas is confirmed by various researchers, which prevents water loss from the plant body. The cortex also plays an important role in the storage of water. Salt-affected *Panicum* plants have well-developed cortical regions. Bigger cortical cells store more water, nutrients and excessive salts in comparison to small cortical cells. The endodermis in *P. antidotale* root act as a barrier that prevents the loss of water from root and also prevent the absorption of toxic nutrients and excessive salts. Endodermis helps in conservation of water

Drought-driven anatomical changes

Plants adapting Drought Avoidance (DA) respond to increase the uptake of water from the extensive root system and rolling of leaves [78]. The vascular bundle sheath's parenchyma or sclerenchyma cells, which form the purported bundle sheath extensions increase the photosynthetic capacity of leaves by creating mesophyll compartments and appear to be advantageous in protecting mesophyll from drought stress. The well-developed bulliform cells are one of the most noticeable characteristics of xerophytic grasses; they are crucial for leaf rolling and are regarded as a major factor for the survival of such species under extreme aridity.

Plants that have evolved to desert conditions typically have thick epidermis [79], which is securely linked to excessive water loss through leaf surfaces [80]. Reduced stomatal density on both leaf surfaces and sclerification immediately underneath vascular tissues helps to reduce water loss [81]. *Panicum* has more developed mesophyll, indicating that they have a wide photosynthetic area that may have been mostly utilized for survival rather than expansion [82]. Better vascular tissue growth in terms of size and vessel area was the third essential tactic, and it may enhance the movement of solutes and photosynthates in hostile environments.

Under drought stress, mesophyll thickness and metaxylem vessel size increased in the *P. antidotale*, which would have allowed for more effective water conduction and photosynthetic activity [83].

Physiological adaptations of *P. antidotale*

Elevation-driven physiological changes

At higher elevations, *P. antidotale* utilizes efficient antioxidant mechanisms to mitigate reactive oxygen species (ROS) and reduce lipid peroxidation [84]. To counteract this toxicity, *P. antidotale* employs a highly coordinated, dual-layered antioxidant defense system comprising enzymatic and non-enzymatic components. Enzymatic antioxidants, including superoxide dismutase (SOD), catalase (CAT), and ascorbate peroxidase (APX), act sequentially to neutralize toxic ROS into harmless water and oxygen molecules [85]. Simultaneously, non-enzymatic components such as proline and glutathione function as direct ROS scavengers and vital cellular osmo-protectants. By upregulating this integrated defense network, *P. antidotale* effectively maintains redox homeostasis, preserves membrane integrity, and sustains critical metabolic functions even in highly degraded environments. The difficulties presented by frequent temperature changes, greater solar radiation, and limited water conditions cause a decrease in photosynthetic pigments at higher elevations, which limits plant development [86]. Ionic contents in both roots and shoots decrease along the elevation gradient. At higher elevations, where nutrient-poor soils predominate, this reduction is especially noticeable and negatively affects the ionic profile of plants. Additionally, changing climatic conditions have a negative impact on the ion concentrations in vegetative plant sections.

SOD and POD activity, however, decline with elevation rise. The species' reduced amounts of photosynthetic pigments at high elevations might be the cause of this decline [38]. On the other hand, CAT activity rises with a modest gradient in altitude.

Salinity-driven physiological changes

During salinization, a rise in sodium ion concentration along with a reduction in potassium ion concentration within the cell cytoplasm causes an imbalance of osmotic potential. Thus ion compartmentalization is compulsory to diminish ionic toxicity via i) proton antiporters (Na^{+}/H^{+}) located on the vacuolar membrane, ii) osmoregulation by accumulation of ions (Na^{+} and Cl^{-}) in vacuole, compatible or organic solutes in cytosol and proton (H^{+} and K^{+}) gathered in cell cytoplasm [87]. Oxygen is considered an essential substance in plants, involving photosynthesis, respiration, oxidative Phosphorylation, and metabolism for the production of energy [88]. Imbalance production of oxygen (high and low concentration) may lead to the production or activation of plant's reactive oxygen intermediates [89], causing damaging effects on macromolecules, cytoplasmic membranes, dysfunctioning of metabolic processes, and ultimately can cause cell's death. *P. antidotale* showed a defensive mechanism of antioxidant or osmo-protectants solutes as a result of oxidative stress.

