**Title:**

# High silicon concentrations in grasses are linked to environmental conditions and not associated with $C_4$ photosynthesis

**Running title:**

Grass Si levels not tied to $C_4$ photosynthesis

**Authors:**

William H. Brightly[1], Sue E. Hartley[2], Colin P. Osborne[2], Kimberley J. Simpson[2], and Caroline A.E. Strömberg[1]

**Address:**

[1]Department of Biology and the Burke Museum of Natural History and Culture, University of Washington, Box 351800, Seattle WA 98195-1800

[2]Department of Animal and Plant Sciences, University of Sheffield, Sheffield S10 2TN, UK

**Author for correspondence:**

William H. Brightly

Tel: +1 860 480 4705

Email: whbright@uw.edu

**ABSTRACT:**

The uptake and deposition of silicon (Si) as silica phytoliths is common among land plants and is associated with a variety of functions. Among these, herbivore defense has received significant attention, particularly with regards to grasses and grasslands. Grasses are well known for their high silica content, a trait which has important implications ranging from defense to global Si cycling. Here, we test the classic hypothesis that $C_4$ grasses evolved stronger mechanical defenses than $C_3$ grasses through increased phytolith deposition, in response to extensive ungulate herbivory ('$C_4$-grazer hypothesis'). Despite mixed support, this hypothesis has received broad attention, even outside the realm of plant biology. Because $C_3$ and $C_4$ grasses typically dominate in different climates, with the latter more abundant in hot, dry regions, we also investigated the effects of water availability and temperature on Si deposition. We compiled a large dataset of grasses grown under controlled environmental conditions. Using phylogenetically informed generalized linear mixed models and character evolution models, we evaluated whether photosynthetic pathway or growth condition influenced Si concentration. We found that $C_4$ grasses did not show consistently elevated Si concentrations compared with $C_3$ grasses. High temperature treatments were associated with increased concentration, especially in taxa adapted to warm regions. Although the effect was less pronounced, reduced water treatment also promoted silica deposition, with slightly stronger response in dry habitat species. The evidence presented here rejects the '$C_4$-grazer hypothesis.' Instead, we propose that the tendency for $C_4$ grasses to outcompete $C_3$ species under hot, dry conditions explains previous observations supporting this hypothesis. These finding also suggest a mechanism via which anthropogenic climate change may influence silica deposition in grasses and, by extension, alter the important ecological and geochemical processes it affects.

**Keywords:** $C_4$ photosynthesis, grass, grassland, herbivore, phytolith, silicon

## INTRODUCTION:

Phytoliths are microscopic bodies of solid, amorphous silica ($SiO_2*nH_2O$) that are deposited in plant tissues, and represent the major sink of silicon (Si) within most plants (Richmond and Sussman, 2003; Piperno, 2006). Members of all major plant lineages produce phytoliths, although the degree of deposition differs substantially between taxa (Hodson et al., 2005; Piperno, 2006; Katz, 2015; Trembath-Reichert et al., 2015; Strömberg et al., 2016). Several groups typically accumulate high concentrations of phytoliths, with grasses (Poaceae) being a particularly prominent and well-studied example (Jones and Beavers, 1964; Kaufman et al., 1985; Sangster et al., 2001; Hodson et al., 2005). Within grasses, silicon (deposited in phytoliths or as a bio-active element) has been linked to various functions, including increased pathogen resistance (Datnoff et al., 1997; Fauteux et al., 2005), as well as the alleviation of heavy metal toxicity (Sangster et al., 2001; Imtiaz et al., 2016), drought stress (Hattori et al., 2005; Kaya et al., 2006; Pei et al., 2010; Meunier et al., 2017), and salt stress (Imtiaz et al., 2016). However, it is the hypothesized role of phytoliths as an herbivore deterrent that has received the most attention.

A large body of work examining the relationship between grass phytolith deposition and herbivore feeding behavior has shown that grasses growing in heavily grazed areas usually have elevated silica concentrations (McNaughton and Tarrants, 1983; McNaughton et al., 1985; Cid et al., 1989). Defoliation by herbivores can also lead to the induction of silica deposition, although the effect is frequently delayed and sensitive to the type and amount of damage (Massey and Hartley, 2006; Reynolds et al., 2012; Soiniene et al., 2013; Huitu et al., 2014; Quigley and Anderson, 2014; Hartley and DeGabriel, 2016). Whether inducible or constitutive, high silica concentrations significantly alter feeding behavior in a variety of herbivores. Laboratory experiments have shown that insects and small mammalian herbivores select forage based upon silica content (Gali-Muhtasib et al., 1992; Massey and Hartley, 2006; Massey et al., 2007), and experience substantial negative fitness effects when fed a high silica diet (Massey et al., 2006; Massey and Hartley, 2006; Massey and Hartley, 2009; Reynolds et al., 2009; Huitu et al., 2014; Calandra et al., 2016).

The high degree of silicification in many grasses is an important and often underappreciated ecological aspect of the communities where they constitute the defining vegetative component (e.g., Street-Perrot and Barker, 2008; Song et al., 2017). Grasslands are an important component of the global Si cycle, and their Neogene expansion appears to have caused important changes to its structure (Kidder and Gierlowski-Kordesch, 2005; Street-Perrot and Barker, 2008; Conley and Carey, 2015). Over geologic timescales, Si cycling is closely linked to the global carbon (C) cycle via silicate weathering, which draws down $CO_2$ from the atmosphere, which is ultimately incorporated in carbonate minerals. This process plays a central role in controlling long term trends in the concentration of atmospheric $CO_2$ (Street-Perrot and Barker, 2008). Over shorter time scales, carbon sequestration by Si accumulating producers, like grasses, and their impact on Si fluxes and, thus weathering rates, are also key links between these two geochemical cycles (Conley, 2002; Street-Perrot and Barker, 2008; Conley and Carey, 2015; Song et al., 2017). Beyond their role in global nutrient cycles, grass-dominated habitats are ecologically, economically, and culturally important, covering more than 40% of Earth’s land surface, supporting diverse and charismatic faunal communities, and providing many other important ecosystem services (Shantz, 1954; Gibson, 2009). Despite their importance, grasslands and savannas are frequently converted for anthropogenic use (e.g., agriculture). In North America, alone, native tall-grass prairie has been reduced to approximately 10% of its original extent, with an overall 70% reduction in the native grasslands of the Great Plains (Samson et al., 2004). These habitats consequently possess a higher Conservation Risk Index than any other terrestrial biome (Gibson, 2009). Nevertheless, their importance as conservation targets is often misunderstood (Griffith et al., 2017; Veldman et al., 2019. High silica concentrations in grasses have been invoked by hypotheses attempting to explain the predominance of hypsodonty (i.e., high crowned cheek teeth) in mammalian herbivores of modern, grass-dominated ecosystems. This pattern has often been interpreted as representing an adaptation for coping with increased levels of tooth-wear resulting from a grass-rich, and therefore silica-rich diet (Stirton, 1947; Stebbins, 1981; McNaughton and Tarrants, 1983; Flynn et al., 2003). However, recent paleontological evidence shows a temporal mismatch between the appearance of open grass-dominated habitats and the evolution of this putative adaptation for grazing, which has cast doubt upon the role of grass phytoliths in the evolution of hypsodonty, instead implicating other, exogenous abrasives (such as windblown dust; Jardine et al., 2012; Strömberg et al., 2013; Dunn et al., 2015; Semprebon et al., 2016, 2019). Silica in grasses also appears to be relatively ineffective at preventing feeding in large mammals in comparison to its deterrent effect on small mammals and insects (Cid et al., 1989; Massey et al., 2009; Hartley and DeGabriel, 2016; Strömberg et al., 2016).

Today, the most conspicuous habitats with abundant large grazers (e.g., Serengeti) are grasslands and savannas dominated by grasses possessing the $C_4$ photosynthetic pathway. $C_4$ photosynthesis describes a coordinated suite of anatomical and biochemical modifications to the ancestral $C_3$ photosynthetic pathway, that concentrate $CO_2$ around the key photosynthetic enzyme RuBisCO. Doing so minimizes the energetically costly process of photorespiration, which is initiated when RuBisCO accepts $O_2$ (rather than $CO_2$) as a substrate (Sage and Monson, 1999; Gibson, 2009). $C_4$ photosynthesis, allows for greater photosynthetic efficiency under certain environmental conditions, most notably in habitats that are hot (RuBisCo's oxygen affinity is temperature dependent) and dry (plants are able to maintain a lower stomatal conductance for a given photosynthetic output, thus limiting water loss), though C4 plants are not restricted to these habitats (Ehleringer, 1978; Ehleringer et al., 1997; Sage and Monson, 1999; Gibson, 2009; Osborne and Freckleton, 2009; Watcharamongkol et al., 2018). Because $C_4$ grasses are dominant in many heavily grazed habitats, and because their dominance can be dependent upon grazers (Owen-Smith, 1989; Sage, 2001; Bouchenak-Khelladi et al., 2009), some authors have hypothesized that $C_4$ grasses have experienced stronger selection for this defense than $C_3$ lineages, resulting in higher silica concentrations in the former (Bouchenak-Khelladi et al., 2009). A number of observations are apparently consistent with this hypothesis (hereafter referred to as the '$C_4$-grazer hypothesis'). Early studies investigating the role of silica in grass-herbivore dynamics did observe high silica concentrations in many of the $C_4$ grasses native to these habitats (e.g., McNaughton and Tarrants, 1983; McNaughton et al., 1985). Investigations of tooth wear in ungulates have also noted differences in wear patterns between grazers of $C_4$ dominated regions and those of other herbivores (Soulonias and Semprebon, 2002). The '$C_4$-grazer hypothesis' was also likely influenced by the observation that $C_4$ grasses are generally less digestible than $C_3$ grasses, although this disparity is primarily related to differences in leaf anatomy, rather than silica concentrations (e.g., Caswell et al., 1973; Caswell and Reed, 1976; Wilson and Hattersley, 1983; Wilson et al., 1983; Heidorn and Joern, 1984; Bernays and Hamai, 1987). However, the few studies that have directly tested the '$C_4$-grazer hypothesis' have returned mixed results. Bouchenak-Khelladi et al. (2009) recovered a trend towards higher silica concentrations among $C_4$ grass lineages, particularly within the Aristidoideae and Chloridoideae subfamilies, while McInerney et al. (2011) and Strömberg et al. (2016) found no differences between $C_3$ and $C_4$ lineages. To our knowledge, no other mechanism has been proposed to explain potential differences in silica content based upon photosynthetic pathway.

One drawback, shared by all of the studies testing the '$C_4$-grazer hypothesis', is a lack of robust control for growth conditions (but see Hodson et al., 2005 and McInerney et al., 2011 for methods intended to correct for this). This is an important consideration, because environmental conditions such as soil type, nutrient availability, temperature, and water availability all impact silica uptake and deposition (Deren et al., 1992; Soininen et al., 2013; Hartley and DeGabriel, 2016; Quigley et al., 2020). Temperature and water availability are of particular interest because $C_3$ and $C_4$ grasses tend to dominate in regions that differ with respect to these two climatic variables, with $C_4$ grasses being more abundant in hot and (seasonally) dry areas (Teeri and Stowe, 1976; Ehleringer, 1978; Ehleringer et al., 1997; Sage and Monson, 1999; Edwards and Still, 2008; Gibson, 2009; Osborne and Freckleton, 2009). Previous work has suggested that drier conditions tend to promote silica deposition (Johnston et al., 1967; Blecker et al., 2006; Power et al., 2016; Issaharou-Matchi et al., 2016; Quigley et al., 2017), and temperature appears to have a positive relationship with silica deposition, although this relationship is not always consistent (Barber and Shone, 1966; Mitani and Ma, 2005; Johnson and Hartley, 2018; Johnson et al., 2019). However, neither of these two effects has been examined in more than a handful of species.

Using a new dataset compiled from grasses grown under controlled conditions in growth chambers (Atkinson et al., 2016), we examine whether **(1)** photosynthetic pathway influences the leaf concentration of Si (as a proxy for silica), with the prediction that $C_4$ grasses accumulate more Si than $C_3$ lineages. We also examine whether **(2)** adaptation to grassland habitats influences Si concentration (hereafter the ‘grasslands hypothesis’), with the prediction that taxa typically occupying grassland and savanna habitats deposit more Si than grasses restricted to other habitat types (e.g., forest understory). This represents a generalization of the ‘$C_4$-grazer hypothesis’ that accommodates paleontological evidence that the habitat types in which many grazing ungulates emerged were dominated by $C_3$ rather than $C_4$ grasses for most of their histories (Strömberg, 2011). Finally, using plants grown under different temperature and watering regimes, we test whether **(3)** water availability and temperature affect the level of Si deposition, and whether the temperature and water conditions to which species are adapted impact these responses.

## MATERIALS AND METHODS:

### Sample Collection:

Leaf material for use in elemental analyses was sourced from grasses grown in growth chambers at the University of Sheffield as part of the study by Atkinson et al., (2016), which was focused on differences in growth patterns between $C_3$ and $C_4$ taxa. Individuals sampled in this study were grown under three different treatments, hereafter referred to as standard, reduced temperature, and reduced watering treatments. Standard growth conditions were a 14-hour day with a daytime temperature of 30°C and a nighttime temperature of 25°C, comparable to growing season temperatures in some tropical savannas (e.g., Darwin, Australia or Campo Grande, Brazil; Global Climate Normals 1961-1990). In the reduced temperature treatment the daytime and nighttime temperatures were reduced to 20°C and 15°C respectively, conditions approximately equivalent to growing season temperatures in parts of northern Europe, albeit with a smaller range in daily temperature (Global Climate Normals 1961-1990). Under all but the reduced watering treatment, plants were given a non-limiting supply of water, with plants watered twice daily (Atkinson et al., 2016). Under the reduced watering treatment, this was reduced in frequency to twice a week. All plants were provided with a non-limiting nutrient supply, via the application of Long Ashton nutrient solution (Hewitt, 1966) two times per week. Plants were grown in a 90/10 vermiculite/sand mixture, which was the sole source of silicon available to plants (Atkinson et al., 2016). Though the nutrient solution did not provide any Si, Long Ashton is slightly acidic (~4.5), and pH does influence Si availability (Imtiaz et al., 2016; Quigley et al., 2017). However, this trait does not appear to influence the pH of the actual soil solution in the root zone of growing plants (Smith et al., 1983).The reduced temperature and watering treatments were conducted subsequent to the standard treatment using the same growth chambers. Unfortunately, because of the large number of plants and limited space in growth chambers (see Atkinson et al., 2016), it was not feasible to replicatethese two environmental treatments. Additional treamtments that examined the combined effects of temperature and water availability, or included longer growth periods were also infeasible for these reasons.. From here on we discuss the effects of temperature and water treatments, recognizing that other, unmeasured environmental variables may also have differed between them.

Plants were harvested, dried, and leaf material collected. Whenever possible, the entire lamina, or the laminae of multiple leaves, was collected. This ensured that concentration estimates were robust to problems associated with heterogeneity in phytolith distribution across the lamina (Sangster, 1977; Hodson and Sangster, 1988; O'Reagain and Mentis, 1989; de Melo et al., 2010), which may confound other methods of quantifying Si deposition (e.g., Bouchenak-Khelladi et al., 2009; Supporting Information, Methods S1). From standard growth conditions, we sampled 274 individuals, representing 124 species, 69 genera and 20 tribes. This sample included at least six lineages that independently evolved C4 photosynthesis (Aliscioni et al., 2012; Spriggs et al., 2014), but excluded the subfamilies Arundinoideae, Bambusoideae, and the grade of early-diverging grasses (Anomochloideae, Pharoideae, Pueliodeae). However, as plants in these subfamilies all differ substantially in habit from the grasses that are the primary subject of the 'C4-grazer hypothesis', their exclusion is not seen as a major bias. A subset of the species in the standard treatment dataset was also sampled from the reduced temperature (82 individuals, 36 species), and reduced watering treatments (134 individuals, 53 species). Sample sizes were largely driven by what material was available in sufficient quantities for elemental analysis (i.e., ≥ 100 mg), but was comparable in number of taxa to previous studies, although differing slightly in coverage (Supporting Information Methods S1). In the reduced temperature treatment, three species (*Brachypodium distachyon* [L.] P. Beauv., *Poa arida* Vasey, and *Puccinellia distans* [Jacq.] Parl.) lacked counterparts from the standard dataset, while two species (*Brachypodium distachyon* and *Puccinellia distans*) from the reduced watering treatment lacked counterparts in the standard dataset. In both cases this was because sufficient material could not be collected from individuals grown under standard conditions.

Plants used in this study were harvested between one and five weeks after germination to allow for the determination of growth rates across the study species (the central focus of the original study; Atkinson et al., 2016). This setup, coupled with the sampling goals of our study (i.e., large number of species, multiple individuals per species) meant that we ultimately sampled leaves from plants of a variety of ages. Sampled individuals ranged in age from 10 to 60 days post germination (median 38), with the vast majority (83%) between 30 and 45 days (Supporting Information Table S1). There was also substantial variation in total dry mass of sampled plants, (0.03 to 9.71 grams, median 0.53), although only a small proportion of this variation could be attributed to differences in age (Supporting Information, Methods S1).

