

ROUTLEDGE HANDBOOK OF GRASSLANDS

This comprehensive handbook represents a definitive state-of-the-art overview of grasslands from multiple, interdisciplinary and global perspectives.

Despite the real and intrinsic values that grasslands offer, they are globally subject to fragmentation, habitat and species loss, and they are increasingly threatened by climate change. From a human societal perspective, grasslands are central to much of our culture and represent areas where agriculture first arose. The *Routledge Handbook of Grasslands* brings together an interdisciplinary team of global authors to present a much needed and vitally important overview of the new and ongoing debates around the values of and threats to grasslands. Reflecting the broad range of issues, debates and threats, this handbook is divided into five parts:

- Part I: Deep Roots, Dynamic Futures: Understanding the Science of Grasslands
- Part II: Living Complexity: Grassland Function, Biodiversity, and Renewal
- Part III: Working Landscapes: Innovation and Tradition in Grassland Stewardship
- Part IV: Social-Ecological Ties: Grassland Services, Justice, and Governance
- Part V: Landscapes of Meaning: Cultural and Creative Perspectives on Grasslands

Drawing on the experience of researchers, practitioners and managers, this handbook is the only grassland-oriented text to include social, economic, policy and cultural value dimensions of grasslands, as well as an up-to-date coverage of the agronomy and ecology of these environments. This handbook concludes with a forward-thinking chapter that discusses the future of grasslands, further directions, threats and innovations.

The *Routledge Handbook of Grasslands* is essential reading for students and scholars of grassland ecology, management and conservation as well as policy and management practitioners involved in grassland management and governance, as well as natural resources more broadly.

Heather A. Hager is an ecologist and natural sciences research facilitator at Wilfrid Laurier University, Canada, and an award-winning textile artist.

David J. Gibson is a plant ecologist and Emeritus in the School of Biological Sciences at Southern Illinois University Carbondale, USA. He is the author of *Grasses and Grassland Ecology* (2009) and co-editor of *Grasslands and Climate Change* (2019).

Jonathan A. Newman is a temperate grassland ecologist and Vice President: Research at Wilfrid Laurier University, Canada. He is co-author of *Defending Biodiversity* (2017) and co-editor of *Grasslands and Climate Change* (2019).

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*Edited by Heather A. Hager, David J. Gibson
and Jonathan A. Newman*

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6

PHYSIOLOGICAL AND ANATOMICAL TRAITS OF GRASS SPECIES

Diversification facilitates persistence in grassy ecosystems

Jesse B. Nippert and Brent R. Helliker

Introduction

Grasses have relatively similar anatomy and physiological function compared to other families of flowering plants. Leaf-level traits are expressed over a fairly short vertical distance (aboveground), often in a similar light environment. The majority of grass species exist in environments with episodic availability of water and soil nutrients. As such, grasses often grow over a short period of time each year in response to changes in resource availability. Based on this apparent similarity in form and responses to changes in resource availability, one might hypothesize that a specific set of environmental conditions would converge on a particular growth strategy that constrains grass species' success. Yet, grass species are adapted to both broad climatological and disturbance gradients including grazing and fire. Thus, can we gain a fresh perspective on the broad successes of grasses by examining their unique morphological and physiological adaptations? How do these trait attributes vary within subfamilies of Poaceae, and confer ecological success in particular environments? In this chapter, we compare general photosynthetic pathway responses and, when possible, provide examples from specific Poaceae subfamilies (Panicoids, Chloridoids, Poooids, and Aristidoids). These subfamilies were chosen because they comprise many dominant grass species within what we broadly consider grasslands (e.g. bamboo-dominated systems aren't generally considered "grasslands"). In such a manner, we discuss physiological constraints imposed by species distributions that reflect landscape patterns of resource availability and temperature constraints.

Evolutionary linkages to trait physiology

The global-scale emergence of Poaceae at the beginning of the Cenozoic era as a dominant family of Angiosperms reflects lineage-specific environmental selection, and provides clear examples of both divergent and convergent evolution. Poaceae begins in Gondwana, with varying phylogenetic analyses pointing to subsequent lineage origins in South America, Africa, or Australia [1]. The first grass-like species had biogeographic origins in moist environments and likely existed under forest

canopies [2,3]. Over time, grasses expanded beyond the dense canopies into open environments, specializing in high-light, drier environments [1,4] (see Chapter 2).

One of the clearest examples of convergent evolution in biology—and one of the most critical aspects of Poaceae success globally—has been the evolution of the C_4 photosynthetic pathway. Despite accounting for only ~3% of all species of plants and approximately half of all grass species [5,6], C_4 grasses cover around 17% of the land surface, accounting for ~20% of total terrestrial gross productivity [7,8]. In Poaceae, the C_4 pathway has evolved independently more than 20 times over a 30-million-year period [9–11], presumably in environments where high rates of photorespiration provided strong selective pressure for a modification of the C_3 photosynthetic pathway [12–14]. C_4 evolution is thought to be selected for by high temperature, but the primacy of additional selective agents has changed through time: water limitation in the mid-Oligocene, lower CO_2 concentrations, and increased aridity in the mid-to-late Miocene [15–17].

Four grass subfamilies dominate grassland communities globally, including Panicoideae (mix of C_3 and C_4), Chloridoideae (mostly C_4), Aristidoideae (mostly C_4), and Pooideae (C_3). These four lineages have evolved to occupy different climate spaces. The Pooideae are cold-climate specialists, having evolved traits to survive freezing and cellular and membrane damage [2,18,19]. Both the Pooideae and Chloridoideae live in dry climates, though droughts are not as pronounced in Pooideae-dominated areas [2,20]. The Panicoideae, Aristidoideae, and Chloridoideae are warm-climate specialists, with the Chloridoideae living in hotter, drier environments and the Panicoideae inhabiting comparatively more mesic sites [2,20–22]. Climate space variability also exists within a particular subfamily, but doesn't always fit neatly within climate axes. For example, C_3 Panicoids typically occupy a more constrained niche space (mean annual temperature: 15–25°C; mean annual precipitation: 500–2,000 mm) compared to the greater climate diversification seen in C_4 Panicoid species [23]. Phylogeny, C_4 subtype, and environmental conditions (particularly water availability) interact to influence grass form and anatomy and the underlying physiological responses [3,24,25]. For example, Chloridoideae species tend to be shorter, have longer and more narrow leaves than Panicoideae species [25]. These phylogenetic morphology distinctions are not consistently reflected by ecophysiological differences, which vary more from C_4 subtype and environment [25]. This simple result comparing anatomical and physiological traits among Chloridoideae and Panicoideae species underscores the necessity of including environmental data and phylogeny (including tribes) to understand both evolutionary and ecological processes within grassy ecosystems.

