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Review

Strategies and Adaptations of Permanent Grasslands in Different Environments

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Abstract

Grassland biomes have developed a multitude of successful strategies and adaptations to various, often adverse environmental conditions through evolution. Grasslands have a wide tolerance to climatic conditions (temperature, precipitation) and can also tolerate temporary drought periods well. An important parameter for assessing drought tolerance of grass stands is the ratio of root biomass to above-ground phytomass, the R:S (root: shoot ratio). A higher value indicates the crop's adaptation to drought-induced stress. In permanent grasslands in Central Europe, we recorded a significant proportion of root biomass (6.69-10.31 t ha^{-1}) with an R:S ratio of 5.16. Other positive strategies include the ability of grasses to reproduce both vegetatively and generatively. Grass species exclusively prefer wind pollination; thus, they are not dependent on insect pollination. For different climatic zones, they have a suitable type of photosynthesis (C_3 or C_4). Grasslands are very well adapted to frequent grazing of phytomass or defoliation (mowing, fire), subsequently regenerating effectively. They are rich in high species biodiversity, contributing to their high eco-stability in agricultural landscapes. We also recorded grassland responses to the presence of heavy metals in the soil. Based on the bioconcentration factor (BCF < 1), grasslands (in Central Europe) acted as excluders of several heavy metals (Cd, Co, Cr, Pb, Mn, Cu, Fe, and Ni). These heavy metals are primarily accumulated in the soil and roots, with the above-ground part of the crop not being contaminated. Permanent grasslands are also effective in carbon sequestration and, based on several observations, are well adapted to the negative consequences of climate change.

Keywords: adaptation of grasses, environmental stress, grass biome, grassland, permanent grassland

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Introduction

Grasslands are globally one of the largest terrestrial biomes on Earth. O'Mara [1] states that they cover an estimated 50 million km^2 or 37% of the Earth's surface. Dong et al. [2] specify that at the regional level, Sub-Saharan Africa has the largest grassy area (17.9 million km^2). Asia (excluding the Middle East) ranks as the second continent in the size of grassland, about 8.89 million km^2. The following continents are South America (including Central America and the Caribbean), Europe, North America, and Oceania (including New Zealand and Australia); their grassland areas range from approximately 6.0 to 7.0 million km^2

There are various types of grasslands, and in this article, we refer to secondary grasslands dominated by communities of unsown plants, termed "semi-natural" grassland ecosystems. Although their plant communities are natural, the maintenance of these ecosystems depends on anthropogenic activities such as grazing, mowing, or burning regimes. In Slovakia, the term "permanent grasslands" is used in agricultural practice. Permanent grasslands are predominantly an extensive type of agricultural land use. There are variations in understanding how many years a grassland area is considered "permanent," commonly applying a threshold of 5 years. Grasslands are utilized through grazing or mowing, and their above-ground biomass serves as a source of bulk feed for both domestic and wild herbivorous animal species [3-5]. Permanent grasslands do not include grass areas of airports, sports facilities, urban and recreational sites, military locations, nor areas of annual grasses and fodder crops grown on arable land.

In permanent grasslands, the vegetation is dominated by grass species (the Poaceae family), as well as clovers and herbs from various other families, and the presence of scattered woody vegetation and trees occupying no more than 30% of the area is common. Besides their productive function, permanent grasslands also provide a range of important non-productive functions and ecosystem services, such as ecological, environmental, social, and so on [6, 7]. Zhang et al. [8] state that preserving ecosystem services and reducing ecosystem degradation are important goals for achieving sustainable development.

Throughout their lives, grasslands, like other ecosystems, are often exposed to the effects of external environmental factors, which can frequently have negative impacts. In extreme cases, the situation can lead to plant stress, adversely affecting their growth and vitality. Stress represents a strain on the plant organism caused by exceptionally adverse environmental conditions of the surrounding environment and the organism's response to the newly arisen situation. Stress is also a reaction of plants to unfavorable changes in growth conditions. The origin of stress factors can be abiotic or biotic. Abiotic stress may be of a physical or chemical nature, while biotic stress can be caused by viruses, bacteria, fungal diseases, and the like [9-12]. The consequences of stress are often devastating, leading to a reduction in the efficiency of biochemical and physiological processes in plants, a decrease in the activity of the plant's photosynthetic apparatus, as well as genetic changes and mutations. The most common result of stress is damage, injury, or even death of plants. Nawaz et al. [13] state that plants exposed to various abiotic and biotic stressors, including environmental pollution and global warming, pose significant threats to biodiversity and ecosystem services. When plants are simultaneously exposed to biotic and abiotic stressors, such as cadmium and drought, they experience significant reductions in above-ground biomass, imbalances in oxidative homeostasis, nutrient assimilation, and restricted root growth. This demonstrates how the synergistic interactions of multiple stressors lead to detrimental physiological impacts. [13]. However, there are also situations where plants develop defensive mechanisms in the form of adaptations, tolerance, resistance, and resilience to environmental stressors [12, 13]. Specifically, grass species or grassland biomes have developed very effective defensive mechanisms and strategies throughout evolution.

Experimental

The study is based on a synthesis of information and conclusions from several relevant works by renowned authors who have dealt with the issues of grasslands and their adaptations to environmental stressors. The work is supplemented by a significant portion of the authors' own results. Although some results were partially published in various scientific journals and publications [3, 6, 14-17], this study offers a comprehensive view of the evaluated issues, enriched with unpublished results and assessments.

The aim of this study was to evaluate the life manifestations, strategies, resilience, and adaptations of permanent grasslands to a wide range of ecological conditions and environmental stressors.

Results and Discussion

Over the course of evolution, which has lasted several million years (it is stated that grasses appeared on the planet 67 to 65 million years ago [18]), grasslands have developed various effective adaptations, tolerances, and resistances to a wide range of environmental factors, or stressors.