**Silicon Concentration Analysis:**

Estimates of bulk Si concentration were obtained using a portable X-ray fluorescence spectrometer (P-XRF) at the University of York, UK, following the methods of Reidinger et al. (2012). XRF provides accurate estimates of the concentration of elemental silicon (Reidinger et al., 2012), here used as a proxy for the concentration of silica within the leaf. While silicon may exist in other forms in plant tissues, it is primarily deposited as silica phytoliths (Richmond and Sussman, 2003; Hartley et al., 2015; Hartley and DeGabriel, 2016; Imtiaz et al., 2016), the concentration of which is strongly correlated with the abrasiveness of forage (Massey and Hartley, 2006; Massey et al., 2006; Massey et al., 2007; but also see Hartley et al., 2015). In addition, XRF provides comparable estimates, with the benefit of being faster, safer, and often more precise, than traditional gravimetric approaches for estimating silica concentration (Reidinger et al., 2012). Prior to analysis, dried leaf material was homogenized using a ballmill (Qiagen TissueLyser II), and pressed into 13 mm pellets using a manual hydraulic press (Atlas 15T; Reidinger et al., 2012) at 11 tons. To partially account for *u*-Drift in the instrument (i.e., variation in measured response between consecutive runs using identical parameters; Johnson, 2012; Reidinger et al., 2012), each pellet was analyzed twice, approximately 30 minutes apart, with a reading taken from each side of the pellet. Si concentrations for individuals were obtained by averaging these values. For species represented by more than one individual, intraspecific variation in Si concentration was quantified using the coefficient of variation (CV) of untransformed Si concentration values.

**Classification of Variables:**

Species were classified as either $C_3$ or $C_4$ (Osborne et al., 2014). Of the 124 species from the standard conditions dataset, 34 were $C_3$, and 90 were $C_4$. In the reduced temperature dataset, there were 19 $C_3$ species and 17 $C_4$ species. The reduced watering dataset contained 20 $C_3$ species and 33 $C_4$. We also considered several variables related to each species' "selective environment" (i.e., the conditions in which each species typically occurs; Brandon, 1990). These were habitat type (grassland/savanna, other), habitat wetness (wet, dry, broad), and the mean annual precipitation (MAPs) and mean annual temperature (MATs) averaged across each species' range. To record MAPs and MATs, species occurrence data were downloaded from the Global Biodiversity Information Facility (GBIF.org) using the *rgbif* package (v. 1.3.0; Chamberlain et al., 2017) in the R software environment (v. 3.6.1; R Core Team, 2019). Records that were deemed unreliable were excluded from this dataset (Supporting Information Methods S2) using tests available in the R package *CoordinateCleaner* (v 2.0-11; Zizka et al., 2019). For each observation, MAT and MAP were extracted from WorldClim 2 climate surfaces (Fick and Hijmans, 2017) and then averaged to the species level. Classification of habitat type and habitat wetness was completed via a literature survey (Supporting Information Methods S2). Habitat wetness was based upon the local soil water conditions favored by each taxon; for example, a species could be classified as "wet" despite occupying a region with a low MAP (i.e., restricted to wetlands in a dry region).

**Statistical Analysis:**

Statistical analysis was completed in the R software environment (v. 3.6.1; R Core Team, 2019). Silicon concentration was noticeably right hand skewed, and was therefore natural log-transformed prior to all analyses, unless stated otherwise. All phylogenetic comparative analyses employed the maximum credibility tree of Atkinson et al. (2016). The phylogenetic signal of Si concentration was measured with Pagel's $\lambda$ (Pagel, 1999) in the package *phytools* (v. 0.6.99; Revell, 2012). The effects of all predictors were tested by fitting multivariate generalized linear mixed models (glmm) using Markov chain Monte Carlo (MCMC) sampling, as implemented in the package *MCMCglmm* (v. 2.29; Hadfield, 2010). Phylogenetic information was incorporated by including an inverted phylogenetic covariance matrix as a random effect in each model. All other variables were included as fixed effects. Models were given weakly informative priors, and, for each, a single chain was run for a total of 100,000 generations, sampling every tenth generation, and discarding the first 3,000 generations as a burn-in. Trace plots and effective sample sizes were inspected to ensure adequate convergence upon the posterior. For each model, the coefficient of determination of the fixed effects, and its 95% confidence interval, was obtained following the method of Nakagawa and Schielzeth (2013).

We tested whether plant age and/or mass (the latter natural log transformed) affected Si concentration in each dataset, and included them as covariates in subsequent models, where appropriate (see results). The effect of temperature treatment was tested in taxa grown under both standard and reduced temperature conditions, while the effect of watering treatment was tested in taxa grown under both standard and reduced watering conditions. We tested for interactions between temperature condition and MATs, and watering condition and both MAPs and habitat wetness to assess whether the conditions to which species were adapted modified their response to changes in growth condition. The '$C_4$-grazer' and 'grasslands' hypotheses were tested in all three growth treatments, with photosynthetic pathway and habitat type (respectively) as fixed effects. In all three treatment groups, we also tested a model including all five predictors (photosynthetic pathway, habitat type, MATs, MAPs, habitat wetness) as fixed effects.

**Character Evolution Model Fitting:**

Five models of character evolution were fit to species average Si concentration using the *OUwie* package (v. 1.5; Beaulieu and O'Meara, 2016). For this analysis, we treated $C_3$ and $C_4$ taxa as occupying separate evolutionary regimes (where possible). The models compared were a single rate Brownian Motion (BM) model (BM1), a multi-rate BM model (BMS) with different rates for $C_3$ and $C_4$ lineages, an Ornstein Uhlenbeck (OU) model with a single universal optimum (OU1), an OU model allowing for different optima for $C_3$ and $C_4$ lineages (OUM), and an OU model allowing for differences in optima and rate in $C_3$ and $C_4$ lineages (OUMV). These same models were fit using habitat type to define two evolutionary regimes (grassland/savanna, other). Note that, for the latter analysis, OUMV models were discarded as not all eigenvalues from the decomposition of the Hessian matrix were positive, indicating that parameter estimates were unreliable. For the same reason, OU models allowing the alpha parameter to vary between regimes (i.e., OUMA and OUMVA) were excluded from our analyses.

Prior to analysis, Si concentration values were shifted (i.e., Si% + 1) before natural log-transformation (excluding negative values increased model stability). Evolutionary regimes at internal nodes were inferred based on the results of ancestral state estimation of photosynthetic pathway and habitat type, which was completed via stochastic mapping (Supporting Information Methods S3; Nielsen, 2002; Huelsenbeck et al., 2003) in the *phytools* package (v. 0.6.44; Revell, 2012). After models had been fit, the maximum likelihood parameter values were extracted and used to perform 1,000 parametric bootstrap replicates of each model. Weighted Akaike Information Criterion (AIC) values were calculated for models with the R package *MuMIn* (v. 1.42.1; Barton, 2018) and used to obtain the weighted average (and its standard deviation) for each model parameter from the bootstrap output for each of our predefined evolutionary regimes. These were subsequently used to compare regimes. Model fitting was only carried out using the largest of our three datasets (i.e., standard treatment) due to sample size limitations, OU models being especially sensitive to small sample sizes (Cooper et al., 2016).

## RESULTS:

### Patterns of Si Concentration:

Silicon concentration estimates showed a large degree of variation under all three treatments, with several taxa showing very high concentrations, especially when considering the relatively young age of plants. Under standard conditions, Si concentration ranged from 0.2 to 5.2%, with a mean of 1.1%. The reduced watering treatment showed a similar range in values (0.3% to 4.6%) although the mean value was slightly higher (1.3%). In contrast, the higher Si concentrations observed under standard and reduced watering conditions were absent in the reduced temperature treatment (0.2 to 1.4%), which resulted in a lower mean concentration (0.7%). In general, taxa showing high Si concentrations under one treatment showed high Si concentrations under other treatments, although; this pattern was less pronounced in the reduced temperature treatment (Supporting Information Notes S1).

### Sample Collection and Phylogenetic Signal:

Under standard conditions, plant age and mass both showed a positive relationship with Si concentration (age: $p = 0.003$, mass: $p = 0.013$), although the combined effects only explained a small proportion of the variation ($R^2 = 0.026$ [95% CI: 0.008, 0.048]). The effect of plant mass was also significant under reduced temperature ($p = 0.032$), although this was only apparent when age ($p = 0.075$) was also included, with neither significant on its own (age: $p = 0.41$, mass: $p = 0.63$). Together, age and mass explained only a small proportion of the variation in Si concentration, although the coefficient of determination from the posterior sample varied quite a bit ($R^2 = 0.055$ [95% CI: << 0.001, 0.129]). Neither mass nor age were significant under reduced watering (age: $p = 0.86$, mass: $p = 0.63$). Mass and age were therefore included as covariates in analyses using the standard and reduced temperature datasets, and discarded for those using the reduced watering dataset.

Among species grown under both standard and reduced temperature treatments (i.e., those for which the effect of temperature was assessed) only plant mass was significant (age: $p = 0.21$, mass: $p = 0.003$), although its effect disappeared when other predictors were included in the model. For species grown under both standard and low watering treatments, age ($p = 0.003$) and mass ($p = 0.017$) individually showed a significant effect, although the effect of mass was not significant when age was accounted for ($p = 0.33$). However, age on its own did not explain much of the variation in Si concentration ($R^2 = 0.013$ [95% CI: 0.013, 0.028]). Nevertheless, plant age was included as a covariate for analyses assessing the effects of watering changes; mass was discarded.

Tests of phylogenetic signal returned significant results under standard ($\lambda = 0.56$, $p < 0.001$) and reduced watering conditions ($\lambda = 0.93$, $p < 0.001$). Phylogenetic signal was strongest under reduced watering conditions, with a value of $\lambda$ close to the expectation under a Brownian

Motion model of evolution (i.e., λ = 1). Under reduced temperature conditions, however, the estimated value of λ was lower than in the other two datasets, and not significantly different from zero (λ = 0.29, $p$ = 0.07).

**Effect of Photosynthetic Pathway and Selective Environment on Si Concentration:**

Under standard conditions (Fig. 1), the effects of photosynthetic pathway ($p$ = 0.22) and habitat type ($p$ = 0.29) on Si concentration were not significant. However, in models including all of our predictors, the effect of MATs was significant ($p$ = 0.019), with species from warmer regions having higher Si concentrations. A model including MATs as the only fixed effect (in addition to age and mass) supported the same effect ($p$ = 0.014). However, in this model, the fixed effects explained only a small portion of the total variation in Si concentration ($R_2$ = 0.043 [95% CI: 0.014, 0.077]).

Under reduced temperature conditions, the effect of photosynthetic pathway was non-significant ($p$ = 0.65), as was the effect of habitat type ($p$ = 0.93). Results under reduced watering conditions were similar, with photosynthetic pathway ($p$ = 0.081) and habitat type ($p$ = 0.111) non-significant. Under neither reduced temperature nor reduced watering conditions was any of our five predictors (photosynthetic pathway, habitat type, MATs, MAPs, habitat wetness) found to be significant.

**Character Evolution Model Fitting:**

When evolutionary regimes were defined by photosynthetic pathway, three models contributed substantially to our final weighted parameter values, with OU models heavily favored over Brownian Motion (weighted AIC values - BM1< 0.01, BMS< 0.01, OU1= 0.36, OUM= 0.30, OUMV= 0.34). Brownian Motion represents random evolution of a character while OU models modify this so that trait values are drawn to an "optimum" value. The better fit of OU models to our data, however, may be related to other factors (e.g., intraspecific variation) causing our data to deviate from a strict Brownian model, rather than evidence that Si concentration evolved following an OU model (Cooper et al., 2016). Theta ($\theta$) represents the "optimum" evolutionary value of a trait in an OU model (i.e., the value toward which species are pulled), with the OUM and OUMV models allowing differences in this parameter between $C_3$ and $C_4$ regimes. Weighted $\theta$ values for $C_3$ and $C_4$ regimes were similar ($C_3 = 0.54 \pm 0.19$, $C_4 = 0.58 \pm 0.22$), with substantial overlap in the distribution of values between the two regimes (Fig. 2). Sigma squared ($\sigma_2$) values represent the rate of change in a trait; of the models applied here, the BMS and OUMV models allow variation in $\sigma_2$ values between regimes. Final, weighted $\sigma_2$ values were lower in $C_4$ taxa ($C_3 = 18.1 \pm 23.1$, $C_4 = 14.8 \pm 19.4$), although there was again substantial overlap in the distribution of values between regimes (Fig. 2). Alpha ($\alpha$) represents the strength with which values are drawn towards the optimum in each regime. Because OUMA and OUMVA models were unstable (see Methods), final $\alpha$ values for the $C_3$ and $C_4$ regimes were identical ($C_3 = 123.1 \pm 145.3$, $C_4 = 123.1 \pm 145.3$).

When regimes were defined based on habitat type, the OU1 and OUM models were favored, with BM models again being rejected (BM1< 0.01, BMS< 0.01, OU1= 0.73, OUM= 0.27). However, in contrast to our photosynthetic pathway results, which did not favor any single model, we found that the OU1 model had weighted AIC values much higher than any other model. This model treats grassland and non-grassland taxa as belonging to a single, global regime. As a consequence, weighted $\theta$ (grassland = $0.50 \pm 0.13$, non-grassland = $0.51 \pm 0.14$), $\sigma_2$ (grassland = $30.5 \pm 43.5$, non-grassland = $30.5 \pm 43.5$), and $\alpha$ (grassland = $114.1 \pm 139.4$, non-grassland = 114.1 ± 139.4) parameter values were similar for both grassland and non-grassland taxa, with distributions again showing substantial overlap (Fig. 2).

**Growth Conditions Effect on Si Concentration:**

Most species (31/36) grown in the reduced temperature treatment tended to have lower average Si concentrations ($p < 0.001$) than they had under standard conditions, with a median increase of 55% from reduced temperature to standard conditions (Fig. 3). The effects of temperature treatment explained a greater proportion of the total variation in Si concentration than plant age or photosynthetic pathway ($R_2 = 0.085$ [95% CI: 0.032, 0.146]). There was also a significant interaction between the effect of temperature treatment and $MAT_S$ ($p = 0.015$), with larger Si concentration differences between standard and reduced temperature plants in species adapted to warmer climates (Fig. 4). In models including this interaction, the effect of $MAT_S$ ($p < 0.001$) remained significant, although the effect of temperature treatment was no longer significant on its own ($p = 0.89$), suggesting that elevated concentration in species of warm regions under standard conditions were largely driving this effect. Fixed effects combined in this model to explain a considerable amount of the total variation in Si concentration ($R_2 = 0.194$ [95% CI: 0.082, 0.316]).

The reduced watering treatment was associated with higher Si concentrations in most of species (39/53), with a median increase of 22% in average Si concentration (Fig. 3). This effect was statistically significant ($p < 0.001$), although age and watering treatment explained only a small amount of the variation in Si concentration ($R_2 = 0.036$ [95% CI: 0.015, 0.061]). There was no significant interaction between watering treatment and $MAP_S$ ($p = 0.66$). However, there was a weak interaction with habitat wetness (dry: $p = 0.044$; wet: $p = 0.071$), such that species adapted to dry habitats showed a slightly larger change in Si concentration under reduced watering than species of other habitats (Fig. 4). The effect of watering treatment on its own was not significant ($p$ = 0.101) when accounting for this interaction. Fixed effects in this model explained a small proportion of the total variation in Si concentration ($R_2$ = 0.049 [95% CI: 0.022, 0.082]).

**Intraspecific Variation in Si Concentration:**

In all three datasets, Si concentration varied substantially within species, with median species CV values of 17%, 19%, and 20% for the standard, reduced temperature, and reduced watering datasets respectively. Several species had intraspecific CV values comparable to, or exceeding the interspecific CV values of each dataset; however, these values are of questionable accuracy given the small sample sizes in many taxa. Small sample size promotes more extreme CV values, which don't accurately reflect the true level of variation within a species. However, the median values are unlikely to overestimate the level of variability in Si concentration, and may in fact underestimate it (Supporting Information Notes S2). There was relatively little overlap between datasets as to which species varied most in Si concentration. Only four species (*Avena sativa* L., *Bothriochloa barbinodis* [Lag.] Herter, *Digitaria setigera* Roth, and *Setaria viridis* [L.] P. Beauv.) surpassed the 75th percentile in more than one dataset, and several taxa with high intraspecific CV values in one dataset fell below average in the others (e.g., *Eragrostis tef* [Zuccagni] Trotter, *Vulpia myuros* [L.] C.C. Gmel.).