Species of these dominant grass lineages can co-exist within particular regions, taking advantage of seasonal and interannual climate variability. As an example within the Great Plains of North America, Pooideae dominate the northern portion, Panicoideae dominate the east-central to southeast, and the Chloridoideae dominate the west-central and southwestern regions [26]. This phylogenetic distribution reflects the inter-continental climate of North America with a N-S temperature axis (cold-warm) and an E-W precipitation axis (wet-dry) [8]. In locations with strong gradients of rainfall and temperature over smaller spatial scales, these three lineages of grasses can co-dominate the landscape [20,27]. Pooideae species take advantage of cooler spring and early summer temperatures while Panicoideae and Chloridoideae species become more dominant grasses on the landscape during mid- and late summer.

Climate space provides boundaries on trait responses

Climate is both a structuring and selective agent for ecological dynamics and terrestrial plant species assemblages. Within temperature ranges of –7 to +30°C and annual rainfall regimes between 400 and 1,600 mm [28], grassland or savanna ecosystems are common, reinforced within

these particular assemblages by frequent disturbances including grazing and fire which modify the plant species assemblages therein (see Chapter 13). As such, both intra- and interannual climatic variability interacts with top-down pressures to influence ecological dynamics (and physiological responses) in many grasslands (see Chapters 8 and 14).

In grasslands, it is common to have separate functional groups for woody species, graminoids (grasses and close relatives), and forbs. Grasses have been further organized into their own functional groups to better represent their functional diversity. One common method groups species into plant functional types (PFTs) based on whether they perform either C_3 or C_4 photosynthesis [26]. This classification scheme includes a basic physiological difference, but assumes that responses within a photosynthetic pathway are more similar than species responses across photosynthetic pathways. For subfamilies that have both C_3 and C_4 species within their lineages, does this assumption hold? Studies show that PFTs based on photosynthetic pathways overlook large amounts of trait variation within Poaceae, especially within the C_4 PFT [29], as C_4 photosynthesis has evolved independently many times [11]. Instead, organizing grasses by their evolutionary lineage better incorporates grass trait diversity by capturing more ecologically meaningful differences than PFTs [26,29,30]. For the remaining sections of this chapter, we illustrate the diversity of anatomical and physiological trait responses that exist within Poaceae, providing lineage-based examples that underlie grass distributions whenever possible.

Grass morphology and leaf anatomy

Grasses utilize both sexual and asexual forms of reproduction to regulate population dynamics. For annual grass species, sexual reproduction constitutes a more significant role with populations regulated by seed bank longevity, germination cues, rates of growth, and generation time. Within perennial grass species, asexual reproduction plays a more significant role with the recruitment of new tillers via existing belowground clonal stems (rhizomes). Grasses often invest large amounts of biomass belowground. Belowground “bud banks” (Figure 6.1) in perennial grass species can be very responsive to changing environmental conditions or to disturbances such as fire and grazing, and this may be an important mechanism underpinning spatial and temporal variability in the population dynamics and productivity of grasses [31–33]

The majority of grass species regardless of life history, photosynthetic pathway, or phylogeny have several common features. Grass leaves are comprised of the sheath, culm (if present), and the blade which extends outward and functions as the primary organ for photosynthesis and transpiration. The acropetal growth of leaves from an intercalary meristem results in younger tissue with higher physiological activity at the base of leaf blades as compared to the tips [34]. Grass leaf blades show similar leaf-size/climate relationships and geometrical allometries with eudicots, with the interesting exception of bundle sheath and bulliform cells [35].

That bulliform and bundle sheath cells scale differently from other leaf cells is possibly indicative of the special role that each cell type has developed in grasses (Figure 6.2). These cell types have been hypothesized [36,37] and more recently shown [38] to be an important component of leaf-water storage. The bundle sheath cells serve as the symplastic interface for water flow from xylem to the evaporative sites within the leaf, where expression of aquaporins controls the rate of water flux [39]. In C_3 grasses, larger bundle sheaths are suggestive of both greater water storage and progenitors to the evolution of C_4 photosynthesis as the Calvin-Benson cycle is ensconced within the bundle sheath as part of the C_4 carbon concentrating mechanism [40]. Historically, the adaptive significance of bulliform cells has been actuating leaf folding or rolling in times of