When grasses face unfavorable conditions resulting in ROS production, which negatively influences the plant metabolism by accumulation of ions (ionic toxicity), osmotic, and oxidative stress [90]. To protect against osmotic stress, proline accumulates in the cytoplasm and functions as an osmo-protectant. Populations populating high salinities also acquire total soluble carbohydrates and glycine betaine for osmo-protection. The soil containing high concentrations of salts and inorganic solutes like Na^{+}, Cl^{-}, and Mg^{2+} is known as saline soil [91]. Such soil was categorized into further three types based on the salt concentration, for example, saline soil, sodic soil, and saline-sodic soil. The electrical conductivity of saline soil (white alkali) is more than 4 while the exchangeable sodium percentage and sodium absorption ratio are less than 15 and the pH is 8.5. The electrical conductivity of sodic soil (black alkali) is less than 4 whereas the exchangeable sodium percentage and sodium absorption ratio are more than 15 with almost 8.5

pH. The electrical conductivity of saline sodic soil is greater than 4 while the exchangeable sodium percentage and sodium absorption ratio are greater than 15 with around 8.5 pH [92].

Plants have developed a variety of defense mechanisms to fight this oxidative stress. These defense mechanisms include activating antioxidant enzymes such as peroxidases (POD), superoxide dismutase (SOD), ascorbate peroxidase (APX), catalase, and other non-enzymatic antioxidants like flavonoids, phenolic compounds, ascorbic acid, and tocopherols. These enzymes help plants scavenge reactive oxygen species. While the concentration of non-enzymatic antioxidants often falls under salt stress because of their interaction with other antioxidants, levels, and activity of different enzymatic antioxidants rose in plants developing under salinity stress [93].

Drought-driven physiological changes

Drought is a shortage of water due to periodically low rainfall in an area. Plants showed four main mechanisms to overcome the prevailing drought conditions such as drought resistance or tolerance, drought avoidance, drought escape, and drought recovery [94]. In drought resistance mechanism, plants can face the extreme shortage of water by involving various tolerant features at physiological, morphological, biochemical, and cellular levels to overcome such stress conditions. In drought escape, plants complete their growing season or life cycle before the onset of dry weather conditions.

Drought avoidance is the ability of plants to sustain or maintain tissue water content even in low availability of water in soil. They adopt different strategies to maintain the water status in the body [95] Figure 3. Drought is a main abiotic stress that delimits the several physiological and morphological activities of the plant and ultimately leads to a great decrease in growth, yield, and productivity. Due to water-scarce conditions plants underwent a water shortage, and in resulting it showed a significant decrease in cell size, cell turgor, and biomass production.

When plants are exposed to severely dry environmental conditions, the primary function of plants is stomatal closure, regarded as the main adaptive component in such conditions, and water scarcity is considered as the main constraint of photosynthesis [96]. Closure of stomata reduces the concentration of CO_2 influx and free electrons that are used in the formation of reactive oxygen species. Deficiency of CO_2 is regarded as the main devastating effect due to the closure of stomata, resulting in a reduction of photosynthetic rate [97].

Plants adapting to drought avoidance (DA) respond to slower developmental processes and increased water use efficiency. Furthermore, DA may be fatal for prolonged periods of drought conditions, therefore, plants represent alternative strategies of drought avoidance and drought tolerance according to their growth requirement to minimize the drought occurrence and duration.

Drought-driven modification Case study

According to Ho [98] report widespread leaf rolling in *Tristachya leiostachya* and *Loudetiopsis chrysothrix* under drought stress, bulliform cells are actively involved in leaf rolling to prevent water loss in *P. antidotale* . Flowers and Colmer noted in many grasses that a good defense against drought stress in grasses is the presence of thick leaves, which are caused by mesophyll and cortical cells. Although parenchymatous cells are the primary storage cells of the leaf and are thus crucial in situations where moisture supply is restricted, there have been a few reports of increased leaf thickness under drought stress due to the parenchyma cells in legume crops. Increased epidermis thickness, sclerenchyma deposition around vascular tissues, and reduced stomata number on both leaf sides may help *P. antidotale* to prevent water loss through leaf surfaces. Additionally, Ibrahim, et al. [99] showed that *P. antidotale* populations that were tolerant to drought were better able to accumulate K^+ in their leaves when subjected to water stress. Drought resistant varieties of *Zea mays* have increased absorption of potassium ions. The capacity of drought-tolerant plants,

such as chickpeas, grasses, and soybeans, to absorb and accumulate macronutrients like N, P, and K under drought stress conditions has long been established.