Life Manifestations and Strategies of Permanent Grasslands to Diverse Environmental Conditions

The occurrence of grass stands in various climatic conditions – grassland biomes are adapted to a broad valence of ecological and environmental conditions, which allows them to occur on all continents of our planet. In the region from the equator to the Tropics of Cancer and Capricorn, tropical grasslands are found, while north and south of the tropics are the grasslands of the temperate zone. Ricklefs [19] states that the occurrence and formation of biomes are primarily shaped by solar energy (expressed as average air temperature) and annual precipitation. In the temperature range from –8 to 20ºC and precipitation from 150 to 1,300 mm, temperate grasslands occur, and at temperatures from 16 to 30ºC and precipitation from 400 to 1,200 mm, savannas (tropical grasslands) are formed. It can be concluded that the grassland biome has an intermediate position between forest and desert. Lin et al. [20] conducted a detailed global meta-analysis of field studies with various types of grassland cover (savanna grassland, temperate grassland, cold grassland, and alpine grassland) to quantify the effects of global changes in precipitation on community structure and function of grassland types. Results showed that regardless of grassland type, increased precipitation increased species richness by 7.8%, decreased belowground biomass by 20.0%, and increased aboveground biomass by 22.9%, but interestingly, decreased precipitation increased belowground biomass by 17.7%, decreased aboveground biomass by 22.8%, and decreased species richness by 13.7% [20]. Yan et al. [21] state that there is a significant positive correlation between aboveground biomass and annual precipitation, while there is no significant correlation between belowground biomass and annual precipitation.

Reproduction strategy – many grass species have developed both forms of reproduction simultaneously, being capable of reproducing both generatively and vegetatively. Permanent grasslands typically prefer the asexual form of reproduction. The ability of grass species to produce offshoots is also directly related to reproduction. During the process of producing offshoots, two basic types of shoots are formed: vegetative and generative. Offshoot production is an adaptation not only for successful reproduction but also supports the competitive abilities of grasses to form a well-integrated stand [22].

Pollination strategy – grass species are exclusively wind-pollinated (insect pollination has not been recorded). Semi-natural grasslands are large-scale open ecosystems that cannot be efficiently pollinated by insects. For insect pollination, they would need numerous populations of pollinators. Therefore, during evolution, they have developed and exclusively prefer a wind pollination strategy. This fact is also confirmed by the results of pollinating various plant habitats in the Netherlands [23]. Grasses were always pollinated by wind (in 173 grass species) or wind-self (in 7 grass species) in all habitats. Wind-pollinated species (principally grass) benefit from more open vegetation for pollen dispersal. Rech et al. [24] hypothesize that wind pollination is facilitated by open vegetation, as denser vegetation in higher strata might mechanically restrict pollen dispersal. They [24] suggest that wind pollination is made easier by open vegetation because denser vegetation in higher layers could mechanically limit the spread of pollen. Givnish et al. [25] also report that wind pollination in grasses significantly correlates with the shift of grass stands to open habitats and the development of small, inconspicuous flowers without nectar. They suggest that the main ecological driving forces behind the repeated evolution of wind pollination in *Poales* (which includes the *Poaceae* family) are open habitats combined with high local dominance of the same taxa, tall plant growth, strong vegetative spreading, and positive ecological feedback.

Evolution of C_3 and C_4 photosynthesis types – the C_3 plant metabolism is most efficient in temperate and cool climate zones. Likely in connection with a decrease in the amount of CO_2 in the atmosphere, C_4 grasses, whose metabolism is more efficient at higher temperatures, appeared in the Oligocene approximately 25 million years ago. The emergence of C_4 metabolism was a key evolutionary step in the evolution of grasses, occurring independently several times, and currently, more than 5,000 species of C_4 grasses are known. In comparison with C_3 plants, the physiology of C_4 plants provides them with a competitive advantage when the ratio of atmospheric CO_2 to O_2 is low. C_4 plants are capable of increasing the concentration of CO_2 in their leaves and reducing stomatal conductance, leading to better water management. Such adaptations are advantageous in hot environments with direct sunlight and water scarcity. C_4 grasses are characteristic of seasonal, arid, and warm environments and are therefore most common in the prairies of North America, the extensive savannas of Africa, and South America [26]. Another study [27] showed different responses of C_3 and C_4 grasses to climate change. C_3 grasses have thrived during cool seasons and in cooler regions, whereas C_4 grasses have thrived in warmer regions characterized by more rainfall during the warm season and greater temperature fluctuations. When future climate scenarios were factored into models, it was observed that C_3 grass abundance declined across 74% of regions, while C_4 grass abundance increased in 66% of regions. C_3 grasses spread to mid- and higher latitude regions with rising temperatures and decreasing seasonality of precipitation. Conversely, C_4 grasses increased in higher latitude regions but declined in lower latitude, dryer regions. De Deus Vidal et al. [28] mention several grass genera that have C_3 and C_4 types of photosynthesis. For example, they include the following genera in the C_3 group: *Agropyron, Agrostis, Alopecurus, Anthoxanthum, Aphanelytrum, Arthrostylidium, Aulonemia, Avena, Brachypodium, Bromus, Calamagrostis, Cinna, Cortaderia, Cyperochloa, Danthonia, Dichelachne, Elymus, Festuca, Glyceria, Helictotrichon, Chionochloa, Isachne, Jarava, Koordersiochloa, Lamarckia, Nassella, Neurolepis, Ortachne, Phalaris, Phleum, Piptochaetium, Poa, Rhipidocladum, Stipa, Styppeiochloa, Triniochloa, Trisetum*. For example, they include the following genera in the C4 group: *Alloteropsis, Aristida, Arthraxon, Arundinella, Bothriochloa, Bouteloua, Brachiaria, Capillipedium, Cenchrus, Coix, Cymbopogon, Cynodon, Dactyloctenium, Digitaria, Echinochloa, Eleusine, Enneapogon, Eragrostis, Hemarthria, Hyparrhenia, Microchloa, Paspalum, Pennisetum, Setaria, Schizachyrium, Tetrachne, Trachypogon* [28].