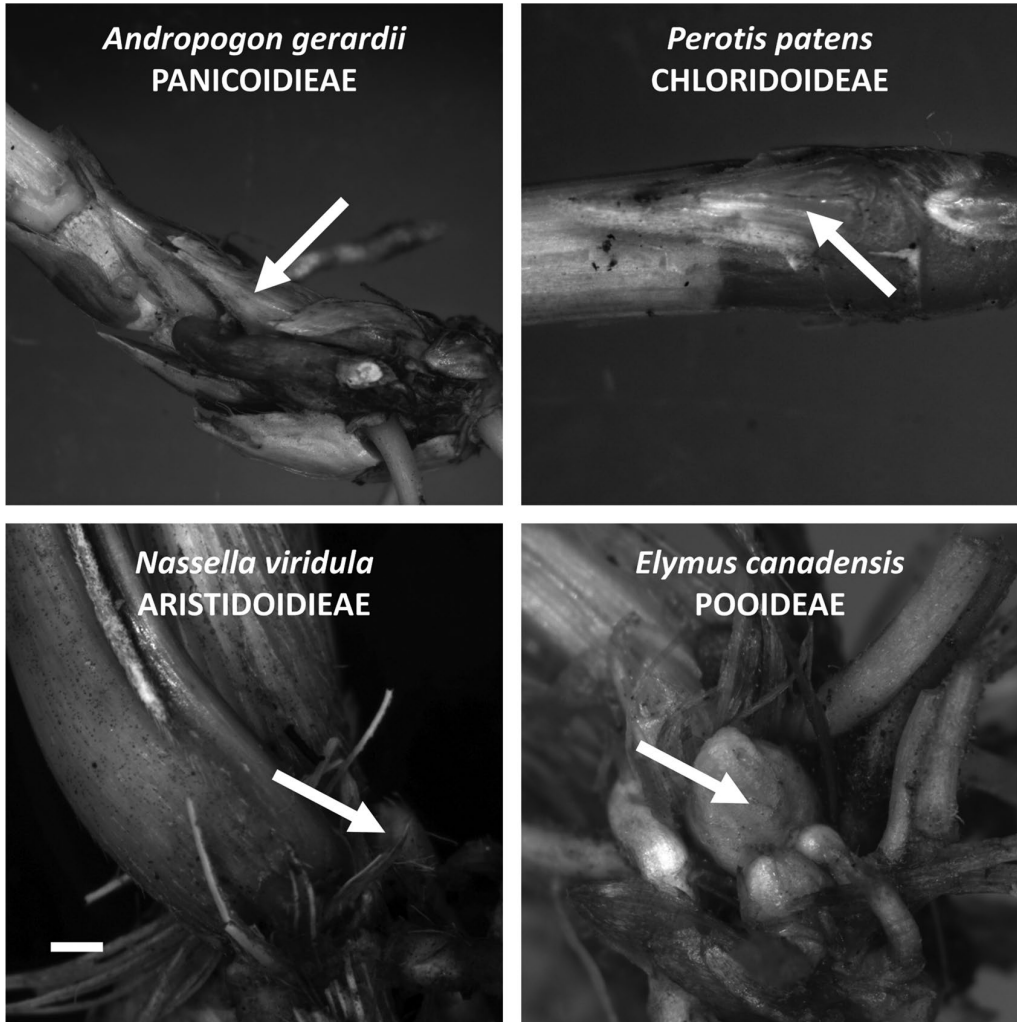


Figure 6.1 Examples of bud bank morphology from species representing varying subfamilies. Arrows identify unique buds. Picture credit: Jacqueline Ott.

drought [41], where the rolled or folded leaf results in lower exposed leaf area, a larger boundary layer, and reduced transpiration. Clear physiological evidence supporting this benefit is lacking [42]. Furthermore, it is our observation that within wild grasses many leaves with bulliform cells do not fold or roll, and many leaves have bulliform cells distributed throughout a leaf cross section, but only fold at the midrib. Lastly, within a species, bulliform cross-sectional area negatively correlates with xylem area across precipitation gradients, suggesting that at drier sites, xylem is more resistant to failure and bulliform-based leaf-water storage is higher [43].

Grasses evolved unique, dumbbell-shaped stomata that, in partnership with subsidiary cells, operate in a manner different to standard, kidney-shaped stomata of eudicots. This morphology

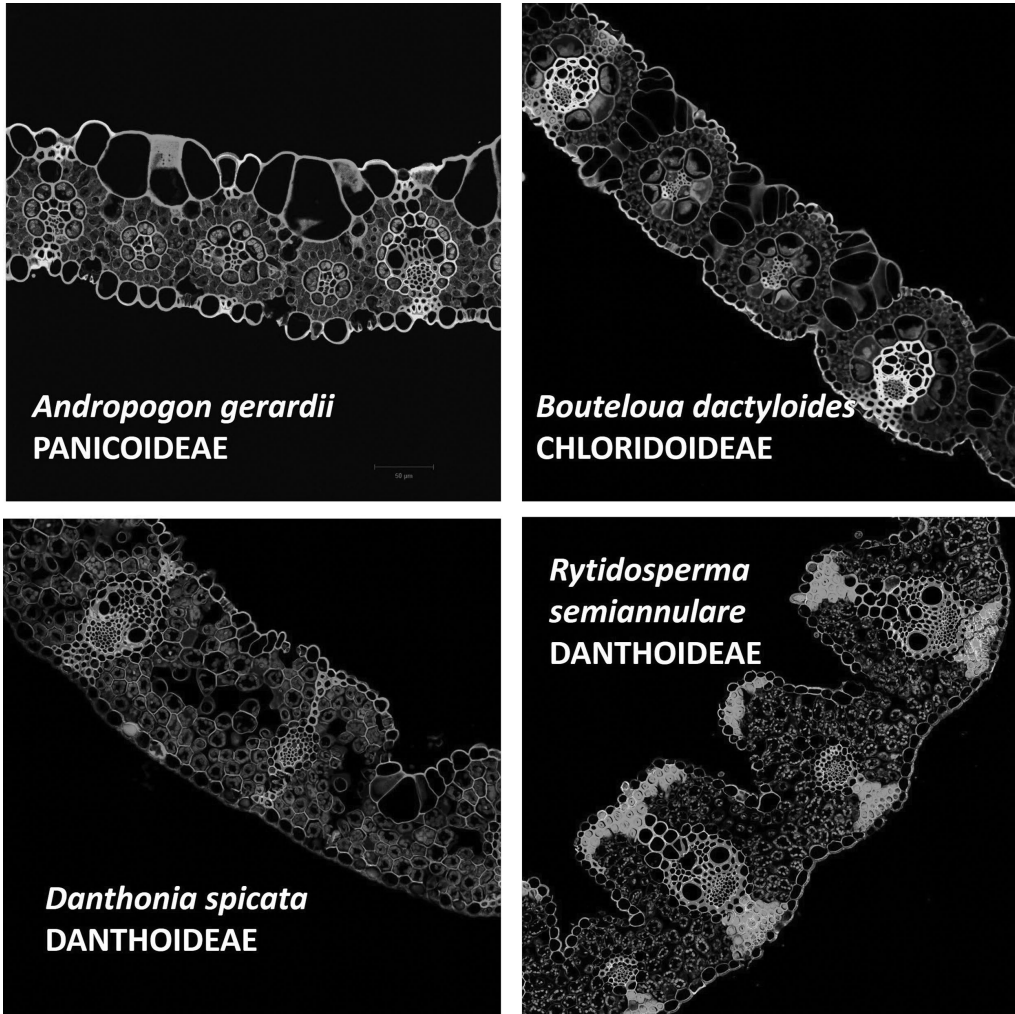


Figure 6.2 Examples of leaf cross-sectional anatomy from three subfamilies. Photo credit: Seton Bachle.

allows for more energy-efficient stomatal movements and greater rates of gas exchange via larger pore apertures [44]. Leaf veins display parallel venation with major and minor veins connected along the leaf by smaller, transverse veins. Major veins typically have larger diameter xylem and are responsible for the majority of acropetal water flow. While the greater resistance of minor veins leads to lower flow, phloem flow in minor veins is likely on par with that of major veins [45]. The minor veins cover a relatively large area of photosynthetically active leaf lamina between major veins, and therefore high phloem flow of carbon is necessary. Optimal operation of C_4 photosynthetic pathway requires a high ratio of bundle sheath to mesophyll cells, and is the impetus for the evolution of much greater vein density compared to C_3 grasses (Figure 6.2). This increased vein density in C_4 grasses is due to an increase in minor veins, as major vein abundance is typically similar between C_3 and C_4 grasses [46].