## DISCUSSION:

### Evolution of Si Defenses in $C_4$ Grasses:

The idea that $C_4$ grasses accumulate more silica than $C_3$ grasses appears to be relatively widely held, despite only mixed support in the literature (Kaufman et al., 1985; Bouchenak-Khelladi et al., 2009; McInerney et al., 2011; Strömberg et al., 2016). In this study, we did not find any strong evidence to suggest that Si concentration differed systematically between $C_3$ and $C_4$ grasses grown under common environmental conditions. While some $C_4$ taxa have high Si concentrations, this trait apparently evolved multiple times in both $C_3$ and $C_4$ lineages (Fig. 1). The idea central to the '$C_4$-grazer hypothesis', that $C_4$ grasses experience disproportionately high grazing pressures, stems from the predominance of $C_4$ grasses in habitats currently sustaining large populations of mammalian grazers (e.g., McNaughton, 1976; Bouchenak-Khelladi et al., 2009; Hempson et al., 2015), where defoliation levels exceed those of most $C_3$ dominated habitats (Sage and Monson, 1999). However, current paleontological consensus indicates that the earliest grass-dominated habitats in many regions consisted primarily of $C_3$ grasses, which were only later replaced by $C_4$-dominated savannas and grasslands (Jacobs et al., 1999; Edwards et al., 2010; McInerney et al., 2011; Strömberg, 2011). These $C_3$-dominated habitats were also inhabited by diverse herbivore communities, including herding ungulates that likely fed on grasses (MacFadden, 1992; Janis et al., 2000; 2004; Mihlbachler et al., 2011; Semprebon et al., 2016; 2019). The modern association between $C_4$-dominance and abundant large grazers, therefore, does not reflect historic patterns (Strömberg, 2006; 2011). The emphasis that the '$C_4$-grazer hypothesis' places on large mammals is also problematic. Compared to insects and small mammals, silica content does not consistently influence forage selection in large mammalian herbivores, nor does it clearly affect their fitness (Cid et al., 1989; Massey et al., 2009; Erickson, 2013; Hartley and DeGabriel, 2016; Strömberg et al., 2016). It is thus unlikely that grasses would respond to the proliferation of large grazers by increasing Si concentration.

Environmental conditions exerted a significant influence on Si concentration, with hot and dry environmental treatments promoting elevated Si concentrations. Given that $C_4$ taxa tend to be most abundant in hot, dry regions (Edwards and Still, 2008; Osborne and Freckleton, 2009), it is possible that previous reports of higher concentrations in $C_4$ grasses (Bouchenak-Khelladi et al., 2009) reflect phenotypic plasticity, instead of selection. Among $C_4$ grasses, Bouchenak-Khelladi et al. (2009) identified the Aristidoideae and Chloridoideae as showing pronounced increases in phytolith deposition. These subfamilies in particular are typical of hot and dry environments (Gibson, 2009; Edwards and Smith, 2010; Visser et al., 2012; Visser et al., 2014).

Overall, the available evidence leads us to reject the '$C_4$-grazer hypothesis.' Even excluding the data presented here, it is consonant with neither recent ecological work nor current paleontological consensus. Given our results, we believe that climatic lineage partitioning may offer a more credible explanation for previous positive results.

The hypothesis that species occupying grass-dominated habitats may experience selection for stronger silica-based defenses (the 'grasslands hypothesis') cites the same mechanism of strong herbivore pressure in grassland environments as the '$C_4$-grazer hypothesis', but relaxes the requirement that the targeted grasses possess the $C_4$ photosynthetic pathway. This hypothesis is therefore more consistent with recent work demonstrating that Earth's grasslands were $C_3$ dominated for most of their histories. The lineages that dominated early $C_3$ grasslands are also still important in many temperate grassland communities (Elias, 1942; Thomasson, 1985; Strömberg, 2005; 2011), potentially conserving the adaptive outcome of these selective pressures in the form of increased silica levels. However, our results did not provide any support for the 'grasslands hypothesis.'

Both the ‘$C_4$-grazer’ and ‘grassland’ hypotheses assume that grasses in grasslands and savannas experience higher herbivore pressure, and thus stronger selection for silica defenses, than grasses found in other ecosystems. While this seems intuitive, to our knowledge it has never been tested directly. Ecological evidence does suggest that more abundant or apparent plants (i.e., grasses surrounded by grasses) often experience higher herbivory, and are thus better defended (e.g., Root, 1973; McNaughton, 1978; Landa and Rabinowitz 1983; McLain and Shure, 1990). However, this is not always the case (e.g., Cates, 1981; Bach, 1988; Barbosa *et al.*, 2009). Furthermore, it is not sufficient that grasses experience higher herbivore pressure in grasslands; they must also experience it from herbivores for which silica is an effective defense. One potential explanation for our results is therefore that the assumption of higher herbivore pressure in grassland ecosystems (by silica-deterred herbivores), made by both hypotheses, is (and/or was) not met.

**Impacts of Environmental Treatments on Si Deposition:**

When other factors are held constant, hot, dry conditions appear to promote the highest Si concentrations in most of the species included in this study. Previous work has shown both water availability and temperature to affect the uptake and deposition of Si (Barber and Shone, 1966; Johnston et al., 1967; Ma et al., 2002; Mitani and Ma, 2005; Blecker et al., 2006; Power et al., 2016; Issaharou-Matchi et al., 2016; Quigley et al., 2017; Johnson and Hartley, 2018; Quigley et al., 2020). These effects, however, are not always consistent. For example, Johnson and Hartley (2018) found mixed responses to an increase of 4 °C among eight Australian grasses, with only three showing a significant effect. The consistency of our results may derive from a larger temperature difference (10 °C) between treatments.

Several studies have demonstrated apparently temperature-dependent changes in the effectiveness of the machinery involved in active uptake of silicic acid (the form of Si taken up by plants) (although see Mitani et al., 2008), but using temperature changes far exceeding those employed here, with low temperatures near freezing (Barber and Shone, 1966; Ma et al., 2002; Mitani and Ma, 2005). It is unclear whether a 10 °C reduction in temperature, with a minimum temperature of 15 °C, would be enough to lower uptake rates through this mechanism alone. Temperature-driven changes in transpiration (Gates, 1968) may also contribute to differences in Si concentration. Although active processes are involved, previous work indicates that transpiration rate also impacts silica accumulation (Hartley, 2015; Kumar et al., 2017; McLarnon et al., 2017). Higher transpiration rates under hot conditions may help explain increased Si concentrations. Transpiration rates likely changed in response to watering treatment as well, although we expect them to be lower under reduced watering (where concentrations were higher), and thus are unlikely to explain the changes observed between treatments. Water availability may also affect the concentration of silicic acid  in the soil solution by affecting leaching rates (with increased rates in wetter sites;Quigley et al., 2017). Plants outside our low watering treatment were watered liberally, and fertilizer did not contain a source of Si, making this an attractive explanation.

A final hypothesis worth considering is the ‘stress hypothesis’ of Johnson and Hartley (2018), which states that increases in Si concentration constitute a plastic response to stress, given silicon alleviates both temperature (Agarie et al., 1998; Wang et al., 2005; Soundararajan et al., 2014) and water stress (Ma, 2004; Hattori et al., 2005; Kaya et al., 2006; Pei et al., 2010; Chen et al., 2011; Meunier et al., 2017). The authors predict that this response would primarily benefit taxa of hot, arid environments (i.e., those most likely to experience these stressors). The observed relationship between MATs and Si concentration under standard conditions, and its dependence on temperature treatment are both explained by this hypothesis. Taxa adapted to warmer regions do show higher average concentrations, but this pattern disappears under cooler temperatures. The interaction between watering treatment and habitat wetness, where dry adapted species showed a more pronounced response to reduced watering, is also theoretically consistent with the 'stress hypothesis'. However, this difference was slight (Fig. 4), and may not translate to a meaningful difference for mitigating drought stress.

Overall, it is difficult to determine with certainty the mechanisms driving the response of Si concentration to changes in environmental conditions. None are mutually exclusive, and several may be acting in concert. A number of the predictions made by the 'stress hypothesis' are, at least partially, supported by our data. However, it is unclear if treatments resulted in meaningful temperature and water stress in some species, and whether more extreme treatments should be explored. All of the mechanisms discussed here warrant further attention, but the possibility that the observed patterns may be explained by a stress mitigation strategy associated with the induction of Si deposition is particularly intriguing. Our results also raise the possibility that athropogenic modification of Earth's climate may lead to changes in the uptake and deposition of Si in grasses. Though predicted changes in temperature are unlikely to reach the magnitude of difference between our treatments, at least in the short-term, grasslands are found in regions likely to experience some of the largest increases in mean annual temperature (Collins et al., 2013). Changes to $CO_2$ concentrations also appear to directly impact Si deposition, but in the opposite direction, with elevated $CO_2$ associated with reduced Si accumulation (Johnson and Hartley, 2018). If pronounced, these climate-Si feedbacks may have meaningful ecological consequences, impacting community interactions or even Si cycling. However, how our results reflect patterns of Si uptake and deposition in natural communities remains to be established. Landscape scale variation in environmental and edaphic conditions contributes to spatial heterogeneity in Si deposition in grasses under natural conditions (e.g., Quigley et al., 2017). Changes in temperature and/or precipitation are, therefore likely to interact with the many other factors (e.g., grazing history, substrate type, taxonomic composition) that vary across natural landscapes and also influence Si concentration. While our findings reveal important information about the magnitude and phylogenetic scope of the effects that temperature and water availability can have on the deposition of Si in grasses, there is still much work to be done in understanding how these factors impact real communities.

**Intraspecific Variation and Other Considerations:**

Our results suggest that Si concentration in grasses is quite variable within species, even when environmental conditions are controlled. Plant age and size contribute to this variation, although their effects appear to be weak under the conditions tested here. Indeed, of all possible pair wise comparisons of individuals within species, approximately half are consistent with a positive effect of age (215 of 423) or mass (240 of 417) on Si concentration. Developmental work indicates that phytolith deposition begins early in leaf development and may proceed rapidly in young leaves, before plateauing (Sangster, 1977; O'Reagain and Mentis, 1989; Piperno, 2006). Thus, for the plants considered here, leaves large enough for elemental analysis likely had similar opportunity for deposition as conspecifics, regardless of plant age or size. Whether this is also true of more mature plants, we cannot say. Indeed, some very high Si concentrations in the Poaceae appear to be the result of continual deposition and long leaf lifespans (Motomura et al., 2002). Overall, 95% of our species had CV values surpassing the approximate average intraspecific CV (5%) estimated by Simpson et al. (1960), although this was based upon zoological data. As another point of comparison, some species showed CV values comparable to or approaching those recorded for seed mass, which is generally considered a highly variable trait among plants (Jordano, 1984; Thompson, 1984; Michaels et al., 1988). High levels of intraspecific variation pose a significant sampling challenge, especially in large groups like the Poaceae. While many of our species were only represented by one or a few individuals, this is still an improvement over previous work (Supporting Information Methods S1). Additionally, one of the benefits of our mixed model approach is that we are able to consider every individual as a unique data point, and therefore better account for variation within species. Despite this advantage, we were fundamentally limited by the amount of material available for each species, and the effects of intraspecific variation, as well as age and/or size may become apparent as intraspecific sample sizes increase.

Taxon sampling is an important consideration in any comparative analysis, with small sampling differences potentially having major impacts on inferences about trait evolution (Ackerly, 2000; Salisbury and Kim, 2001; Finarelli and Flynn, 2006; Heath et al., 2008). How our results are affected is difficult to say, but the fact that they are concordant with those of Strömberg et al. (2016) and McInerney et al. (2011), despite sampling differences, is encouraging (Supporting Information Methods S1). Some of the variation in Si concentration is explained by phylogenetic history, although the strength of phylogenetic signal varies between datasets, and is strongest under the conditions promoting the highest Si concentrations (i.e., hot and dry). Phylogenetic signal may therefore reflect the Si-accumulating *potential* of species.

Phenotypic plasticity is another vital consideration for any comparative work on Si concentration. It may be accounted for by growing plants under controlled conditions. However, this comes with its own issues. When taxon sampling is broad, there may be little overlap in the preferred conditions of individual species, so many may be growing under temperatures and water regimes to which they are not well adapted. A multi-pronged approach with taxa grown under a variety of conditions, as taken here, may therefore prove the most valuable. Inference about broad trends in the evolution of Si concentration may additionally run into complications related to long-term changes in Earth's climate and atmosphere. Climatic conditions have changed substantially over the ~100 million years since grasses first evolved and began to diversify (Zachos et al., 2008; Strömberg, 2011; Gallaher et al., 2019), and it is possible that entirely non-analog conditions existed on Earth during this time (e.g., see discussion in Dunn et al., 2015). Consequently, inferences based on extant grasses growing under modern climatic regimes may not be wholly reliable for reconstructing patterns in the past. Unfortunately, as there is currently no way to make these inferences directly from the fossil record, comparative work on modern taxa is the only method available to us.

## CONCLUSION:

Grassland ecosystems are of vast global importance. They provide many ecosystem services and are an important component of the global silicon cycle, which in turn is linked to global carbon cycling. Silicon also plays an important role in many of the ecological interactions in these ecosystems, notably as an important mechanical defense against grazing (in the form of silica phytoliths). We, tested the classic hypothesis that high grazing pressure in tropical grasslands and savannas led to the evolution of higher silica levels in $C_4$ grasses, but did not find any consistent difference in Si concentration between $C_3$ and $C_4$ grasses and thus rejected this hypothesis. The hypothesis that herbivore pressure in grass-dominated habitats more generally resulted in enhanced silica defenses in ($C_3$ or $C_4$) grassland taxa was not supported either. Growth conditions imparted a pronounced effect upon Si concentration, with hot and dry conditions promoting the highest Si concentrations in most of the sampled taxa. This pattern may ultimately explain why previous authors have found elevated concentrations in $C_4$ lineages. It also suggests a mechanism via which environmental conditions may influence grass-herbivore interactions. More broadly, these results add to our understanding of how global Si cycling may be altered by anthropogenic climate change.

**Acknowledgements:**

For their help and advice during sample collection and XRF analysis, we would like to thank Rebecca Atkinson, Chris Bennett, Emma McLarnon, Millie Mockford, and Ruth Wade. We would also like to thank Tim Gallaher for his advice and input during data analysis. We would also like to thank reviewers for their feedback, which helped in improving this manuscript. This study was partially funded through a U.S. National Science Foundation grant (EAR-253713) to CAES, UW Biology, and Burke Museum of Natural History and Culture. The plant growth experiment was funded by a Natural Environment Research Council grant (NE/I014322/1) to CPO. The authors declare no conflicts of interest associated with this research.

**References:**

Ackerly, D. D. (2000). Taxon sampling, correlated evolution, and independent contrasts. *Evolution*, *54*(5), 1480–1492.

Agarie, S., Hanaoka, N., Ueno, O., Miyazaki, A., Kubota, F., Agata, W., & Kaufmann, P. B. (1998). Effects of silicon on tolerance to water deficit and heat stress in rice plants (Oryza sativa L.), monitored by electrolyte leakage. *Plant Production Science*, *1*(2), 96–103.

Aliscioni, S., Bell, H. L., Besnard, G., Christin, P. A., Columbus, J. T., Duvall, M. R., Edwards, E. J., Giussani, L., Hasenstab-Lehman, K., Hilu, K. W., Hodkinson, T. R., Ingram, A. L., Kellogg, E. A., Mashayekhi, S., Morrone, O., Osborne, C. P., Salamin, N., Schaefer, H., Spriggs, E., … Zuloaga, F. (2012). New grass phylogeny resolves deep evolutionary relationships and discovers $C_4$ origins. *New Phytologist*, *193*(2), 304–312.

Atkinson, R. R. L., Mockford, E. J., Bennett, C., Christin, P. A., Spriggs, E. L., Freckleton, R. P., Thompson, K., Rees, M., & Osborne, C. P. (2016). $C_4$ photosynthesis boosts growth by altering physiology, allocation and size. *Nature Plants*, *2*(5), 1–5.

Bach, C. E. (1988). Effects of Host Plant Patch Size on Herbivore Density : Patterns. *Ecology*, *69*(4), 1090–1102.

Barber, D. A., & Shone, M. G. T. (1966). The absorption of silica from aqueous solutions by plants. *Journal of Experimental Botany*, *17*(52), 569–578.

Barbosa, P., Hines, J., Kaplan, I., Martinson, H., Szczepaniec, A., & Szendrei, Z. (2009). Associational Resistance and Associational Susceptibility: Having Right or Wrong Neighbors. *Annual Review of Ecology, Evolution, and Systematics*, *40*(1), 1–20.

Barton, K. (2018). *MuMIn: Multi-Model Inference*. https://cran.r-project.org/web/packages/MuMIn/index.html

Beaulieu, J. M., & O'Meara, B. (2016). *OUwie: Analysis of Evolutionary Rates in an OU Framework*. https://cran.r-project.org/web/packages/OUwie/index.html

Bernays, E. A., & Hamai, J. (1987). Head size and shape in relation to grass feeding in acridoidea (Orthoptera). *International Journal of Insect Morphology and Embryology*, *16*(5), 323–330.