High biodiversity – another adaptation of grasslands to diverse environmental conditions is their high biodiversity. The grass family *Poaceae* (grasses) is among the most species-rich families of vascular plants. Currently, the *Poaceae* family includes 793 accepted genera and approximately 12,000 species [29]. Kier et al. [30] report the average species richness of vascular plants in grassland biomes. For tropical and subtropical grasslands, savannas, and shrublands, the number is 1,731 species; for temperate grasslands, steppes, and shrublands, 1,372; for montane grasslands and shrublands, 1,397; and for flooded grasslands and savannas, 767 species. Ružičková and Kalivoda [31] recorded that a semi-natural grassland (in Slovakia) consists of 30-70 species of vascular plants. The high diversity of grassland ecosystems allows the spread of various species with different environmental requirements to different areas of the world (cosmopolitan distribution). Thanks to the autoregulatory homeostatic mechanisms in the ecosystem, different types of grasslands respond to fluctuations in external conditions in a compensatory manner so that their production standard fluctuates very little compared to environmental factors. High functional diversity is a prerequisite for the ecological stability and resilience of grasslands to various extreme abiotic and biotic influences.

High silicon concentration in grass tissue – the silicon content across plants varies between about 0.1% and more than 10% on a dry weight basis. Most grasses take up and accumulate silicon (Si) more than any other inorganic constituent [32]. Plants belonging to the family Poaceae have a relatively large silicon content of about 4-5% [33, 34]. Major silicon depositions in grasses occur in the root endodermis, leaf epidermal cells, and outer epidermal cells of inflorescence bracts [35]. Si accumulation is increasingly recognized as playing an important functional role in plant ecology, particularly in terms of its role in relieving the adverse effects of environmental stress [36, 37]. In general, plants with high Si concentrations are less susceptible to attack by pathogens and pests and show increased tolerance to abiotic stresses such as drought, low temperature, or metal toxicity [32, 34, 38-41]. The mechanisms of plant tolerance to stressors through silicon (Si) are very diverse. Different are the mechanisms for tolerance to heavy metals, drought, salinity, diseases, pests, and the like. Also, each plant species may respond to a stressor with a different tolerance mechanism. For example, silicon is known for reducing metal toxicity [41, 42]. The reduced presence of phytotoxic metals in soil may stem from an increase in soil pH and alterations in the metals' speciation (i.e., chemical and physical form) within the soil solution, facilitated by the creation of silicate complexes. The use of sodium metasilicate has been shown to elevate soil pH levels and decrease the amount of exchangeable lead (Pb), thereby diminishing the availability of lead in the soil. Similar effects were observed with the application of amorphous silica (containing 87% SiO_2), which led to an increase in soil pH and a decrease in the bioavailability of cadmium. Furthermore, cadmium in the soil was predominantly found in forms that were specifically adsorbed (attached to carbonates) or bound to iron-manganese oxides in soils treated with silicon amendments. Exogenously applied Si also reduced the availability of chromium in the soil by promoting the formation of precipitate-bound and organic matter-bound Cr fractions. The formation of hydroxyaluminum silicate is believed to play a role in Si-mediated detoxification of aluminum in plants [41, 42]. Plants exposed to abiotic stressors (e.g., drought, exposure to metals, and salinity) show an increased concentration of reactive oxygen species, such as superoxide radical (O_2^-), hydroxyl radical (OH^-), and hydrogen peroxide (H_2O_2). These reactive molecules can harm biomolecules such as DNA, photosynthetic pigments, and proteins. The increased tolerance of Si-supplied plants to such abiotic stresses might be attributed to a reduction in the production of reactive oxygen species and an improvement in their antioxidant defense mechanisms [41-43]. Si plays a significant role in alleviating drought stress in plants by employing multiple mechanisms, including an increase in mineral nutrient uptake, modification of gas exchange attributes, osmotic adjustment, lowering oxidative stress, modification of gene expression, and regulation of compatible solutes and phytohormone synthesis. The decline in crop productivity due to drought and salt stress is primarily caused by the deterioration of gas exchange functions and the decrease in leaf relative water content. Silicon's ability to counter these stress-induced setbacks has been demonstrated [44]. A supply of Si to plants has been shown to reduce the intensities of numerous diseases (e.g., damping off, leaf blights, leaf spots, galls, powdery mildews, root rots, rusts, and wilts). These diseases are caused by different genera of bacteria, fungi, nematodes, and oomycetes, as well as viruses, in many economically important crops. The reduction in plant disease intensity with higher silicon content is explained by the physical barrier hypothesis, which is related to the deposition and polymerization of Si beneath the cuticle, in the cell wall, and inside the bulliform cells. A dense silicon layer beneath the cuticle inhibits the penetration of pathogens into plant tissues [41]. The deposition of Si beneath the cuticle, acting as a physical barrier against plant diseases, also functions in defense against many herbivores and other pests [45]. Grass blades are reinforced with fibrous, very strong tensile structures (rich in silicon), which prevent the grass stem from breaking under the weight of its relatively heavy inflorescences [46].