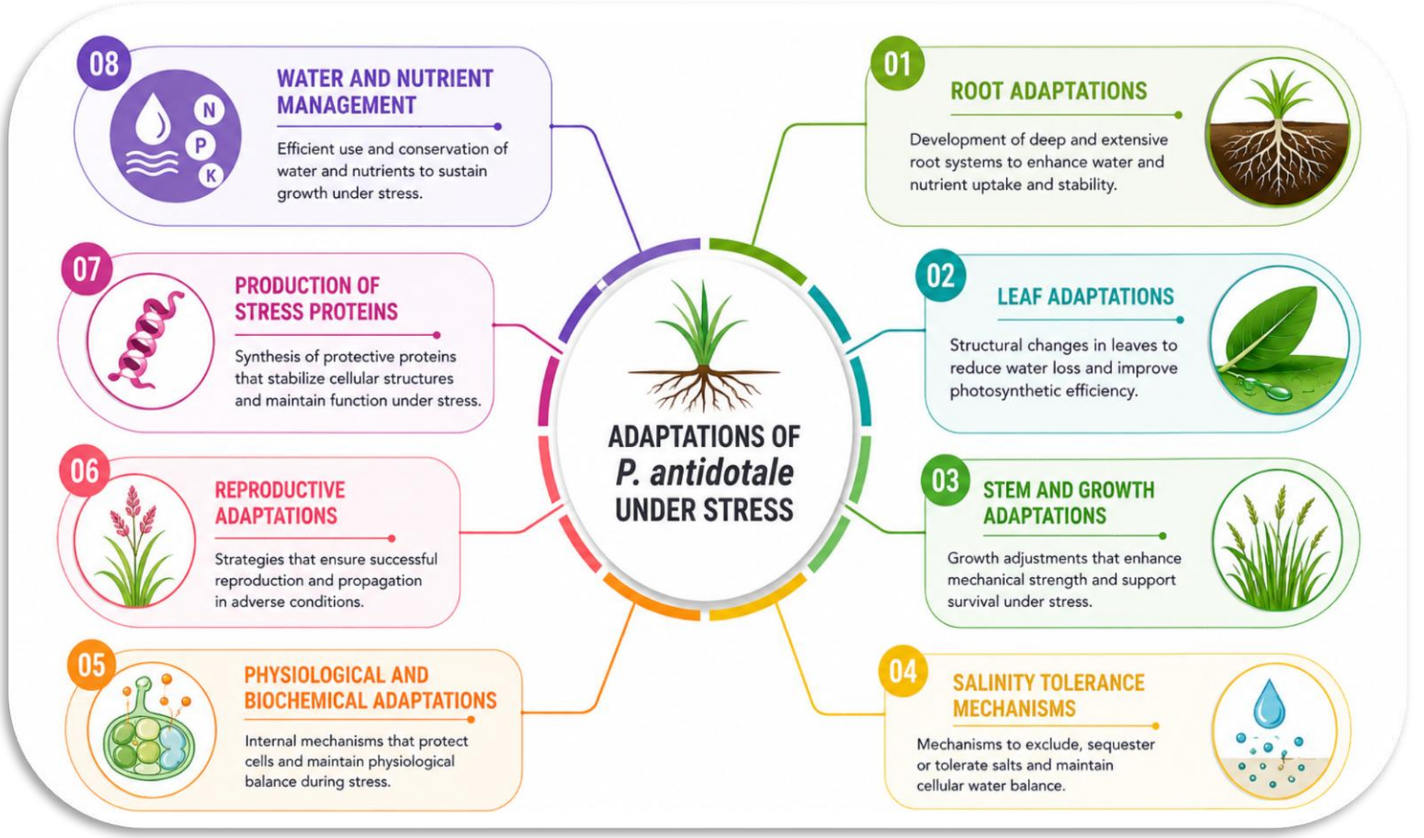

Figure 3. Adaptations of *P. antidotale* under stress conditions. The figure illustrates the key morphological, physiological, biochemical, and reproductive adaptations of *P. antidotale*, including root and leaf modifications, salinity tolerance mechanisms, stress protein production, and efficient water and nutrient management strategies that contribute to enhanced stress tolerance and survival.