Blecker, S. W., McCulley, R. L., Chadwick, O. A., & Kelly, E. F. (2006). Biologic cycling of silica across a grassland bioclimosequence. *Global Biogeochemical Cycles*, *20*(3), 1–11.

Bouchenak-Khelladi, Y., Verboom, G. A., Hodkinson, T. R., Salamin, N., Francois, O., Ní Chonghaile, G., & Savolainen, V. (2009). The origins and diversification of C4 grasses and savanna-adapted ungulates. *Global Change Biology*, *15*(10), 2397–2417.

Brandon, R. N. (1990). *Adaptation and environment*. Princeton University Press.

Calandra, I., Zub, K., Szafrańska, P. A., Zalewski, A., & Merceron, G. (2016). Silicon-based plant defences, tooth wear and voles. *Journal of Experimental Biology*, *219*(4), 501–507.

Caswell, H., & Reed, F. C. (1976). Plant-Herbivore Interactions. The Indigestibility of $C_4$ Bundle Sheath Cells by Grasshoppers. *Oecologia*, *26*(2), 151–156.

Caswell, H., Reed, F., Stephenson, S. N., & Werner, P. A. (1973). Photosynthetic Pathways and Selective Herbivory : A Hypothesis. *The American Naturalist*, *107*(956), 465–480.

Cates, R. G. (1981). Host Plant Predictability and the Feeding Patterns of Monophagous, Oligophagous, and Polyphagous Insect Herbivores. *Oecologia*, *48*(3), 319–326.

Chamberlain, S., Oldoni, D., Barve, V., Desmet, P., Geffert, L., Mcglinn, D., & Ram, K. (2017). *rgbif: Interface to the Global "Biodiversity" Information Facility API*. https://cran.r-project.org/web/packages/rgbif/index.html

Chen, W., Yao, X., Cai, K., & Chen, J. (2011). Silicon alleviates drought stress of rice plants by improving plant water status, photosynthesis and mineral nutrient absorption. *Biological Trace Element Research*, *142*(1), 67–76.

Cid, M. S., Detling, J. K., Brizuela, M. A., & Whicker, A. D. (1989). Patterns in grass silicification: response to grazing history and defoliation. *Oecologia*, *80*(2), 268–271.

Collins, M., Knutti, R., Arblaster, J., Dufresne, J. ., Fichefet, T., Friedlingstein, P., Gao, X., Gutowski, W. J., Johns, T., Krinner, G., Shongwe, M., Tebaldi, C., Weaver, A. J., & Wehner, M. (2013). Long-term climate change: Projections, commitments and irreversibility. In T. F. Stocker, D. Qin, G. K. Plattner, M. Tignor, S. K. Allen, J. Boschung, A. Nauels, Y. Xia, V. Bex, & P. M. Midgley (Eds.), *Climate Change 2013 the Physical Science Basis: Working Group I Contribution to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change* (pp. 1029–1136). Cambridge University Press, United Kingdom and New York, NY, USA.

Conley, D.J. (2002). Terrestrial ecosystems and the global biogeochemical silica cycle. *Global Biogeochemical Cycles*, 16(4), 1121, doi:10.1029/2002GB001894.

Conley, D. J., & Carey, J. C. (2015). Biogeochemistry: Silica cycling over geologic time. *Nature Geoscience*, *8*(6), 431–432.

Cooper, N., Thomas, G. H., Venditti, C., Meade, A., & Freckleton, R. P. (2016). A cautionary note on the use of Ornstein Uhlenbeck models in macroevolutionary studies. *Biological Journal of the Linnean Society*, *118*(1), 64–77.

Datnoff, L. E., Deren, C. W., & Snyder, G. H. (1997). Silicon fertilization for disease management of rice in Florida. *Crop Protection*, *16*(6), 525–531.

de Melo, S. P., Monteiro, F. A., & de Bona, F. D. (2010). Silicon distribution and accumulation in shoot tissue of the tropical forage grass Brachiaria brizantha. *Plant and Soil*, *336*(1), 241–249.

Deren, C. W., Datnoff, L. E., & Snyder, G. H. (1992). Variable silicon content of rice cultivars. *Journal of Plant Nutrition*, *15*(11), 2363–2368.

Dunn, R. E., Strömberg, C. A. E., Madden, R. H., Kohn, M. J., & Carlini, A. A. (2015). Linked canopy, climate, and faunal change in the Cenozoic of Patagonia. *Science*, *347*, 258–261.

Edwards, E. J., & Smith, S. A. (2010). Phylogenetic analyses reveal the shady history of C4 grasses. *Proceedings of the National Academy of Sciences of the United States of America*, *107*(6), 2532–2537.

Edwards, E. J., & Still, C. J. (2008). Climate, phylogeny and the ecological distribution of C4 grasses. *Ecology Letters*, *11*(3), 266–276.

Edwards, E. J., Osborne, C. P., Strömberg, C. A. E., Smith, S. A., Bond, W. J., Christin, P. A., Cousins, A. B., Duvall, M. R., Fox, D. L., Freckleton, R. P., Ghannoum, O., Hartwell, J., Huang, Y., Janis, C. M., Keeley, J. E., Kellogg, E. A., Knapp, A. K., Leakey, A. D. B., Nelson, D. M., … Tipple, B. (2010). The origins of C4 Grasslands: Integrating evolutionary and ecosystem science. *Science*, *328*(5978), 587–591.

Ehleringer, J. R. (1978). Implications of quantum yield differences on the distributions of C3 and C4 grasses. *Oecologia*, *31*(3), 255–267.

Ehleringer, J. R., Cerling, T. E., & Helliker, B. R. (1997). C4 photosynthesis, atmospheric CO2 , and climate. *Oecologia*, *112*, 285–299.

Elias, M. K. (1942). *Tertiary priarie grasses and other herbs from the high plains*. Geological Society of America Special Papers 41.

Erickson, K. L. (2014). Prairie grass phytolith hardness and the evolution of ungulate hypsodonty. *Historical Biology*, *26*(6), 737–744.

Fauteux, F., Rémus-Borel, W., Menzies, J. G., & Bélanger, R. R. (2005). Silicon and plant disease resistance against pathogenic fungi. *FEMS Microbiology Letters*, *249*(1), 1–6.

Fick, S. E., & Hijmans, R. J. (2017). WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas. *International Journal of Climatology*, *37*(12), 4302–4315.

Finarelli, J. A., & Flynn, J. J. (2006). Ancestral state reconstruction of body size in the Caniformia (Carnivora, mammalia): The effects of incorporating data from the fossil record. *Systematic Biology*, *55*(2), 301–313.

Flynn, J. J., Wyss, A. R., Croft, D. A., & Charrier, R. (2003). The Tinguiririca Fauna, Chile: Biochronology, paleoecology, biogeography, and a new earliest Oligocene South American

Land Mammal "Age." *Palaeogeography, Palaeoclimatology, Palaeoecology*, *195*(3–4), 229–259. https://doi.org/10.1016/S0031-0182(03)00360-2

Gali-Muhtasib, H. U., Smith, C. C., & Higgins, J. J. (1992). The effect of silica in grasses on the feeding behavior of the prairie vole, Microtus ochrogaster. *Ecology*, *73*(5), 1724–1729.

Gallaher, T. J., Adams, D. C., Attigala, L., Burke, S. V., Craine, J. M., Duvall, M. R., Klahs, P. C., Sherratt, E., Wysocki, W. P., & Clark, L. G. (2019). Leaf shape and size track habitat transitions across forest–grassland boundaries in the grass family (Poaceae). *Evolution*, *73*(5), 927–946. https://doi.org/10.1111/evo.13722

Gates, D. M. (1968). Transpiration and Leaf Temperature. *Annual Review of Plant Physiology*, *19*(1), 211–238. https://doi.org/10.1146/annurev.pp.19.060168.001235

GBIF.org. (2020). *GBIF Occurrence Download*. doi: 10.15468/dl.heuwwg

Gibson, D. J. (2009). *Grasses and Grasslands*. Oxford University Press.

*Global Climate Normals (1961-1990)*. (n.d.). National Centers for Environmental Information, National Oceanic and Atmospheric Administration. www.ncdc.noaa.gov/wdcmet/data-access-search-viewer-tools/global-climate-normals-1961-1990

Griffith, D. M., Lehmann, C. E. R., Strömberg, C. A. E., Parr, C. L., Pennington, R. T., Sankaran, M., Ratnam, J., Still, C. J., Powell, R. L., Hanan, N. P., Nippert, J. B., Osborne, C. P., Good, S. P., Anderson, T. M., Holdo, R. M., Veldman, J. W., Durigan, G., Tomlinson, K. W., Hoffmann, W. A., … Bond, W. J. (2017). Comment on "The extent of forest in dryland biomes." *Science*, *358*(6365), 27–30.

Hadfield, J. D. (2010). MCMC methods for multi-response generalized linear mixed models: The MCMCglmm R package. *Journal of Statistical Software*, *33*(2), 1–22.

Hartley, S. E. (2015). Round and round in cycles? Silicon-based plant defences and vole population dynamics. *Functional Ecology*, *29*(2), 151–153.

Hartley, S. E., & DeGabriel, J. L. (2016). The ecology of herbivore-induced silicon defences in grasses. *Functional Ecology*, *30*(8), 1311–1322.

Hartley, S. E., Fitt, R. N., McLarnon, E. L., & Wade, R. N. (2015). Defending the leaf surface: Intra- and inter-specific differences in silicon deposition in grasses in response to damage and silicon supply. *Frontiers in Plant Science*, *6*(FEB), 1–8.

Hattori, T., Inanaga, S., Araki, H., An, P., Morita, S., Luxová, M., & Lux, A. (2005). Application of silicon enhanced drought tolerance in Sorghum bicolor. *Physiologia Plantarum*, *123*(4), 459–466.

Heath, T. A., Hedtke, S. M., & Hillis, D. M. (2008). Taxon sampling and the accuracy of phylogenetic analyses. *Journal of Systematics and Evolution*, *46*(3), 239–257.

Heidorn, T., & Joern, A. (1984). Differential herbivory on C3 versus C4 grasses by the grasshopper Ageneotettix deorum (Orthoptera: acrididae). *Oecologia*, *65*, 19–25.

Hempson, G. P., Archibald, S., & Bond, W. J. (2015). A continent-wide assessment of the form and intensity of large mammal herbivory in Africa. *Science*, *350*(6264), 1056–1061.

Hodson, M. J., & Sangster, A. G. (1988). Observations on the distribution of mineral elements in the leaf of wheat (Triticum aestivum L.), with particular reference to silicon. *Annals of Botany*, *62*(5), 463–471.

Hodson, M. J., White, P. J., Mead, A., & Broadley, M. R. (2005). Phylogenetic variation in the silicon composition of plants. *Annals of Botany*, *96*(6), 1027–1046.

Huelsenbeck, J. P., Nielsen, R., & Bollback, J. P. (2003). Stochastic mapping of morphological characters. *Systematic Biology*, *52*(2), 131–158.

Huitu, O., Forbes, K. M., Helander, M., Julkunen-Tiitto, R., Lambin, X., Saikkonen, K., Stuart, P., Sulkama, S., & Hartley, S. (2014). Silicon, endophytes and secondary metabolites as grass defenses against mammalian herbivores. *Frontiers in Plant Science*, *5*(SEP), 1–10.

Imtiaz, M., Rizwan, M. S., Mushtaq, M. A., Ashraf, M., Shahzad, S. M., Yousaf, B., Saeed, D. A., Rizwan, M., Nawaz, M. A., Mehmood, S., & Tu, S. (2016). Silicon occurrence, uptake, transport and mechanisms of heavy metals, minerals and salinity enhanced tolerance in plants with future prospects: A review. *Journal of Environmental Management*, *183*(September), 521–529.

Issaharou-Matchi, I., Barboni, D., Meunier, J. D., Saadou, M., Dussouillez, P., Contoux, C., & Zirihi-Guede, N. (2016). Intraspecific biogenic silica variations in the grass species Pennisetum pedicellatum along an evapotranspiration gradient in South Niger. *Flora: Morphology, Distribution, Functional Ecology of Plants*, *220*, 84–93.

Jacobs, B. F., Kingston, J. D., & Jacobs, L. L. (1999). *The Origin of Grass-Dominated Ecosystems*. *86*(2), 590–643.

Janis, C. M., Damuth, J., & Theodor, J. M. (2000). Miocene ungulates and terrestrial primary productivity: Where have all the browsers gone? *Proceedings of the National Academy of Sciences of the United States of America*, *97*(14), 7899–7904.

Janis, C. M., Damuth, J., & Theodor, J. M. (2004). The species richness of Miocene browsers, and implications for habitat type and primary productivity in the North American grassland biome. *Palaeogeography, Palaeoclimatology, Palaeoecology*, *207*(3–4), 371–398.

Jardine, P. E., Janis, C. M., Sahney, S., & Benton, M. J. (2012). Grit not grass: Concordant patterns of early origin of hypsodonty in Great Plains ungulates and Glires. *Palaeogeography, Palaeoclimatology, Palaeoecology*, *365–366*, 1–10.

Johnson, J. (2014). Accurate Measurements of Low Z Elements in Sediments and Archaeological Ceramics Using Portable X-ray Fluorescence (PXRF). *Journal of Archaeological Method and Theory*, *21*(3), 563–588.

Johnson, S. N., & Hartley, S. E. (2018). Elevated carbon dioxide and warming impact silicon and phenolic-based defences differently in native and exotic grasses. *Global Change Biology*, *24*(9), 3886–3896.

Johnson, S. N., Ryalls, J. M. W., Barton, C. V. M., Tjoelker, M. G., Wright, I. J., & Moore, B. D. (2019). Climate warming and plant biomechanical defences: Silicon addition contributes to herbivore suppression in a pasture grass. *Functional Ecology*, *33*(4), 587–596.

Johnston, A., Bezeau, L. M., & Smoliak, S. (1967). Variation in Silica Content of Range Grasses. *Canadian Journal of Plant Science*, *47*(1), 65–71.

Jones, R. L., & Beavers, A. H. (n.d.). Variation of opal phytolith content among some great soil groups in Illinois. *Soil Science Society of America*, *28*(5), 711–712.

Jordano, P. (1984). Seed Weight Variation and Differential Avian Dispersal in Blackberries Rubus ulmifolius. *Oikos*, *43*(2), 149–153.

Katz, O. (2015). Silica phytoliths in angiosperms: Phylogeny and early evolutionary history. *New Phytologist*, *208*(3), 642–646.

Kaufman, P. B. (1985). Structure and Function of Silica Bodies in the Epidermal System of Grass Shoots. *Annals of Botany*, *55*(4), 487–507.

Kaya, C., Tuna, L., & Higgs, D. (2006). Effect of silicon on plant growth and mineral nutrition of maize grown under water-stress conditions. *Journal of Plant Nutrition*, *29*(8), 1469–1480.

Kidder, D.L., & Gierlowski-Kordesch, E.H. (2005). Impact of Grassland Radiation on the Nonmarine Silica Cycle and Miocene Diatomite. *Palaios*, *20*(2), 198–206.

Kumar, S., Milstein, Y., Brami, Y., Elbaum, M., & Elbaum, R. (2017). Mechanism of silica deposition in sorghum silica cells. *New Phytologist*, *213*(2), 791–798.

Landa, K., & Rabinowitz, D. (1983). Relative Preference of Arphia Sulphurea ( Orthoptera : Acrididae ) for Sparse and Common Prairie Grasses. *Ecology*, *64*(2), 392–395.

Ma, J. F. (2004). Role of silicon in enhancing the resistance of plants to biotic and abiotic stresses. *Soil Science and Plant Nutrition*, *50*(1), 11–18.

Ma, J. F., Tamai, K., Ichii, M., & Wu, G. F. (2002). A rice mutant defective in Si uptake. *Plant Physiology*, *130*(4), 2111–2117.

MacFadden, B. J. (1992). *Fossil horses*. Cambridge University Press.

Massey, F. P., & Hartley, S. E. (2006). Experimental demonstration of the antiherbivore effects of silica in grasses: Impacts on foliage digestibility and vole growth rates. *Proceedings of the Royal Society B: Biological Sciences*, *273*(1599), 2299–2304.

Massey, F. P., & Hartley, S. E. (2009). Physical defences wear you down : progressive and. *Journal of Animal Ecology*, 281–291.

Massey, F. P., Ennos, A. R., & Hartley, S. E. (2006). Silica in grasses as a defence against insect herbivores: Contrasting effects on folivores and a phloem feeder. *Journal of Animal Ecology*, *75*(2), 595–603.

Massey, F. P., Ennos, A. R., & Hartley, S. E. (2007). Grasses and the resource availability hypothesis: The importance of silica-based defences. *Journal of Ecology*, *95*(3), 414–424.

Massey, F. P., Massey, K., Roland Ennos, A., & Hartley, S. E. (2009). Impacts of silica-based defences in grasses on the feeding preferences of sheep. *Basic and Applied Ecology*, *10*(7), 622–630.