Regeneration after natural fires – in the case of grasslands, fire is not considered an abiotic stressor. On the contrary, natural fire, for example in savannas, is understood as a very important and beneficial natural agent for the renewal of grasslands. Fire removes dead plant biomass and eliminates tree seedlings. Without fire, the savanna would gradually become overgrown with woody vegetation and change into a forest ecosystem. Ružičková and Kalivoda [31] mention that fire played an important role in the past in Europe and significantly contributed to the formation of the current cultural landscape. They state that controlled fire removes old vegetation but does not damage underground shoots. In the burned stand, new spaces – niches for the germination of seeds that are in the soil, are created, but without the removal of old vegetation, they would not have a chance to germinate. Neary and Leonard [47] note that fire in grasslands primarily affects the aboveground parts of vegetation and generally causes minimal harm to the substantial underground organic matter reservoir in Mollisols, typically found in grassland ecosystems. While fire can significantly alter the landscape's appearance, the degree and duration of these changes in grasslands are typically much less than in forest ecosystems. The rapid regeneration of grass often conceals the effects of fire within a year due to swift regrowth. Permanent grasslands regenerate after fires primarily through vegetative structures (taproots, surface roots, rhizomes, stolons, and root crowns), but also through seed reproductive structures. Grass plant roots are more resilient to damage as they primarily extend into the mineral soil at depths where there is minimal heat exposure. This resilience is due in part to the deep "A" horizons in grassland soils, which are developed through the turnover of fine roots, offering protection against fires of low severity, high intensity, and short duration herbaceous fuel fires. Such fires typically only destroy the surface litter and aboveground plant structures, leaving the roots unharmed. Consequently, grassland vegetation often recovers quickly from fire, regrowing within months to a year. Natural wildfires play a crucial role in the evolution and management of grasslands, serving as a key natural disturbance for millions of years and aiding in the formation of these grass and herb-based ecosystems. Historically, humans have used fire to enhance habitats for wildlife and livestock over many millennia. Today, prescribed fire is an integral part of contemporary grassland management practices [47].

Carbon sequestration – grasslands are very well adapted to higher concentrations and contents of carbon in the environment among terrestrial ecosystems. Elevated atmospheric CO_2 has been shown to result in increased grass production and enhanced water/nutrient-use efficiency [48]. About 20-34% of the world's soil carbon stocks are found in grassland areas [49, 50]. Enhancing soil carbon storage has the potential to offset human-caused increases in atmospheric CO_2 [51]. Keller et al. [51] suggest that highly productive temperate zone grasslands (USA) are crucial for reducing future greenhouse gas emissions resulting from land use change. Grassland soils are a very significant store of carbon, with global carbon stocks estimated at about 343 Gt C, which is about 50% more than the amount stored in forests globally [1, 49]. Bai and Cotrufo [50] state that grasslands store approximately one-third of the global terrestrial carbon stocks and can act as an important soil carbon sink. Recent studies show that plant diversity increases soil organic carbon (SOC) storage by elevating carbon inputs to belowground biomass and promoting microbial necromass contribution to SOC storage. Climate change affects grassland SOC storage by modifying the processes of plant carbon inputs and microbial catabolism and anabolism. Improved grazing management and biodiversity restoration can provide low-cost and/or high-carbon-gain options for natural climate solutions in global grasslands. The achievable SOC sequestration potential in global grasslands is 2.3 to 7.3 billion tons of carbon dioxide equivalents per year (CO_2e $year^{1}$) for biodiversity restoration, 148 to 699 megatons of CO_2e $year^{1}$ for improved grazing management, and 147 megatons of CO_2e $year^{-1}$ for sown legumes in pasturelands. In addition to the significant stocks of carbon, grasslands also contribute to climate change mitigation by sequestering additional carbon. Lal [52] estimated that the soil organic carbon sequestration potential of the world's grasslands is 0.01-0.3 Gt C $year^{1}$. Stypinski and Mastalerczuk [53] state that grasslands in Central Europe bind approximately 9.6 t ha^{-1} C with their total phytomass (of which about 70% is below-ground biomass) and significantly contribute to the reduction of the greenhouse effect. In grasslands, herbaceous vegetation dominates, and carbon is stored primarily in the roots and soil, unlike in forests. A shift to increased investment in root biomass allied to decreased decomposition rates can also lead to enhanced carbon sequestration under high CO_2 levels [54]. Below-ground biomass can extend several meters below the surface and store a large amount of carbon in the soil, leading to the formation of deep, fertile soils with a high content of organic matter. Similarly, Ottaviani et al. [55] state that the majority of plant species in temperate zone grasslands allocate a large part of their biomass below ground. The underground organs of the grassland can contribute to soil carbon sequestration more than their aboveground shoots and stems [56-58]. Hejduk [59] reports that in the soil under permanent grasslands (in the Czech Republic), 1.7 times more C is stored than in arable soil under the same conditions. In the soil under permanent grasslands, 139.0 t ha^{-1} C (510.0 t ha^{-1} CO_2) was determined, in arable soil, 81.1 t ha^{-1} C (297.6 t ha^{-1} CO_2). Because plant productivity in grassland areas is limited by precipitation, carbon stocks are highest in regions where precipitation is greatest, such as the tallgrass prairie in the humid temperate region of the United States. Similarly, as annual temperatures rise, carbon stocks in grasslands decrease due to increased evapotranspiration

[60]. Dass et al. [61] and Liu et al. [62] state that with climate change, the frequency of droughts and fires is increasing in many regions of the world. They assume that grasslands in arid and semi-arid areas could become more reliable carbon sinks than forests due to their high resilience to drought and fire. Gibson and Newman [63] also point out that grasslands, besides capturing greenhouse gases (mainly CO_2 into the underground biomass), contribute to their production (N_2O from the soil, CH_4 from livestock, and CO_2 from fires). For intensively grazed to degraded grasslands, the practice of sustainable management systems is recommended. In the management of grasslands, local farmers are advised to implement adaptive strategies and measures (for example, in the restoration of grasslands, selecting pasture plants that would increase CO_2 sequestration and reduce CH_4 and N_2O gas emissions, weed control strategies, minimizing mechanical operations that use fossil fuels, and so on).