Photosynthesis

Grasses, particularly the Panicoids and the Pooids, can develop dense canopies that reduce incoming radiation by 90–99% with leaf area indices similar to deciduous forest [47]. Compared to woody species which invest heavily in stems, the structural investment in leaves illustrates the significance of light capture for grasses, leading to maximal photosynthetic rates, fast growth, reduced subcanopy light, and a competitive advantage over coexisting species.

A defining feature of leaf physiology among grass species is the occurrence of two varying photosynthetic pathways—the ancestral C_3 vs. the derived C_4 . Among the tribes discussed here, Panicoids contain C_3 and C_4 , Pooids are all C_3 , while Aristidoideae and Chloridoideae are predominantly C_4 (except for the genus *Sartidia* and the species *Aristida longifolia* in Aristidoideae and the genus *Ellisochloa* in Chloridoideae which are all C_3) [48]. The distinction of C_3 or C_4 impacts the physiological response to changes in light, CO_2 , N, and water availability, along with responses to temperature. C_3 grasses have lower light requirements for photosynthesis (and thereby, higher quantum efficiencies) than C_4 grasses, reflecting the greater metabolic energy required by C_4 grasses [27]. Varying responses to CO_2 and N among species of these contrasting photosynthetic pathways reflect biochemical differences arising between carboxylation processes. For a more detailed physiological description of C_4 photosynthesis, see references [3, 13, 23].

Approximately 85% of all vascular plant species use solely the C_3 photosynthetic pathway, including 40–45% of all known grass species [6]. The general biochemical processes that underlie the light reactions of photosynthesis are similar among all higher plants, with light energy captured and converted to cellular energy in the form of ATP and NADPH, which is then used to power the reduction of carbon in the Calvin-Benson (or C_3) cycle. The nomenclature of C_3 and C_4 refers to the first organic acid formed during the initial carboxylation step. These carboxylation reactions are the starting point for all known complex organic molecules, underlie all ecological and evolutionary complexity on Earth, which underscores the fundamental significance of the photosynthetic processes in plants.

C_4 photosynthesis can be described as the spatial separation of carbon fixation and carbon reduction processes between mesophyll and bundle sheath cells, such that CO_2 diffusing into leaf mesophyll spaces is fixed by the enzyme PEP-carboxylase and reduced to a 4-C acid malate or aspartate. These organic acids are then transported into the bundle sheath cells—where the full Calvin-Benson cycle is sequestered—and decarboxylated by three different decarboxylating pathways (NAD-ME, NADP-ME, or PEP-CK) that often vary by phylogeny. Following phylogenetic classification in Sorrell et al. [48], there are five subfamilies of Poaceae with species that perform C_4 photosynthesis: Aristidoideae, Chloridoideae, Panicoideae, Arundinoideae, and Micrairoideae. Chloridoideae species predominantly contain the NAD-ME and PEP-CK subtypes, while Aristidoideae species are predominantly NADP-ME. Micrairoideae only contains species with the NADP-ME pathway. Panicoideae lineages do not fit neatly within one C_4 subtype, containing species that include all three subtypes: PEP-CK, NAD-ME, and NADP-ME, as well as C_3 – C_4 intermediates [49]. On the most superficial level, C_4 photosynthesis results in lower rates of photorespiration and higher RuBisCO enzymatic kinetics compared to C_3 photosynthesis. This outcome results from the low intercellular CO_2 concentration in mesophyll spaces (resulting from the high affinity of PEP-C for CO_2) and the very high CO_2 concentrations contained inside the leaf bundle sheath cells. These high concentrations of CO_2 surrounding RuBisCO reduce the likelihood of an oxygenation reaction and maximize enzyme activity. Under these conditions, RuBisCO operates under CO_2 concentrations that rival those in which it initially evolved [50]. These dynamics of C_4 photosynthesis result in varying resource use efficiencies and responses to temperature compared to C_3 species, which also vary among evolutionary origins of subfamilies and grass tribes.

C dynamics

While multiple selective pressures were responsible for the convergent evolution of C_4 photosynthesis in grasses [3,11,13,16], an overriding selective pressure resulted from the negative consequences of photorespiration. High bundle sheath CO_2 concentrations effectively negate photorespiration, while also optimizing photosynthesis. In other words, even if atmospheric $[CO_2]$ varies seasonally, centuries, or over geologic time, operational photosynthetic rates are near maximal enzymatic capacity all the time, given that other resource availabilities (water, light) are met. The consequences of photorespiration in C_3 vs. C_4 plants are displayed well by examining photosynthetic responses (Pn) to changing internal leaf CO_2 concentrations (Ci) using A/c_i curves (Figure 6.3). While the general shape of these curves does not vary among pathways, traits derived from these curves, including the CO_2 compensation point, photosynthetic saturation point, and the maximal carboxylation and electron transport rate ($V_{c_{max}}$, J_{max}), do vary. The CO_2 compensation point for C_3 species ($[CO_2]$ whereby C gain exceeds C losses via respiration and photorespiration is much higher for C_3 species), and the initial curve slope (indicative of carboxylation capacity $V_{c_{max}}$) is lower for C_3 vs. C_4 species. The inflection point between linearly increasing and saturated photosynthetic rates is higher in C_3 , often exceeding 200 ppm, while it's typically <50 ppm in C_4 species.