McInerney, F. A., Strömberg, C. A. E., & White, J. W. C. (2011). The Neogene transition from C 3 to C 4 grasslands in North America: stable carbon isotope ratios of fossil phytoliths . *Paleobiology*, *37*(1), 23–49.

Mclain, D. K., & Shure, D. J. (1990). Spatial and Temporal Density Dependence of Host Plant Patch Use by the Ragwort Seed Bug , Neacoryphus Bicrucis (Hemiptera : Lygaeidae). *Oikos*, *58*(3), 306–312.

McLarnon, E., McQueen-Mason, S., Lenk, I., & Hartley, S. E. (2017). Evidence for active uptake and deposition of Si-based defenses in tall fescue. *Frontiers in Plant Science*, *8*(July), 1–11.

Mcnaughton, A. S. J. (2011). *Serengeti Ungulates : Feeding Selectivity Influences the Effectiveness of Plant Defense Guilds Source : Science , New Series , Vol . 199 , No . 4330 ( Feb . 17 , 1978 ), pp . 806-807 Published by : American Association for the Advancement of Science Stabl*. *199*(4330), 806–807.

McNaughton, S. J. (1976). Serengeti Migratory Wildebeest : Facilitation of Energy Flow by Grazing. *Science*, *191*(4222), 92–94.

McNaughton, S. J., & Tarrants, J. L. (1983). Grass leaf silicification: Natural selection for an inducible defense against herbivores. *Proceedings of the National Academy of Sciences*, *80*(3), 790–791.

Mcnaughton, S. J., Tarrants, J. L., Mcnaughton, M. M., & Davis, R. D. (1985). Silica as a Defense against Herbivory and a Growth Promotor in African Grasses. *Ecology*, *66*(2), 528–535.

Meunier, J. D., Barboni, D., Anwar-ul-Haq, M., Levard, C., Chaurand, P., Vidal, V., Grauby, O., Huc, R., Laffont-Schwob, I., Rabier, J., & Keller, C. (2017). Effect of phytoliths for mitigating water stress in durum wheat. *New Phytologist*, *215*(1), 229–239.

Michaels, H. J., Benner, B., Hartgerink, A. P., Lee, T. D., & Rice, S. (1988). Seed size variation: magnitude, distribution, and ecological correlates. *Evolutionary Ecology*, *2*(2), 157–166.

Mihlbachler, M. C., Rivals, F., Solounias, N., & Semprebon, G. M. (2011). Dietary Change and Evolution of Horses in North America. *Science*, *331*, 1178–1182.

Mitani, N., & Ma, J. F. (2005). Uptake system of silicon in different plant species. *Journal of Experimental Botany*, *56*(414), 1255–1261.

Mitani, N., Yamaji, N., & Ma, J. F. (2008). Characterization of substrate specificity of a rice silicon transporter, Lsi1. *Pflugers Archiv European Journal of Physiology*, *456*(4), 679–686.

Motomura, H., Mita, N., Suzuki, M. (2002). Silica accumulation in long-lived leaves of *Sasa veitchii* (Carrière) Rehder (Poaceae-Bambusoideae). *Annals of Botany*, 90, 149-152, doi:10.1093/aob/mcf148.

Nakagawa, S., & Schielzeth, H. (2013). A general and simple method for obtaining R2 from generalized linear mixed-effects models. *Methods in Ecology and Evolution*, *4*(2), 133–142.

Nielsen, R. (2002). Mapping mutations on phylogenies. *Systematic Biology*, *51*(5), 729–739.

O'Reagain, P. J., & Mentis, M. T. (1989). Leaf Silicification in Grasses - A Review. *Journal of the Grassland Society of Southern Africa*, *6*(1), 37–43.

Osborne, C. P., & Freckleton, R. P. (2009). Ecological selection pressures for C4 photosynthesis in the grasses. *Proceedings of the Royal Society B: Biological Sciences*, *276*(1663), 1753–1760.

Osborne, C. P., Salomaa, A., Kluyver, T. A., Visser, V., Kellogg, E. A., Morrone, O., Vorontsova, M. S., Clayton, W. D., & Simpson, D. A. (2014). A global database of C4 photosynthesis in grasses. *New Phytologist*, *204*, 441–446.

Owen-Smith, N. (1989). Megafaunal Extinctions: The Conservation Message from 11,000 Years B.P. *Conservation Biology*, *3*(4), 405–412.

Pagel, M. (1999). Inferring the historical patterns of biological evolution. *Nature*, *401*(6756), 877–884.

Pei, Z. F., Ming, D. F., Liu, D., Wan, G. L., Geng, X. X., Gong, H. J., & Zhou, W. J. (2010). Silicon Improves the Tolerance to Water-Deficit Stress Induced by Polyethylene Glycol in Wheat (Triticum aestivum L.) Seedlings. *Journal of Plant Growth Regulation*, *29*(1), 106–115.

Piperno, D. R. (2006). *Phytoliths: a Comprehensive Guide for Archaeologists and Paleoecologists*. AltaMira Press.

Power, S. A., Barnett, K. L., Ochoa-Hueso, R., Facey, S. L., Gibson-Forty, E. V. J., Hartley, S. E., Nielsen, U. N., Tissue, D. T., & Johnson, S. N. (2016). DRI-Grass: A new experimental platform for addressing grassland ecosystem responses to future precipitation scenarios in South-East Australia. *Frontiers in Plant Science*, *7*(September), 1–14.

Quigley, K. M., & Anderson, T. M. (2014). Leaf silica concentration in Serengeti grasses increases with watering but not clipping: Insights from a common garden study and literature review. *Frontiers in Plant Science*, *5*(OCT), 1–10.

Quigley, K. M., Donati, G. L., & Anderson, T. M. (2017). Variation in the soil 'silicon landscape' explains plant silica accumulation across environmental gradients in Serengeti. *Plant and Soil*, *410*(1–2), 217–229.

Quigley, K. M., Griffith, D. M., Donati, G. L., & Anderson, T. M. (2020). Soil nutrients and precipitation are major drivers of global patterns of grass leaf silicification. *Ecology*, *0*(0), 1–10.

Reidinger, S., Ramsey, M. H., & Hartley, S. E. (2012). Rapid and accurate analyses of silicon and phosphorus in plants using a portable X-ray fluorescence spectrometer. *New Phytologist*, *195*(3), 699–706.

Revell, L. J. (2012). phytools: An R package for phylogenetic comparative biology (and other things). *Methods in Ecology and Evolution*, *3*(2), 217–223.

Reynolds, J. J. H., Lambin, X., Massey, F. P., Reidinger, S., Sherratt, J. A., Smith, M. J., White, A., & Hartley, S. E. (2012). Delayed induced silica defences in grasses and their potential for destabilising herbivore population dynamics. *Oecologia*, *170*(2), 445–456.

Richmond, K. E., & Sussman, M. (2003). Got silicon? The non-essential beneficial plant nutrient. *Current Opinion in Plant Biology*, *6*(3), 268–272.

Root, R. B. (1973). Organization of a Plant-Arthropod Association in Simple and Diverse Habitats : The Fauna of Collards. *Ecological Monographs*, *43*(1), 95–124.

Sage, R. F. (2001). Environmental and evolutionary preconditions for the origin and diversification of the C4 photosynthetic syndrome. *Plant Biology*, *3*(3), 202–213.

Sage, R. F., & Monson, R. K. (Eds.). (1999). *C4 Plant Biology*. Academic Press.

Sage, R. F., & Monson, R. K. (Eds.). (1999). *C4 Plant Biology*. Academic Press.

Salisbury, B. A., & Kim, J. (2001). Ancestral State Estimation and Taxon Sampling Density. *Systematic Biology*, *50*(4), 557–564.

Samson, F. B., Knopf, F. L., & Ostlie, W. R. (2004). Great Plains ecosystems: past, present, and future. *Wildlife Society Bulletin*, *32*(1), 6–15.

Sangster, A. G. (1977). Characteristics of silica deposition in Digitaria sanguinalis (L.) scop. (Crabgrass). *Annals of Botany*, *41*(2), 341–350.

Sangster, A. G., Hodson, M. J., & Tubb, H. J. (2001). Silicon Deposition in Higher Plants. In *Silicon in Agriculture* (pp. 85–113).

Semprebon, G. M., Rivals, F., & Janis, C. M. (2019). The role of grass vs. Exogenous abrasives in the paleodietary patterns of North American. *Frontiers in Ecology and Evolution*, *7*(MAR), 1–23.

Semprebon, G. M., Rivals, F., Solounias, N., & Hulbert, R. C. (2016). Paleodietary reconstruction of fossil horses from the Eocene through Pleistocene of North America. *Palaeogeography, Palaeoclimatology, Palaeoecology*, *442*, 110–127.

Shantz, H. L. (1954). The Place of Grasslands in the Earth ' s Cover. *Ecology*, *35*(2), 143–145.

Simpson, G. G., Roe, A., & Lewontin, R. C. (1960). *Quantitative Zoology*. Dover Publications, Inc.

Soininen, E. M., Bråthen, K. A., Jusdado, J. G. H., Reidinger, S., & Hartley, S. E. (2013). More than herbivory: Levels of silica-based defences in grasses vary with plant species, genotype and location. *Oikos*, *122*(1), 30–41.

Solounias, N., & Semprebon, G. M. (2002). Advances in the Reconstruction of Ungulate Ecomorphology with Application to Early Fossil Equids. *American Museum Novitates*, *3366*(3366), 1–49.

Song, Z., Liu, H., Strömberg, C. A. E., Yang, X., & Zhang, X. (2017). Phytolith carbon sequestration in global terrestrial biomes. *Science of the Total Environment*, *603–604*, 502–509.

Soundararajan, P., Sivanesan, I., Jana, S., & Jeong, B. R. (2014). Influence of silicon supplementation on the growth and tolerance to high temperature in Salvia splendens. *Horticulture, Environment, and Biotechnology*, *55*, 271–279.

Spriggs, E. L., Christinb, P. A., & Edwards, E. J. (2014). C4 photosynthesis promoted species diversification during the miocene grassland expansion. *PLoS ONE*, *9*(5).

Stebbins, G. L. (1981). Coevolution of grasses and herbivores. *Annals of the Missouri Botanical Garden*, *68*(1), 75–86.

Stirton, R. A. (1947). Observations on evolutionary rates in hypsodonty. *Evolution*, *1*(1), 32–41.

Street-Perrott, F. A., & Barker, P. A. (2008). Biogenic silica: a neglected component of the coupled global continental biogeochemical cycles of carbon and silicon. *Earth Surface Processes and Landforms*, *33*, 1436–1457.

Strömberg, C. A. E. (2005). Decoupled taxonomic radiation and ecological expansion of open-habitat grasses in the Cenozoic of North America. *Proceedings of the Natural Academy of Sciences*, 102(34), 11980-11984, doi:10.1073/pnas.0505700102.

Strömberg, C. A. E. (2006). Evolution of hypsodonty in equids: testing a hypothesis of adaptation. *Paleobiology*, *32*(2), 236–258.

Strömberg, C. A. E. (2011). Evolution of Grasses and Grassland Ecosystems. *Annual Review of Earth and Planetary Sciences*, *39*(1), 517–544.

Strömberg, C. A. E., Di Stilio, V. S., & Song, Z. (2016). Functions of phytoliths in vascular plants: an evolutionary perspective. *Functional Ecology*, *30*(8), 1286–1297.

Strömberg, C. A. E., Dunn, R. E., Madden, R. H., Kohn, M. J., & Carlini, A. A. (2013). Decoupling the spread of grasslands from the evolution of grazer-type herbivores in South America. *Nature Communications*, *4*(February 2016).

Team, R. C. (2019). *R: A language and environment for statistical computing*. R Foundation for Statistica Computing. https://r-project.org

Teeri, J. A., & Stowe, L. G. (1976). International Association for Ecology Climatic Patterns and the Distribution of C4 Grasses in North America. *Oecologia*, *23*(1), 1–12.

Thomasson, J. R. (1985). Miocene fossil grasses: possible adaptation in reproductive bracts (lemma and palea). *Annals of the Missouri Botanical Garden*, *72*, 843–851.

Thompson, J. N. (1984). Variation among individual seed masses in Lomatium grayi ( Umbelliferae) under controlled conditions: magnitude and partitioning of the variance. *Ecology*, *65*(2), 626–631.

Trembath-Reichert, E., Wilson, J. P., McGlynn, S. E., & Fischer, W. W. (2015). Four hundred million years of silica biomineralization in land plants. *Proceedings of the National Academy of Sciences of the United States of America*, *112*(17), 5449–5454.

Veldman, J. W., Aleman, J. C., Alvarado, Swanni, T., Anderson, T. M., Archibald, S., Bond, W. J., Boutton, T. W., Buchmann, N., Buisson, E., Canadell, J. G., de Sa Dechoum, M., Diaz-Toribio, M. H., Durigan, G., Ewel, J. J., Fernandes, G. W., Fidelis, A., Fleishman, F., Good,

S. P., Griffith, D. M., … Zaloumis, N. P. (2019). Comment on "The global tree restoration potential." *Science*, *366*(6469), 1–5.

Visser, V., Clayton, W. D., Simpson, D. A., Freckleton, R. P., & Osborne, C. P. (2014). Mechanisms driving an unusual latitudinal diversity gradient for grasses. *Global Ecology and Biogeography*, *23*(1), 61–75.

Visser, V., Woodward, F. I., Freckleton, R. P., & Osborne, C. P. (2012). Environmental factors determining the phylogenetic structure of C 4 grass communities. *Journal of Biogeography*, *39*(2), 232–246.

Wang, L., Nie, Q., Li, M., Zhang, F., Zhuang, J., Yang, W., Li, T., & Wang, Y. (2005). Biosilicified structures for cooling plant leaves: A mechanism of highly efficient midinfrared thermal emission. *Applied Physics Letters*, *87*(19), 1–3.

Watcharamongkol, T., Christin, P.A., Osborne, C.P. (2018). $C_4$ photosynthesis evolved in warm climates but promoted migration to cooler ones. *Ecology Letters*, 21, 376-383, doi: 10.1111/ele.12905.

Wilson, J. R., & Hattersley, P. W. (1983). In vitro digestion of bundle sheath cells in rumen fluid and its relation to the suberized lamella and C4 photosynthetic type in Panicum species. *Grass and Forage Science*, *38*(3), 219–223.

Wilson, J. R., Brown, R. H., & Windham, W. R. (1983). Influence of leaf anatomy on the dry matter digestibility of C3, C4, and C3/C4 intermediate types of Panicum species. *Crop Science*, *23*(1), 141–146.

Zachos, J. C., Dickens, G. R., & Zeebe, R. E. (2008). An early Cenozoic perspective on greenhouse warming and carbon-cycle dynamics. *Nature*, *451*(7176), 279–283.

Zizka, A., Silvestro, D., Andermann, T., Azevedo, J., Duarte Ritter, C., Edler, D., Farooq, H., Herdean, A., Ariza, M., Scharn, R., Svantesson, S., Wengström, N., Zizka, V., & Antonelli, A. (2019). CoordinateCleaner: Standardized cleaning of occurrence records from biological collection databases. *Methods in Ecology and Evolution*, *10*(5), 744–751.

**Supporting Information:**

**Table S1**- raw data for all analyzed samples, full caption given in Methods S1.

**Methods S1** – discussion of sampling with comparison to other recent work.

**Methods S2** – elaboration on literature survey for habitat data, including excerpts from sources used to support all classification.

**Methods S3** – elaboration on methods of ancestral state estimates used in character evolution models, Fig. S1, S2, S3, and S4.

**Notes S1 –** comparison of relative concentration within species included in multiple datasets

**Notes S2** – elaboration on results related to intraspecific variation in Si concentration, and potential biases mentioned in the main text, Fig. S5, S6, and S7.

**Fig. 1** Phylogenetic tree showing variation in silicon (Si) concentration for grasses grown under standard conditions, with subfamilies identified. Branch color represents ln(Si concentration), with coloring at interior nodes obtained via maximum likelihood ancestral state estimation (phytools v. 0.6.99; Revell, 2012). From left to right, colored labels at the tips represent photosynthetic pathway (PP; $C_3$ = green, $C_4$ = tan), habitat type (HT; grassland/savanna = green, other = white), habitat wetness (HW; wet = blue, dry = brown), and the mean annual precipitation (MAPs) and mean annual temperature (MATs) averaged across each species' range.

**Fig. 2** Comparison between predefined evolutionary regimes of weighted parameter values from the bootstrap output of the five character evolution models tested, excluding parameters that were identical for both regimes. Error bars represent weighted standard deviation, based upon weighted Akaike information criterion scores.

**Fig. 3** Kernel density plots of silicon (Si) concentration under different growth conditions, showing only those species grown under both conditions. (a) Individuals of species grown under standard (red) and reduced temperature (blue) conditions, and (b) individuals of species grown under standard (green) and reduced watering (tan) conditions.