Adaptation of Permanent Grasslands to Abiotic Stressors

Drought resistance – grasslands are also well adapted to higher air temperatures and drought. A lack of moisture inhibits the growth of assimilating organs - leaves, as a result of which there is a distribution of the assimilates created to the roots. These adaptations, on the one hand, reduce water losses through transpiration, and on the other hand, by developing the root system, they are capable of obtaining water from considerable depths, which allows grasslands to vegetate even in conditions of water scarcity [16]. In drought conditions, permanent grasslands develop a robust root system. This is also documented by results from central Slovakia [15], where the root biomass weights of permanent grasslands were significantly higher in dry years (10.23 and 10.31 t ha^{-1}) compared to wetter and precipitation-standard years (Table 1).

The dry weight of root biomass is 4-5 times higher than the dry weight of above-ground phytomass from a single harvest, with a reserve of assimilates and other biogenic elements usable for subsequent regeneration after the end of the drought period [6]. An important parameter for assessing the impact of drought is the ratio of the dry weight of the root system to the above-ground phytomass R:S (root to shoot ratio, where the above-ground phytomass is expressed as the yield of phytomass from one cutting of grassland). The R:S ratio is genetically fixed and is a measure of the vegetation's ability to avoid drought [16], and it changes and sensitively reacts to other forms of stress as well. Higher R:S values indicate greater resistance of the vegetation to drought. Tomaškin and Tomaškinová [3, 15] recorded an average R:S value of 5.16 (where the above-ground phytomass is expressed as the yield of phytomass from one cutting) on permanent grasslands (research from 1992 to 1998 in Slovakia), and it was significantly higher than in temporary grassland (cultivated varieties of grasses and clovers grown for 3 to 4 years on arable land), where R:S = 4.27. The results document the higher ecological stability of permanent grasslands against the stress factor of drought. It can therefore be assumed that permanent grasslands may satisfactorily withstand the consequences of global warming and contribute to the stability of the agricultural landscape. The R:S ratio (5.16) recorded in permanent grassland also has another explanatory value: annual and biennial crop plants have this ratio below 1, or close to 1, up to wild perennials (including permanent grasslands), shrubs, and trees where the ratio increases to significantly higher values. Klimešová et al. [64] also state that underground plant organs are of immense importance to plants in arid environments. Belowground plant traits, such as belowground clonal growth organs, bud banks, and the distribution of fine roots, could offer a deeper mechanistic insight into changes in ecosystem functions triggered by environmental shifts. Under extreme

Table 1. The root biomass amount during the individual years (in DM t ha^{-1}).

Year	Total precipitation (mm)		Climatic year	Root biomass weight (in DM t ha^{-1})
	IV – IX	I – XII		Permanent grasslands
1992	287.0	724.1	Dry	10.23 c
1993	336.5	794.7	Dry	10.31 c
1994	564.7	917.3	Standard	9.89 c
1995	568.3	935.7	Wet	7.16 ab
1996	630.9	971.3	Wet	6.69 a
1997	402.8	765.8	Standard	7.65 ab
1998	494.8	829.7	Standard	7.90 b
Average (50 years)	422.0	746.0		
LSD $\alpha_{0.01}$				1.1481

Statistical method: ANOVA – LSD test ($\alpha = 0.01$) a, b, c – significant differences aridification, perennial plants, except those with bulbs, would be banished from the community, giving way to annuals. These annuals generate low amounts of litter and rely solely on ephemeral water resources in the upper soil layers. Středa et al. [65] state that a larger root system contributes to yield stability, as during periods of drought, the root system can supply water from deeper soil layers. However, in periods with sufficient rainfall, the root system becomes a consumer of carbohydrates, which does not lead to a higher yield. The significance of the root system for plant drought resistance is also highlighted by Chloupek et al. [66]. They recommend considering the size of the root system and its ability to tolerate drought when breeding plant varieties.

Adaptation to defoliation – in grasslands, perennial grass species predominate (perennity or multi-year lifespan of species can also be considered an adaptation to the environment), which tolerate the stress of frequent defoliation, whether in the form of grazing, mowing, or other damage to the stand. During the growing season, they are adapted to repeated grazing or mowing and quickly regenerate by forming new leaf areas under favorable conditions. This allows for their continuous use [22]. Hassan et al. [67] state that grazing and mowing significantly affect soil quality and the yield of grassland crops. They recommend choosing appropriate management of cultivation and use of grasslands in accordance with the ecological and environmental conditions of the habitat, respectively.