cell walls is one of the main morphological characteristics linked to drought tolerance in the *P. antidotale*. In *Panicum*, there is a notable increase in both the metaxylem vessel area and the overall vascular region area. In *P. antidotale*, pith area and pith cell size significantly increased when there was a moisture shortage. The ability of large parenchymatous cells to store water is essential in situations when there is a moisture shortage as reported by Ievinsh [100] in *Calotropis peocera*.

Near the root perimeter, *P. antidotale* formed a dense layer of sclerenchyma. Sclerenchyma with thick

Given that this condition was documented previously in drought-stressed *P. antidotale*, a significant decrease in vascular bundle area and phloem area in the stem region of *P. antidotale* possibly helped to limit growth during drought stress by conserving vital energy for survival. The characteristic changes under moisture deficit circumstances were distorted metaxylem arteries and increased sclerification around peripheral vascular bundles and close to the stem periphery. Deformation of metaxylem vessels led to a reduction in vessel area, which

may be an essential adaptation for promoting water conduction under water-deficient situations in *juniper* species was also noted in *P. antidotale*. There are two main reasons for the importance of these morpho-anatomical and physiological responses. First, they show how *P. antidotale* is able to coordinate the structural change (sclerification, leaf rolling) with physiological change (ion accumulation, vascular deformation) to maintain water use efficiency and hydraulic safety. Second, it is a useful structural blueprint for plant breeders to decipher the combination of traits in this case. The ability to identify these specific markers (e.g., adaptive metaxylem plasticity, targeted sclerenchyma deposition) allows for the targeted selection and engineering of highly drought-resistant forage and cereal crops that are more suitable for the more arid agricultural environments.

Salinity-driven modification Case study

Hamdi, et al. [101] observed growth stimulation in early *P. turgidum* seedlings with low salinity (100 mM) under conditions. While plants could not survive in 400 mM NaCl. At low salinity, monocotyledonous halophytes showed minimal growth stimulation, according to earlier observations by Martini and Papafotiou [102] in monocots. Some grasses, such *Pennisetum clandestinum* and *Sporobolus virginicus* are an exception [103].

At different salt concentrations, *P. antidotale* was capable of sustaining leaf water potential that was noticeably lower than that of the soil. Similar to the previously reports, rise in stomatal resistance, the decrease in leaf area and number with increasing salinity helped to minimize water loss. In *Panicum turgidum*, the similar findings were recorded by [104]. The reduction in *P. antidotale*'s leaf water potential caused by salt is consistent with findings for other salt-resistant grasses, including in *Aeluropus lagopoides* by Hussain, et al. [63], *Odyssea paucinervis* by Hussain, et al. [63], *Posidonia oceanica* and *Cymodocea nodosa*, and *Sporobolus virginicus* by Bhagat, et al. [21].

Elevation driven modification Case study

Due to varying climatic conditions and restricted availability of water, plant development and eco-physiological properties responded differently across elevation gradients. In response to increasing variations in elevation from low to high altitudes (600–1400 m), *P. antidotale* biomass significantly declined. As noted by Sharma, et al. [105] in *Vitis vinifera L.*, despite reductions in biomass and leaf area, the increase in leaf number at intermediate elevations points to potential methods for improving plant resistance to pressures caused by altitude. This was observed in *P. antidotale* as well.
Blue panic grass's sclerenchymatous thickness in stem portion appears to rise substantially with height, offering crucial mechanical assistance over soil compaction. Gruss and Moore [106]observed the same outcomes in Salsola imbricate. According to Sutthachai, et al. [107] in rice, there is a rise in pith cell area at medium altitudinal levels, which is associated with greater mechanical strength and the ability to store water and carbohydrates. The same was observed in *P. antidotale*. According to Fatima, et al. [73], the presence of lysogenic aerenchyma in *Panicum* at higher elevations promotes effective gaseous exchange and is similar to characteristics of hydrophytes seen in *Aristida adscensionis L*.