**Fig. 4** Interactions between the effect of environmental treatment and species habitat preference on silicon (Si) concentration. (a) The relationship between mean annual temperature of species' range (MATs) and Si concentration in species grown under both standard (red) and reduced temperature (blue) treatments. (b) Average Si concentration of species adapted to wet (dark green), dry (tan), and broad (light green) habitats, when grown under standard (twice daily) and reduced watering (twice weekly) treatments. Error bars represent standard error.

**Contents:**

**Table S1:** Table including raw data for all individuals included in our analyses. The first three columns respectively include identifying numbers for each specimen from the original study by Atkinson et al. (2016) (sheffield.num), the Burke Museum of Natural History and Culture (burke.num), and our internal collection numbers (collection.num). Taxon and tip, respectively, refer to the accepted taxonomic name and tip in the phylogenetic tree as listed for each individual in the original growth study (Atkinson et al., 2016). The remaining columns refer to ind: the letter assigned to each individual plant within a species, condition: the treatment conditions of growth (see main text), si: individual average silicon (Si) concentration (see main text), har.days: the age in days after germination of each plant at the time of harvest, all.dry.weight.g: the aboveground biomass of each plant after harvesting, photo.pathway: the dominant photosynthetic pathway of each species, grassland.savanna: determination of whether the species is typically present (1) or absent (0) in grassland or savanna type habitats, water.regime: determination of the water availability in the habitats a species is typically found, MAT: the average mean annual temperature across the range of each species (i.e., MATs in the main text), MAP: the average mean annual precipitation across the range of each species (i.e., MAPs in the main text).

**Methods S1: Sampling and Data Collection**

In the present study, we sampled 124 species from 69 genera, representing 20 tribes and 7 subfamilies (excluded are the Arundinoideae, Bambusoideae, Anomochlooideae, Puelioideae, and Pharoideae). Sampling within the PACMAD clade is also biased towards $C_4$ lineages (Supporting Information Methods S3). This sample was determined by what material was available for sampling in sufficient quantities to complete Si concentration analyses. Among recent works looking at levels of Si deposition among $C_3$ and $C_4$ taxa, in a phylogenetic framework, Bouchenak-Khelladi et al. (2009) found support for elevated Si concentrations in $C_4$ lineages, while McInerney et al. (2011) and Strömberg et al. (2016) did not. The latter two studies employed Si concentration data taken from Hodson et al. (2005), and both employed generic level phylogenies. Hodson et al. (2005) included data for 148 species of grass in 78 genera, representing 8 of the 12 subfamilies (the APP grade and the Micrairoideae were not sampled). Data were compiled from published Si concentration estimates, and the authors exploited overlapping taxa to account for variation between studies (though differences could be related to methodology, developmental age, and/or environmental conditions) (Hodson et al., 2005). Bouchenak-Khelladi et al. (2009) sampled a total of 90 genera representing 10 of the 12 subfamilies (only the Puelioideae and Micrairoideae were excluded). These three works and the present study all sample a similar number of taxa. And though there are taxa common between the datasets, differences primarily arise in which taxa are sampled. For example, Bouchenak-Khelladi et al. (2009) include a sample of 20 bamboo genera, including both “woody” and herbaceous members of the subfamily. This is a much larger sample than found in either Hodson et al. (2005), or this study, where bamboos were excluded entirely. Interestingly, the extremely high levels of deposition observed in some bamboos (the highest recorded Si concentration among grasses was recorded in the genus *Sasa*, Motomura et al., 2002) was not recovered. That said, given the main question of this study, whether $C_4$ taxa have evolved higher Si concentrations than $C_3$ taxa, the limitation of our sample to grasses primarily of open or partially closed habitats seems reasonable (notwithstanding the $C_4$ biased sample with the PACMAD clade). We also note that we have provided a slightly larger sample of the Aristidoideae and Chloridoideae, the two predominantly $C_4$ clades identified by Bouchenak-Khelladi et al. (2009) as showing increasing trends in Si deposition.

Comparative work has often considered Si concentration as a genus level trait (Bouchenak-Khelladi et al., 2009; McInerney et al., 2011; Strömberg et al., 2016 though see discussion in the latter two). This may be problematic, given the level of variation in Si concentration below the generic level. Furthermore, treating grass genera as comparable eco-taxonomic units is problematic, especially when generic boundaries are not always clear. High intraspecific variation also complicates comparative work (e.g., Cooper et al., 2016), especially when sample sizes are small. Of the 124 species from our standard conditions treatment, 87 were represented by more than one individual, and 40 were represented by 3 or more (sample sizes were similar in the reduced temperature dataset, and slightly better in the reduced watering dataset). By comparison, Bouchenak-Khelladi et al. (2009) considered only one individual per taxon, while McInerney et al. (2011) and Strömberg et al. (2016) included multiple individuals per taxon (both using different subsamples of Hodson et al., 2005), but these were compiled from different studies (though as mentioned previously, statistical methods were applied to adjust for inter-study variation). Overall, though we consider this study to be among the best to date with regards to sampling at lower taxonomic levels, there is still considerable room for improvement.

Another methodological advantage of this study is the use of X-ray fluorescence spectrometry (XRF), which quickly provides accurate estimates of bulk leaf Si concentration (Reidinger et al., 2012). By comparison, recent work supporting the $C_4$-grazer hypothesis, measured silica deposition as the proportion of epidermal area covered by silica bodies (Bouchenak-Khelladi et al., 2009). However, counting *in situ* silica bodies in small, randomly chosen regions of the leaf epidermis may not adequately control for spatial heterogeneity in Si deposition. This is an important limitation, given that Si deposition has been shown to be heterogeneous across the leaf, with spatial patterns varying with the developmental age of the leaf, and across the family (e.g., Sangster, 1977; Hodson and Sangster, 1988; O'Reagain and Mentis, 1989; de Melo et al., 2010). Our method of sampling and homogenizing the entire lamina (or a substantial portion of it) is more robust to this problem. In contrast, although we argue that XRF provides some advantages, comparisons to previous studies using traditional gravimetric approaches for estimating silica content (e.g., those compiled by Hodson et al., 2005), are unlikely to show substantial differences in estimates.

The sampled plants varied in both age and size and we consequently included both age and plant mass as covariates in our analyses (see main text). Variation in plant mass was substantial; however, only a small proportion of this variation was apparently related to differences in plant age at harvest. We tested this using phylogenetically informed generalized linear mixed models (see Methods in main text), separately for each of our three environmental conditions. We included age as a fixed effect and plant mass as the response. Under all three sets of growth conditions the effect of age was significant ($p < 0.001$), but it typically explained less than 10% of the variation in mass (standard - $R^2 = 0.056$ [95% CI: 0.027, 0.087], reduced temperature - $R^2 = 0.105$ [95% CI: 0.042, 0.181], reduced watering - 0.072 [95% CI: 0.036, 0.112]).

**Methods S2: Classification of Variables:**

The habitat type character was made by first compiling a list of all habitat types each species was known to occupy, based upon a survey of available literature (see below). Habitat types were then grouped into several broad categories describing general habitat structure (grassland/savanna, shrubland, woodland/forest, disturbed/anthropogenic, dune/desert, and wetland). For the analyses run here, this was then simplified to the presence/absence of a taxon in grassland and savanna type habitats. Of the 125 species included in the standard conditions dataset, 73 were found in grassland habitats, while the remaining 52 were not. In the reduced temperature dataset, there were 19 grassland taxa and 17 non-grassland taxa, while the reduced watering dataset had 31 and 22 species of grasslands, and non-grasslands, respectively.

Water regime was coded using a simplified scheme (wet, dry, or broad) compared to that used by Atkinson et al. (2016), to accommodate our smaller sample size (i.e., many of the original groups contained few taxa). In this classification scheme, we attempted to condense a considerable degree of variation into relatively few categories. “Wet” taxa included both those found in mesic environments and those typical of habitats with more abundant moisture (e.g., wetland taxa like *Echinochloa oryzoides*). “Dry” taxa included taxa adapted to xeric environments, as well as those commonly found in dry-mesic habitats. “Broad” taxa were those commonly found in a wide range of habitats. Of the 125 species included in the standard conditions dataset, 49 were listed as primarily occurring in wet habitats, 42 were listed as primarily occurring in dry habitats, and 34 had broad habitat occupation. In the reduced temperature dataset, there were 11 “wet”, 12 “dry”, and 13 “broad” species, while the reduced watering dataset included 17 “wet”, 19 “dry”, and 17 “broad” species.

Mean annual precipitation (MAP) within the geographic range of each species represents a geographically coarser, but quantitative, classification of water availability, compared with our habitat wetness variable. For both MAP and mean annual temperature (MAT), we first downloaded species observation data from the Global Biodiversity Information Facility (GBIF.org) using v. 1.3.0 of the rgbif package (Chamberlain et al., 2017). We limited our search to preserved specimens that had not been flagged by GBIF as having any geospatial issues. We further cleaned up these data using v. 2.0-11 of the package CoordinateCleaner (Zizka et al., 2019) to exclude observations where the same value was entered for both latitude and longitude, observations with coordinates corresponding to the GBIF headquarters or another known instituitional locations (e.g., herbaria), observations entered as either a national capital or the centroid of a nation, and observations where coordinates did not fall within the country where it was identified. Observations were also excluded if either latitude or longitude were entered as zero, or either exceeded the possible bounds. Once cleaned, MAT and MAP at each observation point was extracted using climate data from WorldClim v2 (Fick and Hijmans, 2017) at a 30 second resolution. For each species, MAT and MAP were taken as the average from all available observations. One species (*Cynodon barberi*) did not have any observations that met the criteria we used. Coarser MAP and MAT data for this taxon were available from Atkinson et al. (2016), and these values were used in subsequent analyses.

Ecological information to supplement that taken from Atkinson et al. (2016) was compiled from a variety of sources. Species included in our dataset are listed below, along with excerpts from the sources used to complete their classification. Final classifications for each taxon are in Table S1. For a number of species, very few, or no, published sources, detailing habitat preference, could be found. In these cases, herbarium sheets were consulted for habitat information. Specimens were found using the Global Biodiversity Information Facility (GBIF), and habitat information was taken from images of each herabarium sheet. When possible, preference was given to specimens collected from within the native range of each species. Below, these descriptions are identified by herbarium code, and specimen number.

*Acroceras zizanioides*-

“Sprawling, decumbent, clone-forming perennial to 75 cm tall... Open stream sides, swamps, ditches, near sea level to 500m...”- (Davidse et al., 2004)

“In Southeast Asia the representatives are decumbent or prostrate, perennial forest grasses, often found scrambling over other vegetation. Though reported from elevations <1200m, they occur most commonly in lowland evergreen forests and scrub <800 m, usually forming small colonies in damp, shady, open sites. Being predominant in forest, the grasses have little fodder value, but in Africa other species of the genus are cultivated for pasture and hay.”- (Lazarides, 1980)

“Tropical Africa, southern Mexico to northern Argentina, India. Perennial, rhizomatous...useful grass, good forage and hay, occurs in damp places in shade, roadside ditches, swampy places, seasonally inundatated savannahs, in shallow water...”- (Quattrocchi, 2006)

*Alloteropsis cimicina*-

“The annual *A. cimicina* is a very common ruderal and weed in elevations <700 m, found on a variety of soils in disturbed or cultivated sites and sometimes in dry, deciduous and dipterocarp forests. Both grasses are palatable to grazing animals.”- (Lazarides, 1980)

“Grows in the open or light shade of Dry Teak Forest or Acacia Thorn Forest. Occurs on both flat and sloping areas on sandy-red or red-brown-clay soil.”- (Hodd and Hodd, 1982)

“Old World tropics, Southeast Asia, tropical Africa, Australia. Short-lived perennial or annual, erect or decumbent...weed species, hay, economic and useful plant, roots used in toothache by Lodhas (India), forage, moderate fodder value, useful for erosion control, found in moist areas, along roadsides, lowland, open habitats weedy places, dry open forest, open dry soils, along waste places...”- (Quattrocchi, 2006)

*Andropogon gerardii*-

> "...is most abundant in moist, deep, well-drained soils of prairies, pastures, and meadows in soils ranging from clayey to sandy. It is the predominant grass on tallgrass pairies, as well as on overflow and subirrigated sites in the Great Plains."- (Stubbendieck et al., 2017)
>
> "Big bluestem is climatically adapted throughout the Midwest and Northeast on moderately well drained through excessively well drained soils. It is adapted to a range of other soil limitations such as shallow depth, low pH, and low fertility."- (USDA, NRCS National Plant Data Team, 2020)
>
> "...grows in prairies, meadows, generally in dry soils. It is a widespread species, exending from southern Canada to Mexico, and was once dominant over much of its range."- (Barkworth et al., 2007)
>
> "Northern America, Canada to Mexico, U.S. Long-lived perennial with tufted and solid culms, shortly stoloniferous, rhizomes short or absent...ornamental and weed species, analgesic, carminative and diuretic, naturalized, cultivated, excellent and highly palatable livestock forage when actively growing, fodder, good prairie hay, used by wildlife for food and cover, provides nesting and concealment cover for birds, excellent drought tolerance, good grass for erosion control and revegation, tolerant of various soil types from wet clay to dry sand, occurs along riverbanks, on sandy soils, roadsides and moist meadows, open roadside, at edge of roadside ditch, coastal marshes, prairies and open fields, degraded prairie, foothills, sand hills, pine flatwoods, dry rocky soil..."- (Quattrocchi, 2006)

*Anthephora pubescens*-

“Common on sandy or gravelly soils, sometimes loams. Occurs in areas with rainfall from 175-950 mm, most collections being made between 350 and 500 mm. It is extremely drought tolerant, but intolerant of waterlogging and flooding. Normally recommended in areas with rainfall of 250-650 mm per year.”- (Cook et al., 2005)

“Tropical and South Africa. Perennial, erect...tussock grass...shortly rhizomatous with strong creeping rhizome...pasture grass, forage, usually very palatable, excellent drought resistance, useful to reduce soil erosion, occurs in undisturbed dry veld areas, hillsides, slopes, well-drained ground, rocky sites, deciduous bushland, low rainfall sandy areas, savannah, grassland, in dry areas, sandy soils...”- (Quattrocchi, 2006)

*Apluda mutica*-

“culms to about 3m long”- (Cope, 1982)

“It is very common in the plains and at low elevation in the Himalayas. In hedges and bushy places it usually assumes a climbing habit. It often constitutes a large part of the undergrowth in forests.”- (Cope, 1982)

“Common in thickets and along forest margins, sometimes forming large masses”- (Flora of China vol. 22)

“In medium shade to open throughout the Gir Forest. On flat, or more typically on gentle to steeply sloping hillsides...On treeless or tree-covered hillsides it often forms dense pure stands.”- (Hodd and Hodd, 1982)

“...very wide range of habitats, which include disturbed sites (such as old garden clearings, roadsides, the banks of water courses and ricefields, coconut plantations and beach frontages), rocky slopes particularly on limestone, and primary or secondary communities of grassland, savannah, scrub, deciduous and evergreen forests."- (Lazarides, 1980)

"Southeast Asia, India. Annual or perennial...often rambling among bushes...good fodder value, palatable to stock when young, young grass eaten by buffaloes, a forest grass, garden edges, plains, along bushes, ditch and river banks, wet places, along roadsides, on poor soil, in waste grounds..."- (Quattrocchi, 2006)

*Aristida diffusa*-

"South Africa, Lesotho, Zimbabwe, Botswana. Perennial, caespitose, wiry, flexible leaves, unpalatable, very low grazing value, useful for erosion control, used for making soft brooms, found in shallow and stony soils, dry ground on sandy soils, open places, poor overgrazed veld, roadsides..."- (Quattrocchi, 2006)

*Aristida divaricata*-

"...infrequent in sandy to gravelly soils of open plains, prairies, pastures, and disturbed sites."- (Stubbendieck et al., 2017)

"grows on dry hills and plains, especially in pinyon-juniper-grassland zones, from the southwestern United States through Mexico to Guatemala."- (Barkworth et al., 2007)

"...poor forage, grows on dry rocky hills, sandy fields, desert grassland..."- (Quattrocchi, 2006)

*Aristida funiculata*-

"North Africa to Pakistan, Somalia, Sudan, White Nile region, boundary between the Saharan and Sahelian zones...used for fodder, eaten by cattle in the young stage and when tender, desert grass, on very poor dry rocky soil, dry sandy soils, stony plain..."- (Quattrocchi, 2006)

*Aristida ternipes*-

"...grows on dry slopes and plains and along roadsides..."- (Barkworth et al., 2007)

"...grows on dry pairies, plains, slopes, and roadsides."- (Stubbendieck et al., 2017)

"Venezuela, U.S., Mexico, Colombia. Perennial, caespitose...forage, growing on rocky slopes, on sandy and gravelly bajadas, related to Stipa..."- (Quattrocchi, 2006)

*Arundinella hookeri*-

"Common on mountainsides, open forests, meadows; 1800-3200m."- (Flora of China vol. 22)

"India, Himalaya. Tufted, shortly rhizomatous...low forage value, fodder, grows on rocky slopes..."- (Quattrocchi, 2006)