Anti-erosion function of permanent grasslands – grasslands have developed a very effective strategy for eliminating the mechanically acting stressor of erosion. Erosion causes degradation and loss of soil, which has a direct negative impact on the vegetation cover [68]. Grass species have developed a strategy: their erosion protection is ensured by a robustly developed root system and a dense grass sward, which stabilizes the soil and prevents its removal. Perennial grassland is the main tool for reducing soil degradation [69]. The sward layer contributes to increased water infiltration into the soil. Perennial plants form a permanent soil cover, reducing the leaching of nutrients and erosion [70]. Also, underground biomass and sward significantly enrich the soil with organic matter, which then forms humus, increasing the ability of the stand and soil to retain rainfall water, which loses its surface destructive force. Several authors point out the importance of the sward and rhizosphere in performing an anti-erosion function [15, 16, 69]. The root biomass of grasslands is part of the biological yield, making up a significant portion (sometimes up to 50 – 70%, in spring even 90%) [16]. Jackson et al. [71] report that the biome of tropical grassland/savanna creates on average 14.0 t ha^{-1} and temperate grassland 15.6 t ha^{-1} total root biomass. For comparison: the biome of tropical rainforest averages 48.8, boreal forest 29.2, tundra/alpine 12.5, desert 3.7, and cultivated land 1.5 t ha^{-1} of root biomass. An even more important parameter than root mass is the live fine root area index. Tropical grassland/savanna has an index value of 42.5 m^2 m^{-2}, and temperate grassland up to 79.1 m^2 m^{-2}. All other Earth's biomes have a much smaller index, ranging from 4.6 – 11.6 m^2 m^{-2}. Tang et al. [72] present the results of the underground biomass production of three types of natural grasslands in central China (desert steppe, typical steppe, and meadow steppe). The mean belowground biomass of natural grasslands on the Loess Plateau was simulated using the Bayesian method forecasting model, and the value was 2.885 t ha^{-1}. The meadow steppe had the maximum belowground biomass value (3.578 t ha^{-1}), whereas the desert steppe had the lowest value (1.745 t ha^{-1}). The belowground biomass differed significantly between the desert and typical steppes and the meadow steppe. Compared with the belowground biomass of the meadow steppe, that of the desert steppes was 51.2% lower. The mentioned authors [72] further add that grasslands in northern China produce much more underground biomass (on average 7.22 t ha^{-1}, desert steppe 4.12 t ha^{-1}, typical steppe 6.53 t ha^{-1}, meadow steppe 11.02 t ha^{-1}). Skuodienė et al. [69] recorded root biomass production in permanent grasslands in Lithuania from 8.21 to 14.94 t ha^{-1}. Summarized data on field biomass measurements, obtained in unfertilized temperate grasslands in the Czech and Slovak Republics (Central Europe), showed that root biomass data are rather variable. Total below-ground dry mass varied in a large range of values from 8.31 to 25.92 t ha^{-1} [73]. In central Slovakia, the weight of root biomass of permanent grasslands was recorded in the range of 6.69-10.31 t ha^{-1} (Table 1) [15]. Cleland et al. [74] conducted an interesting analysis of root biomass production at 29 sites of the global grassland network, Nutrient Network, which were fertilized with nitrogen and other nutrients (P, K, and micronutrients). They state that the supply of nutrients (especially the addition of nitrogen) led to a reduction in root biomass. The consequence is significant changes in carbon sequestration and the carbon cycle (as well as other nutrients) in grasslands. The root system of grasslands also has a very good regenerative ability. Old roots gradually decompose, but the root system is simultaneously rejuvenated. Its complete turnover (turnover period of root biomass) takes in Central Europe about 3.5 to 5 years [16]. In the assessment of permanent grasslands at the global level, root turnover time ranged from 0.6 to 19.6 years with a mean value of 3.1 years and large variations among climatic zones. On average, root turnover time was longest in the boreal zone, shortest in the tropical zone, and the temperate zone had intermediate values. Root turnover time varied significantly among vegetation types, with the longest average value in tundra (6.9 years), followed by alpine grassland and meadow (3.4 years), temperate grassland and meadow (2.9 years), desert (2.8 years), and tropical grassland and savanna (1.5 years) [75]. Grassland reduces the effects of erosion compared to arable land by about 25 to 100 times; its anti-erosion effect is significantly greater also because it covers the soil year-round. The anti-erosion effect of individual crops (vegetation cover) can be ranked as follows: well-integrated forest > permanent grassland > fodder crops > annual grasses > winter cereals > spring cereals > root crops [3]. Lieskovský et al. [76] state that in Slovakia, permanent grasslands are increasingly being used for soil erosion protection in vineyards. Permanent grasslands are supported by EU agri-environmental schemes for medium and large farms registered in the viticultural registry. Based on their findings, the authors [76] note that in a vineyard that was hoed for five years and then grassed for the following five years, erosion on the slope's shoulder was three times lower, and sediment on the slope was almost six times lower compared to a cultivated vineyard. Stašek et al. [77] recommend that crops grown on arable land that pose a risk of soil erosion (such as corn) utilize gentle and sustainable forms of land management, such as contour farming and shallow tillage. Brychta et al. [78] highlight the seriousness of the erosion risk, which represents long-term soil losses. They mention several models projecting future trends of soil erosion and recommend creating suitable management and crop rotation systems. These anti-erosion dispositions allow grasslands to successfully vegetate even in the alpine stage of high mountains above the upper forest line (high mountain grasslands, balds), but also in areas of the seacoast with sandy dunes, where fine wind-blown sand, almost constantly moving, attacks the tough grass vegetation [46].

Tolerance and adaptation to chemical substances- Grass species have developed diverse mechanisms, strategies, and adaptations to contamination. For example, in the intake and content of heavy metals based on the bioconcentration factor (BCF), we distinguish three strategy groups: excluders (BCF<1), indicators (BCF = 1), and accumulators to hyperaccumulators (BCF>1). Among grass species, *Agrostis stolonifera*, for instance, belongs to the hyperaccumulators, capable of extracting 300 times more arsenic from the soil than other plants growing freely at the same site [79]. Such species can be used, for example, for the phytoremediation of the environment or phytoextraction [80]. Tomaškin et al. [17] evaluated the intake and accumulation of heavy metals (Cd, Co, Cr, Pb, Zn, Mn, Cu, Fe, and Ni) in the soil – root – above-ground phytomass system of permanent grasslands in central Slovakia over three years 2009 – 2011 (Table 2). Permanent grasslands belong to the plant community *Poa-Trisetetum* (alliance *Arrhenatherion*). The community determined grasses, especially the dominant Trisetum flavescens and other valuable grasses *Poa pratensis*, *Dactylis glomerata*, and *Arrhenatherum elatius*. *Fabaceae* plants, *Trifolium repens*, *Trifolium pratense*, and *Lotus corniculatus* increase stand value. *Taraxacum officinale* is the most significant species of herb. The authors of the study state that heavy metals are most concentrated in the roots of plants and in the soil. A significantly lower content was determined in the above-ground phytomass. Based on the bioconcentration factor (BCF<1), grasslands acted as an excluder of all evaluated heavy metals (with the exception of Zn, for which grasslands acted as an accumulator, BCF = 2.13). This strategy is also very suitable for the production of bulk feeds, as the concentration of heavy metals in the above-ground parts of the stand is relatively low and does not lead to contamination of the food chain.