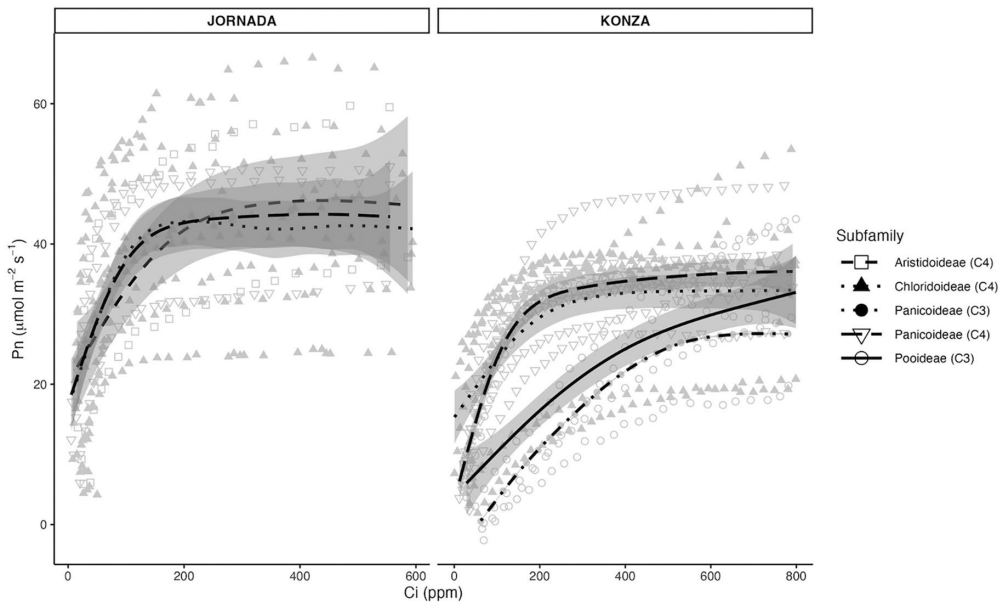


Figure 6.3 A/c_i curves [photosynthetic responses (Pn) to changing internal leaf CO_2 concentrations (Ci)] representing species from four major subfamilies in North American grasslands. Points represent discrete data by species, while curves represent mean responses by species within a subfamily, with 95% CI illustrated by shading. Data on the left were measured at the black grama desert grassland Jornada Experimental Range, outside Las Cruces, NM. Data on the right were measured in tallgrass prairie, at the Konza Prairie Biological Station, Manhattan, KS. Data arise from Ho et al., unpublished.

Environmental conditions and phylogeny impact photosynthetic responses. Figure 6.3 shows varying curve shapes among species representing four subfamilies from hot/dry (Jornada) and warm/wet (Konza) grassland sites. All data were collected at times with optimal growing season temperatures, and available soil moisture. At Jornada, the overall curve shape and initial slopes are similar among all species/subfamilies, but note the large range of saturating photosynthetic values in this community. By comparison, species and subfamilies measured at Konza were more distinct, especially the C_3 Pooids and Panicoids. Saturating photosynthetic rates of C_4 species at Konza are lower compared to Jornada, likely reflecting differences in leaf N availability (%N per leaf area) among locations. These data illustrate that while there are “general trends” with regard to leaf photosynthesis that vary among grass species of C_3 and C_4 pathways, environmental conditions and phylogeny provide important structural roles impacting physiological responses.

N dynamics

For all grass species regardless of photosynthetic pathway, one of the largest N sinks is photosynthetic enzymes [51]. The compartmentalization of the Calvin-Benson cycle inside bundle sheath cells impacts leaf N requirements for C_4 grasses. Because of a higher operational efficiency of RuBisCO, overall N requirements are lower in C_4 vs. C_3 species [23]. Leaf N requirements are often compared among species in the context of photosynthetic nitrogen-use efficiency (PNUE), or the rate of C assimilation per unit of leaf N (on an area or mass basis). PNUE varies among grass species with varying C_4 subtypes. Lineages and species using NADP-ME have higher PNUE than lineages with NAD-ME [52–54]. These differences among subtypes may reflect larger leaf areas in species with NADP-ME, with fewer subtype/lineage differences when compared based on leaf mass [52]. Higher PNUE in C_4 grasses may facilitate the colonization and growth of these species in N-poor environments [23], and allow for greater investment belowground (roots, rhizomes, bud banks) compared to C_3 grasses [10]. We require more phylogenetic comparisons among grass subfamilies in contrasting *in situ* environmental conditions to understand the role of evolutionary history as a driver of N trait diversity in Poaceae, and improve predictions of grassland responses to future change.

Temperature

Temperature plays a key role in rates of C assimilation for all autotrophic species. RuBisCO oxygenation increases relative to carboxylation as temperatures increase, resulting in higher photorespiration in C_3 plants [55]. Conversely, the enzymatic activity of PEP-carboxylase is cold-temperature sensitive. These varying temperature sensitivities among photosynthetic pathways were identified as the mechanisms driving a crossover temperature model of 22°C [56] whereby C_3 grass species distribution and abundance are greater at higher latitudes [57] and altitudes [58] than C_4 species. While temperature undoubtedly has differing physiological impacts on C_3 vs. C_4 species, the biogeographic pattern (C_3 in northern latitudes and altitudes) also reflects varying evolutionary history within the grasses. The subfamily Pooidae acquired cold tolerance traits during the Oligocene [2,18], and then subsequently diversified and expanded into colder environments [19]. Given that this one lineage of C_3 grasses (Pooids) occupies colder regions, temperature-based assessments of species distributions must include both physiological mechanisms along with the evolutionary history of grass taxa [59,60] and climate histories [61] of particular regions.

Water relations

Similar to other higher plants, grasses regulate leaf gas exchange via stomata, which allow for the inward diffusion of CO₂ to support photosynthesis. As a consequence of the inward diffusion of CO₂, water is lost via the stomata at a ratio often exceeding 100:1. This lost water vapor must be replaced by the conductance of liquid water to the evaporative sites within a leaf, and water must be extracted from the soil to maintain this continuous chain of water molecules from leaf xylem to the root endodermis. Grasses differ from other higher plants in several aspects of this soil-plant-atmosphere continuum, and here, we highlight several areas where there are clear unknowns for future study within the context of soil and atmospheric drought.

Atmospheric drought is manifest through changes in the evaporative gradient from the leaf to the atmosphere, the leaf-to-air vapor pressure deficit (VPD_L; units of kPa). While stomatal responses to VPD_L can vary greatly across species and within species, stomatal conductance typically decreases as VPD_L increases, reducing water loss at the expense of decreasing carbon gain. Measurements of leaf-level stomatal conductance (g_s), tree canopy conductance, and ecosystem-level surface conductance can be used to assess stomatal sensitivity to changes in VPD_L over a variety of scales by:

$$g_s = -m \times \ln(\text{VPD}_L) + g_{s\text{-ref}}$$

where g_{s-ref} is a reference conductance at a relatively standard VPD_L = 1 kPa (mmol m⁻² s⁻¹) and *m* describes the sensitivity of g_s to changes in VPD_L [62].

Previous work has shown that grass stomata are more responsive than other stomatal types in response to changes in both VPD_L and light [44,63], but recent work on wild grasses shows that stomatal responses to changing VPD_L are not particularly fast [38], and previous hypotheses concerning grass stomatal responses were developed based upon the physiological responses of domesticated grasses (crops). In both field and lab measurements, wild grasses (all Panicoideae) have relatively low stomatal sensitivity (*m*) and C₄ species had a significantly lower *m* than C₃ species [38], in accordance with C₄ grasses having lower overall stomatal conductance (g_{s-ref}) as compared to C₃ grasses. Compared to a survey of published data for wild grasses, domesticated grasses, and a broader phylogenetic grouping of higher plants, the stomatal sensitivities of wild grasses were significantly lower than that of crops, and while not significantly different, mean *m* for wild grasses was lower than that of herbaceous dicots and ferns (Figure 6.4). At the ecosystem scale, grasslands display a similarly muted *m* as leaf-level measurements [64]. With high soil moisture content, both g_{s-ref} and *m* were low as compared to forests and showed little difference from mesic to xeric grassland sites [64]. As soil moisture declined, *m* remained relatively constant until soil became very dry, while g_{s-ref} declined with soil moisture.