Higher altitudes are linked to a rise in stem epidermal thickness of *P. antidotale*. As noted by Basharat, et al. [108] in *Cenchrus ciliaris*, this thickness, in conjunction with increased sclerenchyma deposition, strengthens plants against drought stress, which is an essential response in arid environments. Conversely, cortical cell area and sclerenchyma thickness decrease with increasing height; this is especially noticeable in *K. macrantha*. This decrease in certain *Aveneae* grasses at high elevations is highlighted by Fatima, et al. [73], who also point out a tendency toward streamlined structures to deal with challenging conditions.

Challenges and Future Perspectives

P. antidotale is highly adaptable to environmental stressors, but has several limitations in growth and survival. Climate change comprises of increasing temperatures, erratic precipitation and extreme weather, posing significant threats to the natural habitats [109]. In addition, habitat fragmentation and over harvesting for fodder can cause genetic erosion and a decrease in genetic diversity, which can result in greater stress [110]. The growth potential and yield of *P. antidotale* is also reduced by soil degradation, salinization and unsustainable farming practices. Furthermore, its ecological balance is under threat because of the competition with exotic species for the essential resources such as sunlight, nutrients and water.

The future research directions that are needed to address these challenges are in the direction of high resolution molecular and genomic approaches. In particular, there is a need for detailed, genome-wide analyses and expression profiling under combined salinity and drought stress to gain insight into underlying regulatory networks. Identification of the regulatory function of the important families of transcription factors, like WRKY, MYB and bHLH will open up very specific molecular targets for crop improvement. Use of CRISPR/Cas9 genome editing to control these specific transcription factors or their downstream targets precisely provides a fast and targeted approach to create crops with improved osmotic adjustment and metabolic stability.

Apart from biotechnology, there is a need for sustainable management strategies to be practically applied in order to improve field cultivation. In drylands, for example, application of biochar has been found to improve water holding capacity, structural stability, and other soil characteristics; in polluted and degraded soils, certain types of biofertilizers (such as plant growth promoting microbes) can aid in bioremediation of heavy metals and in improving nutrient uptake. Incorporating *P. antidotale* into specific agroforestry systems can also practically help in the stabilization of arid soils and decrease soil erosion, which will have a positive impact on the sustainable provision of good quality forage. The use of these sophisticated climate-smart farming techniques and in situ/ex situ conservation to safeguard genetic variation can be effective in the ecological restoration and sustained productivity of *P. antidotale*.

Conclusion

P. antidotale is a highly resilient C_4 grass whose survival in challenging dry and semi-arid regions is governed by a complex integration of morpho-anatomical and physiological traits. This review establishes that its exceptional tolerance to combined drought and salinity is driven by specific structural adaptations such as increased sclerification, broadened metaxylem vessels, and active leaf rolling coupled with robust antioxidant defense systems that mitigate oxidative damage. To fully harness this resilience, future research must move beyond descriptive studies and prioritize comprehensive genome-wide analysis and expression profiling of stress-responsive regulatory networks. Specifically, deciphering the roles of key transcription factor families, such as WRKY, MYB, and bHLH, will provide the molecular targets necessary for advanced breeding and genetic engineering. Practically, translating these genomic insights will accelerate the development of climate-smart forage cultivars. Furthermore, strategically deploying *P. antidotale* in sustainable land management practices, including agroforestry and the bioremediation of degraded soils, offers actionable solutions to soil deterioration and habitat fragmentation. Ultimately, as climate change accelerates the expansion of extreme abiotic stressors, *P. antidotale* emerges not merely as an essential resource for sustainable livestock production, but as a critical scientific model for understanding and engineering plant resilience in increasingly harsh global environments.

Data availability

Not applicable

Acknowledgments

Not applicable

Conflict of interest

The authors declare that they have no conflict of interest.

Author Contribution

The author(s) confirm contribution to the paper as follows: MI: Conceptualization, literature review, writing—original draft preparation, writing—review and editing. AA and AR: Literature review and writing—original draft preparation. AI and RK: Data curation and writing—original draft preparation. UT: Supervision and writing—review and editing. MH and AS: Writing—review and editing. AS, AB, and MRT: Visualization. All authors contributed to the interpretation of the literature, critically revised the manuscript for important intellectual content, read and approved the final version of the manuscript, and agree to be accountable for all aspects of the work.

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