*Avena fatua*-

"*Avena fatua* var. *fatua* is a disturbance species in fields, waste laces, and along roadsides and railroad tracks."- (Stubbendieck et al., 2017)

“One of the most noxious weeds in our agriculture. It takes up one and a half times as much moisture as wheat and it severely dries up the soil.”- (Komarov et al. (1963))

“Cultivated fields, shingle beaches, tea plantations, s.l.-1510 m.”- (Davis et al. 1985)

“...cosmopolitan grass weed growing on nearly all soil types...A. fatua has its origin in the relatively arid climate of Asia. The species seems to be troublesome wherever cereals are grown in locations with an annual rainfall of 375 to 750 mm (Holm et al., 1977).”- (CABI, 2020)

“North Africa, central Asia, Europe. Annual or perennial...planted as erosion control, drought-resistant, invasive, the most widely distributed of the wild oat species, one of the world’s worst weeds difficult to eradicate because of shattering and dormancy, forage, a useful fodder, palatable when young, naturalized throughout temperate regions, noxious weed species of disturbed lands, sandy soils, disturbed waste areas, open pasture, open habitats, in coarse desert loam, along roadsides, gardens, brackish soil, cultivated lands, on slopes, a weed of other cereals and fields, worst weed problem in barley, wheat and oat fields...”- (Quattrocchi, 2006)

*Avena sativa*-

“Avena fatua var. sativa grows in a wide range of soils and grows best under mesic conditions.”- (Stubbendieck et al., 2017)

“Europe, Egypt to Morocco. Annual...cultivated in many varieties ,frequently escaped and naturalized...soil improver, fodder, forage, grain crop, a very nutritious source of food, crushed grain and straw for feeding horses, under some circumstances capable of poisoning livestock, open grass plain, common in waste places, fallow fields, along roadsides, disturbed areas, dry soil, occasionally in damp ground...”- (Quattrocchi, 2006)

*Boissiera squarrosa*-

“A common desert grass enjoyed by sheep, goats, mules and camels”- (Cope, 1982)

“Steppes, foothills.”- (Komarov et al. (1963))

“...open places, dry stony sites, native pasture species...”- (Quattrocchi, 2006)

*Bothriochloa barbinodis*-

“Cane bluestem is well adapted to sandy loam to loamy calcareous soils with a pH of 7.2 to 8.0 which overflow frequently. It grows on gravelly foot slopes that have a good soil-moisture relationship.”- (USDA, NRCS National Plant Data Team, 2020)

“...grows in a variety of soils, but it is most common in sandy to gravelly soils. It grows well in calcareous soils, tolerates moderate salinity, and often grows in areas that are occasionally flooded by heavy summer rains. It occurs in desert grasslands, prairies, open slopes, plateaus, swales, and roadsides.”- (Stubbendieck et al., 2017)

“...common species, growing at 500-1200 m along roadsides, drainage ways, and on gravelly slopes in desert grasslands, from the southwestern United States through Mexico and Central America to Bolivia and Argentina.”- (Barkworth et al., 2007)

“North America, South America, US Perennial bunchgrass, densely tufted, erect to spreading, sometimes rhizomatous...seeds dispersed by wind, animal food, forage, palatable before the stems become fully mature and fibrous, recommended for reseeding arid rangelands, leaves diuretic, extremely drought-resistant, full sun, commonly found in semidesert grasslands and chaparral, disturbed habitats, among rocks, along roadsides, open arroyo...”- (Quattrocchi, 2006)

*Bothriochloa pertusa*-

“A tussock-forming perennial, up to 70 cm high.”- (Hodd and Hodd, 1982)

“In the open areas of Acacia Thorn Forest.”- (Hodd and Hodd, 1982)

“Grassy hills, disturbed ground; 1200-1500m.”- (Flora of China vol. 22)

“It will stand up to constant grazing and trampling and is able to withstand moderate periods of drought.”- (Cope, 1982)

“Most commonly found in areas with annual rainfall from 600-900 mm, but also grows at >2,000 mm rainfall and down to 500 mm. Considered as a perennial, drought-evading species, with growth declining rapidly with the onset of dry conditions. Can tolerate short periods of waterlogging...Grows in light shade, but best in full sunlight. Does not grow well when shaded by taller pasture plants or weeds.”- (Cook et al., 2005)

“Asia tropical, India, Indonesia. Perennial, herbaceous...stoloniferous or tufted...shortly rhizomatous...native pasture species, quite palatable, best fed green, eaten when mixed with other grasses, good fodder grass, forage, used for grazing and for stacking, suitable for silage and hay, erosion control, revegetator, turf, lawns, recommended for reseeding eroded land in India, ornamental, cultivated, naturalized, moderate periods of drought-tolerant, withstands heavy grazing and trampling, survives fire, vigorous weed species, sometimes difficult to eradicate, rather common in disturbed as well as undisturbed areas, in moderately damp areas, along roadsides and in rather dry areas, grassland on clay soils and open woodland, limestone, loamy soils, open disturbed roadsides, dry pastures...”- (Quattrocchi, 2006)

*Bouteloua gracilis*-

“ Culms 20-65 cm tall, erect or from geniculate bases...”- (Stubbendieck et al., 2017)

“...grows in pure stands in mixed prairie associations and disturbed habitats, usually on rocky or clay soils and mainly at elevations of 300-3000m”- (Barkworth et al., 2007)

“...grows in a broad range of soils on dry prairies, rocky slopes, mesas, canyons, mountains, and basins. It is most abundant in sandy or gravelly soils, where it often grows in nearly pure stands. It is not found in wet, poorly drained soils...It tolerates drought and close grazing...”- (Stubbendieck et al., 2017)

“...most effective when grown in the dryer parts of the northern and southern Great Plains and southwestern region of the U.S. ...demonstrates good drought, fair salinity and moderate alkalinity tolerance...not tolerant of frequent flooding or submergence. It is also intolerant of shade and acidic soils.”- (USDA, NRCS National Plant Data Team, 2020)

“North America, US Perennial, variable...often with short stout rhizmones...good forage, ornamental, golf courses, turf, naturalized elsewhere, grows in disturbed habitats, grasslands, on rocky or clay soils, pine forest, slopes, scrub, flats, drainages, shrubland...”- (Quattrocchi, 2006)

*Bouteloua repens*-

“...grows in open, usually hilly terrain on many soil types, from sandy ocean shores to montane slopes, reaching elevations of 2500 m.”- (Barkworth et al., 2007)

“...most abundant in sandy or rocky soils. It is found on grasslands, open brushy pastures, dry slopes, roadsides, and stream banks. It is not highly drought tolerant.”- (Stubbendieck et al., 2017)

“North and South America, US, Mexico. Perennial, herbaceous, leaning, not rhizomatous...good forage, growing in small clumps, dry places, montane slopes, dunes and low dunes, sandy ocean shores...”- (CRC World Handbook of Grasses)

*Brachypodium distachyon*-

“Macchie, phrygana, calcareous slopes, steppe, olive groves, fields, s.l.-1250 m.”- (Davis et al. 1985)

“Mediterranean. Annual or perennial...chasmogamous and cleistogamous...invasive, naturalized elsewhere, a weedy species in dry disturbed areas, upland, dry wasteland cliff slopes, dry rocky soil, scrubland, dry red soil, open habitats along roadsides, gardens...”- (Quattrocchi, 2006)

*Briza maxima*-

“Open Pinus brutia woodland, phrygana, rocky limestone slopes, dunes, grassy places, fallow fields and waste places, s.l.-320 m.”- (Davis et al. 1985)

“Common on disturbed and sandy areas.”- (Wilson et al., 2009)

“Shaded sites, roadsides, pastures, weedy on coastal dunes...”- (Jepson eFlora)

“Mediterranean, Europe, Asia temperate. Annual...palatable, low grazing value, widespread weed species, attractive, ornamental grass cultivated and naturalized elsewhere, common in disturbed areas, open sandy soil, along irrigated fields, wetlands and woodlands, well-drained soil, gardens, wasteland, granite rocks, shallow granitic soils, pastures, along roadsides, orchards...”- (Quattrocchi, 2006)

*Cenchrus echinatus*-

“Savannas, disturbed open areas, 100-400m...”- (Davidse et al., 2004)

“...grows in disturbed areas throughout the coastal plain and piedmont of the southern United States, Mexico, Central and South America...”- (Barkworth et al., 2007)

“It can grow in many habitats and is found in dry and moist regions in rainfed and irrigated crops and has been reported as a weed of 18 crops in 35 countries...It prefers moderate moisture and light, sandy, well-drained soils at low elevations (Holm et al., 1977).”- (CABI 2020)

“Tropics and subtropics. Annual...good forage grass when young and before the burs harden, medicinal, anti-malarial use (with leaves of Persea Americana or leaves of Lippia schomburgkiana), tea for kidney problems, and infusion is drunk as a febrifuge in the West Indies, invasive in most tropical countries, a troublesome weed in cultivated land, spines from this plant are very irritating, common on waste ground, near running fresh water, coastal, coastal dunes, near the ocean, open areas, sandy or limestone soils, open ground and waste places, edge of cultivated fields, roadsides, ruderal areas, in turf, on disturbed ground and road verges, road ditch, river sands, poor soils, in vine thickets, on beaches and riverbanks, recently fallow land...”- (Quattrocchi, 2006)

*Cenchrus setigerus*-

“Pakistan, tropical East Africa, through Arabia to India; introduced in several tropical countries. This species is very common throughout the plains and the lower hills and is considered a very fine fodder grass.”- (Cope, 1982)

“Open dry brush and grassland, usually on alkaline soils, sometimes on heavy black clays with impeded drainage. Naturalized elsewhere in dry tropics and subtropics...Adapted to arid and semi-arid climates (annual rainfall as low as 200mm) with a long dry season; responds quickly to light rains...No record of flood tolerance, although some types originate from flooded land...No record of shade tolerance. Few trees or taller species in normal habitat.”- (Cook et al., 2005)

“East and northeast tropical Africa, northwest India, Arabia, Yemen. Perennial bunchgrass or annual...stoloniferous...short rhizomes...cultivated fodder, once established withstands heavy stocking, forage, pasture species or potential pasture grass, high feed value during the pre-flowering stage, tender leaves quite palatable, poor forage value, in India seeds eaten mixed with bajra (millet) for bread making, seeds also eaten raw, adapted to arid and semiarid climates with a long dry season useful against moving sand, very tolerant of drought, naturalized elsewhere, can be a serious riverine weed, found in alluvial flats and water courses, wet to upland soil, open dry bush and grassland, arid deciduous grassland, desert areas, subdesert grassland, hot arid zones, along roadsides, on sandy soils, margins of irrigated fields, sandy and silty soils, free-draining soils, sand plains and sand dunes, alkaline soils, sandstone rocky sites, stony hills, savannah, ravine areas, degraded lands...”- (Quattrocchi, 2006)

*Chloris elata* (*Stapfochloa elata*)-

“Disturbed areas, 100-200m.”- (Davidse et al., 2004)

“Bolivia, Brazil...along roadsides...”- (Quattrocchi, 2006)

Transferred to *Stapfochloa*- (Peterson et al., 2015)

*Cymbopogon citratus*-

"...commonly cultivated and wild, grows well in sandy soils with adequate drainage, semi-deserts, savannah, in clearings, sunny warm and humid conditions."- (Quattrocchi, 2006)

"The species thrive in damp and arid environments in lowland and mid-upland elevations, commonly on rugged hillslopes and in open grasslands."- (Lazarides, 1980)

*Cymbopogon commutatus*-

"Tropical Africa, Asia, India...low to medium palatability, grazed, used for roofing, found in degraded areas, deciduous bushland, open sandstone hillsides, grassy plains, limestone, hillsides, wadi..."- (Quattrocchi, 2006)

*Cynodon barberi*-

"Southern India, Sri Lanka...grazed by cattle, found in wet places, open damp sites, sandy soils, roadsides, gravelly soils..."- (Quattrocchi, 2006)

*Dactylis glomerata*-

"North Africa, Mediterranean, Europe...sometimes a noxious weed species, can withstand heavy grazing, moderately nutritious and highly palatable, cultivated fodder, meadow and pasture grass, forage, cause of hay fever, ornamental honey plant, drought- and shade-tolerant, frost- and heat-resistant, requires good drainage, excellent ground cover, recommended and used for a variety of rehabilitation applications, used for rehabilitation of sites disturbed by mining, may be used for soil erosion control on cut-over forest land, found in moist soils, in timbered areas after fire, in open habitats, gardens, fields, in disturbed places and along road sides, orchards, waste places and depleted sites, meadows, dune hollows, sandy soil, clays and clay loams, in irrigated and high rainfall areas, on logging roads, on normally drained to dry soils..."- (Quattrocchi, 2006)

"Keith (l.c.) regards it as one of the most useful grass for forage and hay, which can grow in semi-arid areas as well."- (Sherif and Siddiqi, 1988)

"Mountain slopes, light forest shade, other grassy places; 1400-3600 m...This is an important pasture and forage grass that has been widely introduced into temperate and subtropical regions throughout the world."- (Flora of China vol. 22)

"Orchardgrass is found from Maine to the Gulf Coast states and from the Atlantic Coast to the eastern Great Plains. It is common throughout the Appalachian Mountains and is especially well-adapted to Maryland, Pennsylvania, West Virginia, Virginia, Kentucky, and Tennessee. It is also found in the high-rainfall regions of the western mountains and in irrigated areas throughout the West. Areas of greatest adaptability in the West are the sagebrush, grass, and pinyon-juniper communities, although the plant has performed well when seeded in the aspen and Douglas fir communities. In the Northeast, orchardgrass is adapted to somewhat poorly drained to well-drained soils."- (USDA, NRCS National Plant Data Team, 2020)

*Dactyloctenium aegyptium*-

“Old World tropics, tropical and subtropical regions...a troublesome weed in crops, drought-resistant, sand-binder and stabilizer, lawns and playing fields, tolerant of alkaline soils, nitrate poisoning has been reported, native pasture species, valuable to excellent fodder grass, forage, quite palatable and nutritious, used by indigenous people to treat amenorrhea and stomach ache, edible grains, seeds dried and ground used for porridge during scarcity in Africa, a decoction from seeds used for kidney inflammations, common in arable land and waste areas, low dry stony hills, in wet places, in disturbed areas near water, rice fields, in gardens and along roadsides, disturbed ground, lowlands in secondary situations, beach sand, loose sand, white sand, reddish brown loamy soils, alluvial soils, waste and cultivated lands, in roadbed, river edges, uncultivated savannah, high rainfall areas, steep wooded hills, fields and open ground, floodplains, generally on poor soil, poor dry soils...”- (Quattrocchi, 2006)

“Disturbed weedy places, especially on sandy soils.”- (Flora of China vol. 22)

“In open areas throughout the Gir Forest. On flat or slightly sloping areas having red clay to sandy red soil. In the absence of grazing it grows erect. In the protected area at Nanava it has become rare after only two years. This suggests that it requires grazing animals to disperse its seeds. It often grows in sparse clumps...It may occur as an understorey to *Themeda quardrivalvis*, dying back as *Themeda quadrivavlis* shades it out.- (Hodd and Hodd, 1982)

“Loosely tufted or stoloniferous annual, prostrate or ascending, 15-60 cm. high; a weed, often on trampled path-sides.”- (Hutchinson et al., 1972)

“Flowering January to April. Disturbed areas near water. Common. Biome: Savanna, Grassland, Nama-Karoo, and Desert. Tropical and warm temperate regions worldwide. Food and drink (seed used as food in times of famine), or pasture, or poisonous (bruised young seed used as a fish poison), or traditional medicine (extracted to treat kidney ailment and coughing), or weed (in ricefields and waste ground, host for viruses).”- (Russell et al., 1990)

*Danthoniopsis dinteri*-

"South Africa...pasture, of little agricultural value, grazed by animals in the young stages, useful for erosion control, common on rocky soil, on mountains..."- (Quattrocchi, 2006)

"Rocky slope 400-500 m"- (Flora Zambesiaca)

*Dichanthelium acuminatum*-

"Vernal plants. Grows in dry to wet, open, sandy or clayey soils of meadows, swamps, bogs, and, occasionally, dry prairie ridges. It tolerates some soil salinity and acidity and can grow in calcareous soils. It has little forage value but may provide limited early green forage. With a few exceptions, it grows in most of the Great Plains and North America."- (Stubbendieck et al., 2017)

"...usually occurs in wetlands and along streams, moist open areas, wet meadows, rich soils, open fields, wet prairies, moist places in woods, along roadsides..."- (Quattrocchi, 2006)

"...common and ubiquitous in dry to wet, open, sandy or clayey woods, clearings, bogs, and swamps, or in saline soil near hot springs, growing in much of the Manual region and extending into northern South America. It is probably the most polymorphic and troublesome species in the genus."- (Barkworth et al., 2007)

*Dichanthelium scoparium*

“…growing in open habitats, low ground, damp and moist soils, moist sand, seasonally flooded places, wetlands, dry to mesic sites, grassland areas, open wet meadows…”- (Quattrocchi, 2006)