Grass water potentials and drought

According to patterns of the leaf-water potential at turgor-loss point (Ψ_{TLP}; MPa) observed primarily in woody plants and herbaceous dicots, grasses should be isohydric and drought intolerant. Ψ_{TLP} is an indicator of incipient plasmolysis [66] and is the Ψ at which the leaf wilts, gas exchange ceases and represents the limit of soil Ψ for plant water uptake [67,68]. Plant Ψ_{TLP} is a strong predictor of drought resistance in dicot-dominated biomes [69]. In comparison, mesic and aridland grasses have Ψ_{TLP} that is somewhere between wet tropical and temperate forests

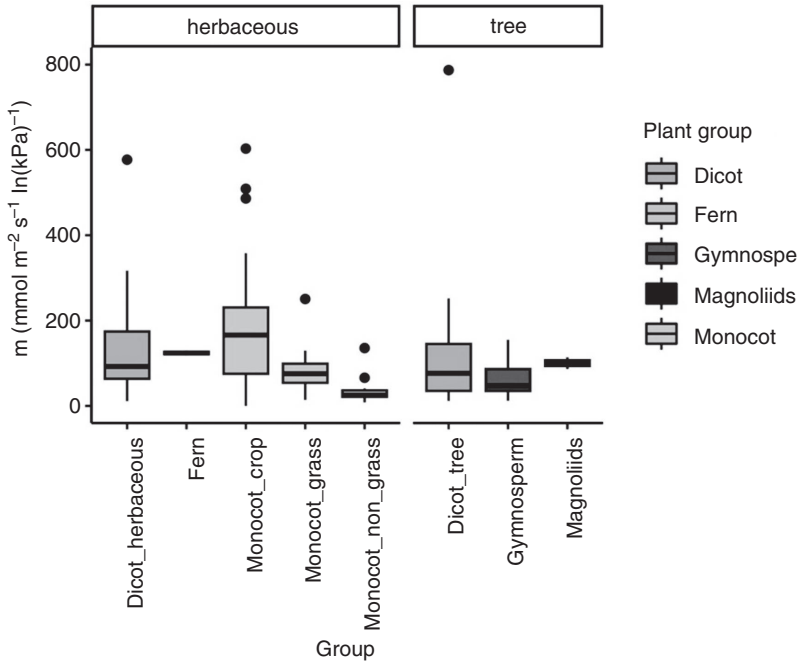


Figure 6.4 Stomatal sensitivity (m) values of grasses as compared to other plant groups [65].

(Figure 6.5). Ψ_{TLp} also yields information on plant hydroscares, which explain the water-potential space over which a plant can operate [70]. One way of delineating a hydroscape is to examine the separation between pre-dawn and mid-day water potential as drought conditions ensue. Plants whose predawn and mid-day water potentials show little difference at relatively high (less negative) predawn values are isohydric and drought intolerant, meaning stomata close early in drought to avoid reaching lower Ψ_{leaf} values. Whereas plants that maintain large differences in predawn and mid-day water potential as drought persists are drought resistant and anisohydric. Anisohydric plants have evolved mechanisms to better resist xylem embolism and can therefore keep stomata open and maintain carbon gain deep into a drought. In woody plants [70], strong correlations exist between well-watered Ψ_{TLp} hydroscape area, and the degree of anisohydry [70]. Here again, based on broad sampling of grass Ψ_{TLp} , grasses would be placed in the isohydric and drought intolerant category. This categorization includes known desert/aridland grasses in the Chloridoideae as well as more mesic grasses of the Panicoideae. One could argue that grasses are drought avoiders and they are active only when seasonal precipitation occurs. The available data do not support this assertion. Rather, grasses can be both extremely productive when water is available, and also extremely drought tolerant when it is not.

The root-to-leaf transport of liquid water from the soil is broadly governed by what has been termed a safety/efficiency tradeoff [71]. If the water potential within xylem becomes too negative, then flow-blocking embolisms can form within xylem conduits. Stomatal conductance is regulated to maintain a greater water potential in the xylem to avoid embolism [72]. Within grasses, decreases in stomatal conductance track with decreases in leaf hydraulic conductance (K_{leaf}) [73,74], demonstrating that a safety-efficiency tradeoff does exist. Thus, g_s decreases to maintain

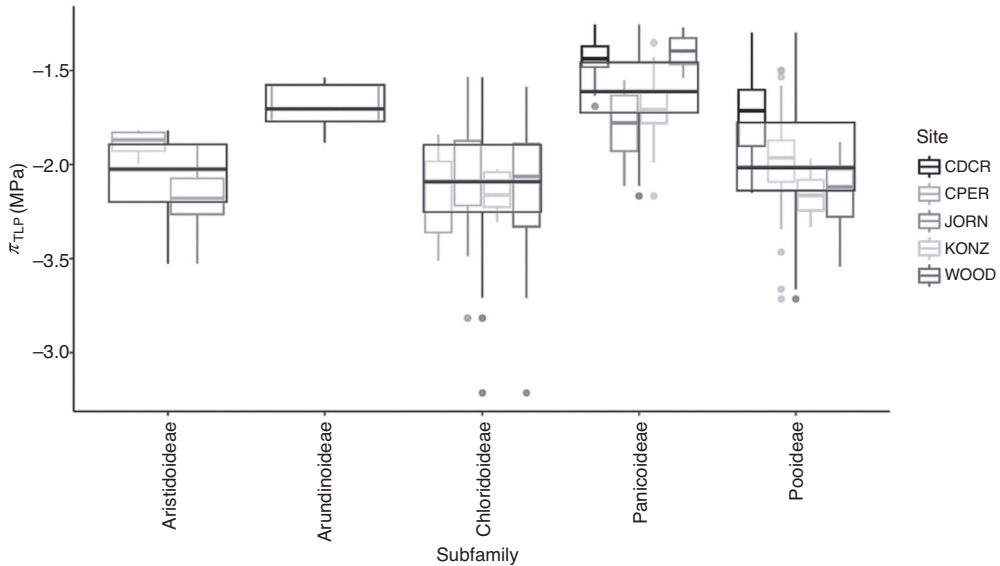


Figure 6.5 Leaf-water potential at turgor-loss point (Ψ_{TLP}) among subfamilies within several Great Plains grassland sites. The sites were Cedar Creek, Minnesota (CDCR); the Central Plains Experimental Research location in Colorado (CPER); the Jornada Basin, New Mexico (JORN); the Konza Prairie Biological Station (KONZ); and the Chase Lake National Wildlife Refuge in North Dakota (WOOD). Data are from Ho et al. [65] unpublished data.

the integrity of the hydraulic transport system. Grasses appear to differ markedly, however, in how the safety/efficiency tradeoff compares to the leaf Ψ_{TLP} .