Response of grasslands to climate change – extreme weather conditions can trigger a rapid and severe response that changes ecosystems and human communities. Increasingly serious and frequent droughts, floods, fires, and hurricanes are likely to affect grassland ecosystems as well. Greater precipitation variability will contribute to more frequent fires, which could reduce the encroachment of woody plants into grasslands. Other widespread disturbances, such as the occurrence of insects, may accelerate the conversion of forests into grasslands. Greater biodiversity and redundancy of species' functional roles in grasslands create greater ecosystem stability and are associated with greater resilience to changing conditions. Restoring degraded grasslands can increase resilience to climate change along with providing protection against soil erosion, carbon loss, and other negative impacts [81]. Grassland adaptation to climate change will be variable, with possible increases or decreases in productivity and increases or decreases in soil carbon stores [1]. Climate change has the potential to drive ecosystem changes for better or worse (impact on stability, biodiversity, and other functions). It is assumed that climate change will affect not only plant growth, but also the allocation of biomass into aboveground and belowground parts of plants [82]. Climate change in the form of global warming will also impact the allocation of plant biomass in grassland vegetation. Yan et al. [21] state that global warming increases vegetation evapotranspiration and reduces soil water availability. To mitigate water stress, plants will allocate more biomass to underground organs. Based on our results as well, we conclude that in the case of higher temperatures and drought, grass species have this strategy of transferring assimilates from aboveground parts to roots very well developed [15]. Středa et al. [83] provide an overview of correlations between the size of the root system and the yield of several crops. They state that it is not always possible to consider a positive relationship between the size of the root system and grain yield. Especially in an extremely dry year, the root system did not affect the grain yield; on the contrary, a larger root system had a negative impact on the grain yield. In an extremely dry year, larger roots likely could not provide some plants with an advantage because water was not available in the soil. Contrary to expectations, it turned out to be an inefficient utilization of assimilates, essentially rendering it a wasteful endeavor. This finding substantially adds to the ongoing debate regarding how the size of the root system influences yield across various environments [83]. Successful adaptation of grasslands to climate

Table 2. Heavy metals concentration in soil and plant biomass (mg kg^{-1}), BCF of permanent grasslands.

Environment	Heavy metals concentration (mg kg^{-1})								
	Cd	Co	Cr	Pb	Zn	Mn	Cu	Fe	Ni
Soil	2.35±0.07 b	13.17±0.68 b	5.99±0.08 b	151.09±2.90 b	48.71±1.84 a	589.27±7.27 b	11.42±0.51 a	2192.90±28.79 b	11.24±0.97 b
Roots	2.27±0.06 b	6.92±0.09 a	7.62±0.14 c	24.45±1.35 a	208.21±2.56 c	353.83±4.53 a	39.25±1.38 b	3569.37±32.65 c	12.52±0.85 b
Sward	1.61±0.07 a	5.93±0.07 a	3.93±0.07 a	12.38±0.34 a	103.93±2.39 b	330.28±3.83 a	11.50±0.69 a	1351.45±18.63 a	8.18±0.56 a
LSD $\alpha_{0.05}$	0.413	2.423	1.088	24.740	18.899	61.180	14.513	813.807	1.900
BCF	0.68	0.45	0.66	0.08	2.13	0.56	1.00	0.62	0.73

Statistical method: ANOVA – LSD test (α = 0.05) a, b, c – significant differences, ±standard error of the mean

change is anticipated by Hebda [84]. He states that due to warming and drought, and thus more frequent fires, there will be a decline in the occurrence of forest ecosystems. At the expense of forests, the ecosystem of grasslands will expand, penetrating into higher altitudes and latitudes. Using a model example from British Columbia (southwestern Canada), he notes that plant species of grasslands will likely become most suitable for the future climate. His model documents the loss of forests and the good adaptation of grasslands to climate change due to global warming. In western North America [85], model projections indicate that by the conclusion of the 21st century, increased temperatures and water scarcity will result in nearly half of the evergreen tree coverage being substituted by shrubs and grasses.

Adaptations of Permanent Grasslands to Biotic Stressors

Coevolution with herbivores – grasslands are adapted to grazing by herbivores, subsequently able to regenerate and restore their leaf area. Against excessive grazing by herbivores, grasslands have developed an adaptation of higher silicon content in grass tissues. We have already mentioned the high concentration of Si, and we add to the text that many grasses are hyper-accumulators of silicon (Si), sometimes accumulating up to 10% of their dry mass, more than any other inorganic constituent [86]. In defending themselves against herbivores, plants can tolerate (e.g., through compensatory regrowth) and/or resist (e.g., via the production of toxic chemicals or defensive structures) herbivory. Many species of grasses, for example, are frequently defoliated by grazing ungulates and often tolerate herbivory by replacing lost biomass [87]. Phytoliths (i.e., microscopic deposits of silica, SiO_2), in particular, confer defense against herbivores through abrasion on their mouthparts and diminished nutrient acquisition via reduced palatability and digestibility of foliage [88]. Grasslands also tolerate trampling and mechanical stress by livestock or wild herds of animals. Lin et al. [20] evaluated the impact of grazing on the community structure and function of global grassland types (savanna grassland, temperate grassland, cold grassland, and alpine grassland). Species richness of global grassland vegetation was positively correlated with grazing intensity. The total vegetation community biomass increased by 11.7% under moderate grazing intensity, while the species diversity of global grassland vegetation increased by 10.7% under moderate grazing intensity. In global grasslands, moderate grazing intensity was most effective in promoting increased species richness of vegetation. Grassland responds to moderate grazing and trampling by animals with compensatory mechanisms. The grassland supports plant growth, thereby reducing the impact of livestock on the grazed vegetation cover [89]. Conversely, long-term and intensive grazing has a negative impact on the composition and function of grasslands and leads to degradation and a reduction in species richness and community biomass [90].