Grasses appear to sit beyond the bounds of what has been described for woody and herbaceous dicots [75] and the “unified theory of photosynthesis and hydraulics” [76]. Previous broad sampling of dicot species and growth forms shows a repeatable relationship between the Ψ_{TLP} , hydraulic conductance (K), and g_s as drought ensues [77,78]. The general relationship is that the capacity of K_{leaf} and g_s is reduced by 50% at ~ 1 MPa more positive than Ψ_{TLP} and g_s should be reduced by 88–90% within a few tenths of MPa more negative than the Ψ_{TLP} . In other words, Ψ_{TLP} is in between the Ψ_{leaf} that represents 50% loss of K_{leaf} and that of near complete stomatal closure. It appears that grasses buck this trend. For the available data on grasses [73,74,79] (see [80] for slight disagreement for some species), Ψ_{TLP} is about 1.0 MPa less negative than 50% loss of g_s and about 1.5 MPa less negative than the Ψ_{leaf} at 50% loss of K_{leaf} . The relationship between K_{leaf50} and g_{s50} (Figure 6.6) demonstrates that safety-efficiency tradeoff does exist in grasses, but the relationship between Ψ_{TLP} , K_{leaf50} and g_s is not in accordance with observations of other plant types.

To fully contextualize the unique grass physiological responses to both soil and atmospheric drought as compared to woody plants, *Andropogon gerardii* provides an ideal example. *A. gerardii* is a dominant C_4 grass (Panicoideae) in the mesic, tallgrass prairie system of North America [81]. *A. gerardii* has a measured Ψ_{TLP} of -1.2 to -1.5 MPa, which places it squarely into the small hydroscape/isohydric/drought intolerant space. VPD_L response curves of *A. gerardii* have low stomatal sensitivity with $m = 67 \text{ mmol m}^{-2} \text{ s}^{-1} \ln(\text{kPa})^{-1}$ (with $m/g_{s-ref} = 0.39$), which is indicative of anisohydry. K_{leaf50} is not reached until ~ 2.5 MPa less negative than the Ψ_{TLP} and g_{s50} is reached at ~ 1 MPa

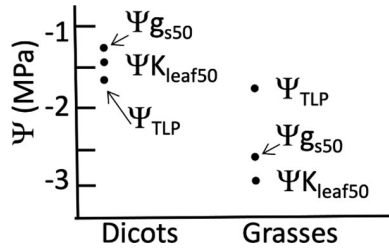


Figure 6.6 Summary data for leaf-water potential at turgor-loss point (Ψ_{TLP}), 50% of maximal stomatal conductance (Ψ_{g50}), and 50% of maximal hydraulic conductance ($\Psi_{K_{leaf50}}$) for dicots [77] and grasses [81,82].

less negative than the Ψ_{TLP} [73]. *A. gerardii* is extremely productive when water is available, with photosynthetic rates exceeding $40 \text{ mmol m}^{-2} \text{ s}^{-1}$, and aboveground net primary productivity values $>800 \text{ g/m}^{-247}$, but it can also be extremely drought tolerant, maintaining photosynthetic rates of $\sim 10 \text{ mmol m}^{-2} \text{ s}^{-1}$ with $\Psi_{leaf} < -5 \text{ MPa}$ [82], indicating that *A. gerardii* was operating at somewhere between 10 and 30% of maximal gs while Ψ_{leaf} was $\sim 4 \text{ MPa}$ below the Ψ_{TLP} . Furthermore, photosynthesis ceased only when Ψ_{leaf} decreased below -6.5 MPa , and these same leaves rebounded when precipitation returned [82].

Grass root anatomy and physiology

For many grass species, allocation of biomass belowground is often double or triple the amount of biomass aboveground [77]. Grasses maintain fibrous root systems that are highly branched, high root length, and small root diameters, resulting in an overall root system that has high surface area and is functionally very absorptive. Fibrous root systems allow for greater total biomass and root length per soil volume, contributing to the soil-binding and reduced erosion of grassy ecosystems [78]. While many wild grass species have maximum rooting depths of several meters, these roots are typically allocated exponentially by depth, with $>80\%$ of the total biomass occurring in the top 30 cm of the soil [77,83–85]. These root allocation patterns illustrate a common grass strategy regardless of photosynthetic pathway or evolutionary history; grasses invest biomass toward resource uptake (water and nutrients) in the portion of the soil that experiences pulses in resource availability [86]. This investment strategy often results in periods of high resource uptake in the most superficial layers of the soil profile [87].

Beyond biomass and total length distributions, root anatomical traits are measured to infer strategies associated with resource uptake efficiency vs. avoidance of water stress. Typically, root traits delineate water acquisition strategies facilitating efficient uptake (many large diameter vessels, lower cortex:stele) or avoidance of water stress (fewer smaller diameter vessels and higher t/b) [88], but it's more rare to see species develop strategies based on rapid uptake *and* stress resistance [89]. Root anatomical traits from Panicoideae species growing in situ illustrate that grasses have traits illustrative of safety (thinner, more numerous root conduits), but whole root-system traits illustrative of efficient water transport (higher whole system hydraulic conductance of shallow compared to deeper roots) [89]. This combination of safe transport at the individual root compared to efficient transport across the entire root system may facilitate grasses to rapidly use water when available but tolerate dry soils under rapidly fluctuating environments [90].