Resistance to diseases and pests – compared to cultivated crops on arable land, grasslands are relatively resistant to diseases and pests. Grasses may suffer from fungal diseases (e.g., molds, rust), mosses, lichens, and common pests, including rodents [22]. Alba-Mejía et al. [91] observe that even conserved grass biomass in the form of silage is often contaminated with mycotoxins. Silaged feeds may contain a mixture of mycotoxins originating from preharvest contamination and/or postharvest contamination by toxigenic fungi commonly found in silage. They present results where grass silage evidently exhibited signs of fungal contamination. To detect contamination of grass silage by fungi, they propose measuring the content of ergosterol and polyphenols. Ergosterol is the main sterol of fungal and yeast mycelial membranes. Determining these fungal metabolites serves to predict the safety of grass silage [91].

Conclusions

Throughout evolution, grasslands have developed several ingenious and effective strategies and adaptations to mitigate the negative effects of various abiotic and biotic factors and stressors:

1. Grassland biomes are adapted to a wide range of ecological and environmental conditions and are found on all inhabited continents.
2. They have concurrently developed both forms of reproduction (generative and vegetative propagation).
3. Grass species are exclusively wind-pollinated (not dependent on insect pollination).
4. In response to diverse climatic conditions, they have developed a suitable C_3 or C_4 type of photosynthesis during evolution.
5. They are rich in species diversity. The occurrence of 1,731 plant species is reported for pre-tropical and subtropical pastures, savannas, and shrublands; for meadows, steppes, and shrublands of the temperate zone, 1,372 species are mentioned; for mountain grasslands and shrublands, 1,397 species; and for flooded pastures and savannas, 767 species. Semi-natural grassland (in Slovakia) consists of 30–70 species of vascular plants.
6. They possess a high content of silicon in their tissues (approximately 4–5%), providing high mechanical resistance and adaptations to excessive grazing and usage. Generally, plants with high Si concentrations are less susceptible to attacks by pathogens and pests, and they show increased tolerance to abiotic stresses such as drought, low temperature, or metal toxicity.
7. They have very good regenerative ability after defoliation and natural fires. Fire can induce various changes in landscape appearance, but the degree of change and duration in grasslands is typically much less compared to forested ecosystems. Grass recovery is usually so rapid that the effects of fire are concealed within one year due to rapid regrowth. Permanent grasslands primarily regenerate after fires through vegetative means (taproots, surface roots, rhizomes, stolons, and root crowns), as well as through seed reproductive structures.
8. They bind high amounts of carbon in the soil and roots, which is advantageous for mitigating global warming on our planet. Grassland soils represent a highly significant carbon store, with global carbon stocks estimated at about 343 Gt C, approximately 50% more than the amount stored in forests worldwide.
9. They are drought-resistant and tolerate prolonged drought well. An important parameter for assessing the impact of drought is the ratio of the dry weight of the root system to the above-ground phytomass, R:S (root to shoot ratio). Higher R:S values indicate greater resistance of the vegetation to drought. In the permanent grasslands of central Slovakia, we recorded an average R:S value of 5.16, which was significantly higher than in temporary grasslands, where R:S = 4.27. These results demonstrate the higher ecological stability of permanent grasslands against the stress factor of drought.
10. They have developed robust root systems and sward, thereby eliminating soil erosion. In central Slovakia, the root biomass weight of permanent grasslands ranged from 6.69 to 10.31 t ha^{-1}. Grasslands reduce erosion effects compared to arable land by approximately 25 to 100 times. Their anti-erosion effect is significantly greater because they provide continuous soil cover throughout the year. The anti-erosion effect of different crops (vegetation cover) can be ranked as follows: well-established forest > permanent grassland > fodder crops > annual grasses > winter cereals > spring cereals > root crops.
11. Several grass species act as excluders of heavy metals, contributing to the protection of the food chain. We evaluated [17] the uptake and accumulation of heavy metals (Cd, Co, Cr, Pb, Zn, Mn, Cu, Fe, and Ni) in the soil-root-aboveground phytomass system of permanent grasslands in central Slovakia. Our results showed that heavy metals are most concentrated in the plant roots and soil, with significantly lower levels detected in aboveground phytomass. Based on the bioconcentration factor (BCF < 1), grasslands functioned as excluders of the assessed heavy metals.
12. Grasslands have the potential to successfully manage the impacts of climate change. Successful adaptation of grasslands to climate change is anticipated by Hebda [84]. He states that due to warming and drought, and consequently more frequent fires, the occurrence of forest ecosystems will decline. At the expense of forests, grassland ecosystems are expected to expand, extending into higher altitudes and latitudes. Using a model example from British

Columbia (southwestern Canada), he notes that plant species characteristic of grasslands will likely become most suitable for future climate conditions. His model documents the loss of forests and the effective adaptation of grasslands to climate change driven by global warming.

13. Compared to crops on arable land, they are relatively resistant to diseases and pests.

In conclusion, the grassland ecosystem (nor any other) will not develop adaptations for the excessive exploitation of natural ecosystems and resources by humans, often to a destructive and devastating extent. To protect and utilize the functions and services of ecosystems sustainably, a change in human behavior is primarily needed. Permanent grasslands (unlike the production of more expensive cereals, legumes, and similar crops) provide a cheaper and more accessible source of bulk feed for livestock and often represent the main source of sustenance in the poorest regions and countries of the world.

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Conflict of Interest

The authors declare no conflict of interest.

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