Whole-plant anatomy and physiology

A holy grail of trait research is the integration of belowground and aboveground anatomical and physiological traits to explain ecological processes [91]. Using root anatomical trait data from 19 perennial grass species grown under controlled conditions, tissue mass density (dry weight/root volume) was negatively correlated with aboveground relative growth rates [88]. These results suggest that grass species investing in thicker root stele cell walls and a higher proportion of stele in the cross-sectional area have slower growth rates but are less susceptible to drought stress [88]. Conversely, species with high root, xylem, and xylem vessel cross-sectional areas were positively correlated with overall plant height, suggesting that a higher hydraulic capacity to move water supports greater aboveground biomass [88]. Similar results comparing relative growth rates and root anatomy have been reported for 18 C_4 grass species [92]. In a large screening experiment of nearly 400 grass species, C_4 grasses generally had faster growth rates and invested more in root growth during seedling establishment compared with C_3 grasses, facilitated by a higher leaf area to mass relationship, not faster growth per unit leaf area [10]. C_4 grasses can more cheaply produce a similar canopy compared to C_3 , and then utilize additional resources for belowground growth [10,93].

Water-use efficiency

Viewing the process of gas exchange in economic terms, water-use efficiency (WUE) describes the “cost” of water loss per unit of CO_2 “gained” via the stomata. A higher WUE denotes that higher rates of photosynthesis occurred per unit of water lost via leaf transpiration. Theoretically, and when measured under ideal conditions, C_4 grass lineages have higher WUE than C_3 grass species [52,93]. Higher WUE in C_4 grasses arises from the unique cellular arrangement in this photosynthetic pathway. The first carboxylation process performed by the carbonic anhydrase and PEP-C have a very high affinity for CO_2 , more so than the affinity of RuBisCO [94]. As a consequence, the $[CO_2]$ in leaf mesophyll spaces (measured as c_i —the intracellular concentration of CO_2) is considerably lower than the c_i in C_3 species. Because the driving diffusional gradient from atmosphere to intercellular spaces is higher in C_4 grasses, CO_2 enters the leaf more readily, even at smaller stomatal apertures. Thus, the higher WUE in C_4 typically represents less water lost (via stomatal conductance) than increased gains in photosynthesis [52].

WUE is often identified by agronomic breeders as a trait of value for crop improvement programs, and by ecologists as a mechanism explaining greater physiological performance of C_4 grasses during drought. Are the differences in WUE between C_3 and C_4 species manifest when an economical increase in C gains vs. water losses matter most? Results are mixed, varying according to scale of inquiry, environmental conditions, and phylogenetic lineage. When measured at the landscape level using eddy flux, the differences in WUE among grasslands dominated by C_3 and C_4 grass species are insignificant, particularly during drought periods [95]. When leaf-level WUE is assessed among grass lineages in field conditions, the results can be mixed, showing few differences among lineages, or contrasting patterns of WUE within the same growing season [96,97]. One consistent finding from field studies with diverse grass assemblages, the “advantage” of higher WUE in C_4 grass species is muted under drought conditions [52,97,98] Indeed, in response to extended periods of extreme drought, grasslands comprised of both C_3 and C_4 species may actually shift toward C_3 dominance [99,100].

So, how can we explain these paradoxical results, and better understand why C_4 grasses often have lower WUE when water availability is low? One potential answer is evidence when you

consider environmental changes across the growing season. Grassland canopies with continuous cover result in boundary layers with high humidity, efficient gas exchange, and high WUE. But during periods of low water availability and drought, grasslands experience increased air temperatures and increased VPD [101]. During these periods, the advantage of a large boundary layer is lost, individual leaf temperatures spike, and leaf rolling may occur [97]. Early in the season, resource pulses are high, and then water and N limit growth later in the growing season. A growth strategy focused on effective capture of resources when plentiful may be more advantageous than the efficient use of limited water resources later in the growing season. In other words, the advantage of high WUE in C_4 species may result from maximizing growth when conditions are favorable, when high rates of photosynthesis translate to rapid growth and biomass accrual. Lower WUE later in the growing season reflects a strategy of enduring low-water conditions during drought and persisting to the next growing season [97].

Frontiers in grass anatomy and physiology

To date, the field of plant ecophysiology has primarily focused on woody plant species, and a few agronomically important herbaceous species. While many leaf-level physiology and whole-plant processes translate from woody to herbaceous and eudicot to monocot, many others do not [79]. Further ecophysiological study of grasses is both academically and socially relevant, given the unique evolutionary history of Poaceae, and the sweeping significance of wild grasses and grasslands to human livelihoods (see Chapter 28).

Grasses are often viewed as being functionally redundant, and less complex than eudicots, resulting in grass species and grassland ecosystems being overlooked for scientific study, conservation, and inclusion in process-based models forecasting ecosystem changes. While grass species have been studied comparatively more in the northern hemisphere, the majority of grass species and grassland ecosystems are endemic to the southern hemisphere. For these reasons, investigation of grass species anatomy and physiology holds much promise of discovery, particularly in the savannas and grasslands of the southern hemisphere. We encourage the scientific community to prioritize description and discovery of the physiological responses across the broad phylogeny of Poaceae, with a particular focus on the responses of sub-dominant grass species and lineages, especially traits measured across gradients of resource availability in natural conditions.

One of the more exciting frontiers for future research is grass water relations. Some specific areas for research should examine (i) why leaf turgor-loss point is not a strong predictor of drought response/distribution, as it is in eudicots, (ii) the relationship between leaf hydraulic conductance and resistance to embolism, and (iii) why many grass species have deep roots. The myth of functional deep roots in grasses persists in the literature, model analyses, and public-facing dioramas to signify the drought tolerance of grasses [102]. This dogma persists because it is seemingly illogical that grasses would invest resources to build and maintain deep roots that aren't functionally significant. While deep grass roots cannot move sufficient water to maintain transpirational demand for a canopy if surface soils are dry [91], they can still move small amounts of water. During the great droughts of the 1930s and 1940s, John Weaver observed populations of grasses that lay dormant for years and were presumed dead. When the rains returned, individuals recruited from bud banks, not seed [103]. As such, deep rooting in grasses may not matter with regard to surviving an individual year of drought, but may be the lifeline for survival of belowground meristems during extreme events. This presumed mechanism is speculation, as the functional significance of deep roots remains untested. Given the forecast possibility of megadroughts in the future, mechanistic understanding of deep root physiology is warranted.

Finally, we encourage the broader community of grass biologists to continue toward an inclusion of phylogeny in assessments of grass species trait responses. “Lineage functional types” account for shared evolutionary history when assessing trait responses, allowing previous natural history to inform current growth responses to environmental niches [26,29,30]. Further investigations linking anatomy and physiology of the wild grasses including both phylogeny and environmental variation are important for understanding the roles of evolutionary history and ecology as structuring agents of change [60]. These assessments have the potential to provide greater detail for predicting future changes in grasslands undergoing global change.

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