“…grows in open, moist, often disturbed sandy soils of lawn areas, pond shores, wetland edges, woodlands, and savannas. It will tolerate somewhat acidic soils. It is grazed by livestock and deer…” -(Stubbendieck et al., 2017)

“…grows in moist, sandy, open, often disturbed areas of the southeastern United States.”- (Barkworth et al., 2007)

“Anthropogenic, dunes, meadows and fields, shores of rivers or lakes, wetland margins”- (Go Botany)

“Throughout the adaptation area of the United States, velvet panicum is identified as either facultative (FAC- equally likely to occur in wetlands or non-wetlands) or facultative wetland (FACW- usually occurs in wetlands, but occasionally found as a non-wetlands) plant...Velvet panicum grows in areas with precipitation ranging from 30 to 55 inches. It prefers coarse and medium textured soils with pH range of 4.5 to 7.5. Velvet panicum is not tolerant of salinity. This plant is found in sandy woods, low areas, and disturbed sites.”- (USDA, NRCS National Plant Data Team, 2020)

*Digitaria ciliaris*

“…grains used as a famine food, economic plant, a variable and poplymorphic species widely naturalized, forage species, good green fodder, best fed after flowering, quite palatable, good pasture, good hay…grows on poor soils, lawn, weedy places, open habitats, along trails, sandy soils and loams, rocky soil along river margin, in sand behind beach, field borders, disturbed areas and waste places, open savannah, coarse sand, alluvial plains, ditches…”- (Quattrocchi, 2006)

"…weedy species, found in open, disturbed areas in most warm-temperate to tropical regions…"- (Barkworth et al., 2007)

"…as a ruderal and weed in waste and disturbed ground, cultivation and gardens. Sometimes it is found near streams and in abandoned clearings in evergreen and deciduous forests. The grass is reputed to be highly palatable and nutritious."- (Lazarides, 1980)

"In open or light shade throughout the Gir Forest. On flat or slightly sloping areas having red-brown to black clay soil."- (Hodd and Hodd, 1982)

"Roadsides, weedy places…a pantropical, weedy annual."- (Flora of China vol. 22)

*Digitaria didactyla*

"…ornamental, cultivated, palatable, native pasture species, provides useful grazing for steers, a pioneer of cleared land, survives droughts and temporary flooding, grown as a lawn grass, playing fields, putting greens, turf grass, good ground cover…grows in damp sandy soils, disturbed sites and swamps, best on sandy loams and loams."- (Quattrocchi, 2006)

"900-1800 mm AAR, survives seasonal dry conditions and drought by losing all leaf. On light soils, responds almost instantly to good rainfall. Can tolerate short term flooding…Tolerates some shade…Very resistant to heavy grazing…Seed reserves can be high in the soil; germinable seed can be spread through dung of cattle on well grazed pastures."- (Cook et al., 2005)

*Digitaria insularis*-

“Digitaria insularis grows in low, open ground of the southern United States, and extends to the West Indies, Mexico, and through Central America to Argentina.”- (Barkworth et al., 2007)

“Culms erect, or geniculately ascending; 70-120 cm long; 5-10 mm diam.”- (Clayton et al., 2016)

“In its native areas in South America it is a plant of low altitude swamps, pastures, railway tracks, roadsides, pastures and disturbed forest. Generally in moist conditions but also occurring in some drier situations”- (CABI, 2020)

“noxious weed, usually avoided by livestock, in wetlands or nonwetlands, in dry regions at lower elevations, pastures, waste places, rangelands, cultivated soils, grazed areas, along roadsides, disturbed places, pineapple fields, coffee plantations, sandy plains, often occurs after burning…”- (Quattrocchi, 2006)

*Digitaria milanjiana*-

“...highly variable grass species which occurs in regions of low (450 mm) to high (1700 mm) rainfall in central and eastern Africa.”- (Hacker, 1984)

“Widespread in native environment, occurring in grassland, savannah or woodland, in tall and short grass associations...Generally not considered shade tolerant.”- (Cook et al., 2005)

“Culms erect, or geniculately ascending, or decumbent; 20-250 cm long...”- (Clayton et al., 2016)

"Perennial or annual, variable…grains eaten by baboons, stock fodder, very high grazing value, highly palatable, natural pasture, forage, suitable for horses and cattle, economic plant, requires moist conditions, prefers fertile soils, it does not tolerate waterlogging, naturalized, colonizer, a weed of cultivation, excellent drought resistance, persistent under heavy grazing, usually found in small patches among trees, occurs on red soil stream banks, woodland and thicket, open spaces, irrigated land, on heavy black seasonally waterlogged soils, seasonally waterlogged grassland, mixed deciduous woodland, sandy soils, on moist sandy soils, disturbed areas and abandoned cultivations."- (Quattrocchi, 2006)

*Digitaria monodactyla*-

"Culms 30-100 cm long."- (Clayton et al., 2016)

"…well grazed, low grazing value, relatively palatable, common in open sour grassland, highland sourveld, mixed bushveld, open habitats, in disturbed areas, on sour sandveld, savannah in stable grassland, sandy soil, on moist soils, on shallow sandy poorly-drained soils. - (Quattrocchi, 2006)

"In dambos, wet grassland, vlei areas in open grassland on sandveld."- (Flora Zambesiaca)

"In undisturbed grassland. In rocky outcrop, on poorly-drained loam soil."- (MNHN 01165742)

"On pantanal in tufts around small termite hummocks."- (NYBG 00713890)

"Cleared forest region. Grass in soaking sandy soil of roadside ditch, growing at side of the water in the ditch."- (NYBG 00713865)

“In tufts or small clumps; culms weak, reclining; around clumps of small brush on campo.”- (NYBG 00713886)

“Yellowish green, forming dense mats, said not to be eaten by cattle; moist campo,”- (NYBG 00713883)

*Digitaria sanguinalis*

“...palatable, fodder, forage grass in pastures, low grazing value, a variable species widely naturalized, invasive, noxious strongly rooted, weed species of maize and peanuts, economic plant, grown for hay, used in making paper, edible seed used as a flour, a decoction of the plant is used in the treatment of gonorrhea, leaves might be cyanogenic…occurs in disturbed places and habitats, cultivated fields, waste places, gardens, sandy soils, lawns, poor soils, along roadsides.”- (Quattrocchi, 2006)

“…most abundant in medium- and fine-textured soils. It is found as a weed in lawns, abused pastures, disturbed sites, gardens, waste places, roadsides, and cultivated fields. It is common in bottomlands and overflow sites where moisture is less limiting. It is rarely found in uplands. It is palatable when it is actively growing but furnishes little forage for livestock or wildlife.”- (Stubbendieck et al., 2017)

“Margins of Alnus woods, shaley slopes, and as a weed of cultivated and waste land, gardens and lawns, s.l.-c 500m.”- (Davis et al. 1985)

“…a common weed in warm temperate and subtropical parts of the Old World and has found its way into most other countries. Like D. ciliaris it is polymorphic…”- (Cope, 1982)

“Anthropogenic (man-made or disturbed habitats). Usually occurs in non-wetlands, but occasionally in wetlands.”- (Go Botany)

*Digitaria seriata*

"Tropical Africa, Kalahari…palatable, mostly on sandy soils…"- (Quattrocchi, 2006)

*Digitaria setigera*

"…weed species, a weed of rice in the tropics, forage, economic plant palatable to stock, occurs in open and disturbed site at edge of lawn, in shady woods, moist regions, waste place…"- (Quattrocchi, 2006)

"Moist slopes, stream banks, roadsides and weedy places…widespread in warm parts of Asia."- (Flora of China vol. 22)

*Digitaria ternata*

"…garden weed species, naturalized, economic plant, palatable, low grazing value, good forage grass, usually on damp places, waste places, scrubby irrigation ditches, in high rainfall areas, gardens, on wet compacted soils, field borders, disturbed ground, shaded disturbed places, uncultivated lands, along roadsides, weedy places…"- (Quattrocchi, 2006)

"Grassy, weedy places…This species is a good forage grass."- (Flora of China vol. 22)

"It can be abundant in upland rice in Indonesia (Kostermans et al., 1987), is common in cereal crops in Ethiopia (Stroud and Parker, 1989) and can be serious in cereal crops in East Africa (Terry, 1984). Reed (1977) notes it as a weed of arable land, frequently invading pastures. Wells et al. (1986) list it as behaving as a ruderal, agrestal, and pasture weed in South Africa, competitive and able to replace other vegetation."- (Weed Science Society of America)

*Diheteropogon hagerupii*

"Tropical Africa. Annual, fodder, on dry sites, sandy places…"- (Quattrocchi, 2006)

GENUS: "species of open habitats, savannah, poor stony soils, rocky hills, impoverished soil, ruderal…"- (Quattrocchi, 2006)

*Echinochloa crus-galli*

"edible seeds, very polymorphic and pioneer grass…seldom grazed by any animal, poor grazing for wildlife and livestock, harsh and unpalatable at maturity, fair to poor forage value for livestock, suitable for ensilage, can be cultivated for hay and as a cereal, seed used as a millet, roasted seed a coffee substitute, young shoots eaten raw or cooked, seeds eaten by songbirds and waterfowl, seeds furnish some food for ground birds, noxious weed species of fields and rice, a vigorous competitor for soil nitrogen in rice crops, invasive, useful for erosion control and habitat rehabilitation…tolerates poor drainage and flooding, intolerant of dense shade and severe drought, usually occurs in wetlands and wet places, in rich soils, in swampy ground, brackish marsh in sown pasture, in freshwater swamps, in moist disturbed sites, in temporarily flooded palustrine wetlands and seasonally wet habitats, in moist poorly drained areas, in shallow water or after drawdown, on silts and clays in ponds and depressions, in shallow water around the periphery of rice fields, in wet and agricultural land, in fields and ditches, river bottoms, marshes, floodplains and along lakeshores and stream banks."- (Quattrocchi, 2006)

"…thrives in wet situations. Suitable habitats are inundated usually for long periods to depths of <1m and germination can take place in shallow water. Consequently, the plants commonly grow in or near lakes, swamps, marshes, canals, streams and ditches, and generally in open, low-lying ground on a range of sandy or clayey, coastal or inland soils. Like *E. colona* the grass is highly palatable, especially to buffalo and cattle, and its grain at times is eaten by village people. Similarly, it behaves as a weed in disturbed and cultivated areas, being especially troublesome in rice fields because of its similar growth requirements."- (Lazarides, 1980)

"…polymorphic weed of warm temperate and subtropical regions, whose numerous intergrading races are apparently the consequence of cleistogamous self-pollination…This is said to be a good fodder grass, once sown for its grain in Lahore district and occasionally still eaten in times of want. It is common in marshy places and rice fields below 3000m."- (Cope, 1982)

"…grows best in low, moist, disturbed areas with high soil fertility. This weed grows in cultivated fields, feed grounds, corrals, waste places, roadsides, ditches, and riverbanks. It produces fair to good forage if grazed in the early growth stages. However, production is unreliable, and it is unpalatable later in the season. It may accumulate nitrates and cause animal poisoning." – (Stubbendieck et al., 2017)

"…widespread in warm temperate and subtropical regions of the world, extending into the tropics. It prefers open sunny places and is largely restricted to wet soils, from loams to clays. It can tolerate drier soils, but can also continue to grow when partially submerged."- (CABI, 2020)

*Echinochloa frumentacea*

"…economic plant extremely palatable, largely cultivated as a cereal for its edible seeds, fodder and widely used forage, requires rich moist and well-drained soil, used as a soil stabilizer and for temporary control of erosion in newly cleared and ploughed sandy soils, a rapid grower, cropping 6 weeks after sowing, sometimes a weedy escape from cultivation, seed cooked and used as a millet, seed can be cooked whole or can be ground into a flour, the plant is useful in constipation."- (Quattrocchi, 2006)

"It grows well in wet soils but will also grow on well-drained upland soils."- (USDA, NRCS National Plant Data Team, 2020)

"Anthropogenic (man-made or disturbed habitats), meadows and fields…Occurs in wetlands or non-wetlands."- (Go Botany)

*Echinochloa haploclada*

"Perennial, aquatic, often wiry, very variable…a good seed producer, useful for erosion control, low grazing value, well grazed only when young, grains eaten by people, occurs on stream banks and in swamps, edge of pond, dry river beds, marshy swamps, moist grassland, marshes, floodplain, grasslands, open areas of the coasts, from sandy loams to alluvial silts, in heavy black clays and areas with open water, paddy fields, in wet areas and on seasonally waterlogged ground, in low wet areas, in seasonally flooded lowlands and ditches…"- (Quattrocchi, 2006)

*Echinochloa oryzoides*-

"Culms erect, forming a narrow tuft up to 1m tall."- (Flora of China vol. 22)

"A genus of c. 30 species distributed in tropical and warm-temperate regions of the world. The grasses are chiefly moisture-loving annuals or perennials..."- (Lazarides, 1980)

"…adapted as a weed of rice (*Oryza*), which it resembles in habit."- (Flora of China vol. 22)

"Often co-existent with *E. crus-galli* as a rice mimetic plant strongly confined to paddy lands."- (Davis et al. 1985)

"…economic plant, occurs almost always in wetlands and in the flooded portion of the rice fields, cereal, widely naturalized, weed species of drains, a common weed of rice fields throughout the world, paddy-rice mimic weed…"- (CRC World Handbook of Grasses)

*Echinochloa picta*

"It resembles E. crusgalli in its preference for very wet conditions and grows in similar situations though usually in deeper water. In low-lying parts of lowland <1500m elevation, the grass is often predominant in the fringing communities of deep rivers, lakes, lagoons, swamps and marshes. The foliage is reported to be high in sugar content and relished by grazing animals. In certain regions, the grain is eaten and the culms are used for thatching and to produce extracts for the preparation of sugar and beverages."- (Lazarides, 1980)

*Echinochloa stagnina*

"Short-lived perennial and annual, aquatic…troublesome weed of paddy fields, a vegetable salt from the ashes, cultivated, rich fodder, coarse but palatable hay, economic plant very productive and highly palatable, readily grazed by stock, grain eaten in time of scarcity, sweet culms useful thatching grass, pith used for caulking boats, in the Niger basin used as sugar, often floating on the water surface, forming dense colonies, grows along rivers and in lakes and lagoons, dry arid and wet zones, sandy soils, in standing water, in stagnant pools and marshes, streamsides, irrigation ditches, swamps, waterways, marshes, rivers, irrigation channels, in cultivated fields, on banks of lakes…"- (Quattrocchi, 2006)

"This species is closely allied to *E. picta*, being similar in habitat though more restricted in its Asian distribution. Often, it occurs as a major constituent of the vegetation of floating islands."- (Lazarides, 1980)

*Ehrharta calycina*

"Africa, South Africa. Perennial bunchgrass, rarely annual...sometimes or rarely stoloniferous, often with a creeping branched rhizome...seeds profusely, reproduces by seed and rhizomes, aggressive and highly invasive weed, a rapidly spreading pest naturalized elsewhere, cultivated fodder, highly palatable, useful pasture species on soils of low fertility, grazed by domestic animals, range reseeding and revegation of disturbed areas, soil stabilization uses, useful to prevent soil erosion and for sand stabilization, drought and frost resistant, susceptible to heavy grazing, common on the coastal sand dunes and sandy places, shady places, stabilized sand dunes, among shrubs, rocky places, a widespread weed of roadsides and bushland on sandy soils, wildlands, heavily grazed veld..."- (Quattrocchi, 2006)

"...grows in a wide range of habitats, usually on deep sandy soils. In California, it is found in sand dunes, dune scrub, coastal sage scrub, coastal grasslands, maritime chaparral, and oak woodlands...In Australia, it grows in disturbed sites such as road sides, in heathland, in *Banksia* woodlands...and in blue gum woodlands...resistant to drought and moderate frost...does not tolerate waterlogging, oxygen-poor soil conditions or high salinity levels...seeds are dispersed primarily by wind...birds and mammals may disperse seeds of *E. calycina* if they become attached to feathers or fur."- (CABI, 2020)

*Eleusine coracana*

"Pantropical, Asia, Africa. Annual or perennial...progenitor of finger millet, weed species, low grazing value, tough and unpalatable as it matures, utilized by livestock in the young stage, toxic to stock, grain crop, fermented for alcoholic drinks, seeds viable for many years, grains used to make flour and cereal, grains eaten by baboons, occurs in disturbed areas, grassland, savannah, slopes, limestone, streams and ditches..."- (Quattrocchi, 2006)

"The annual crop plant, *E. coracana* (African or finger Millet), though relatively worthless as fodder, is cultivated widely as a cereal"- (Lazarides, 1980)

"Cultivated in the Tropics of the Old World. Sometimes grown as a fodder, especially in the southern parts of Libya."- (Sherif and Siddiqi, 1988)

"...is sometimes cultivated in the plains and lower hills...and used to make a kind of porridge or alcoholic beverage. The species may occasionally escape..."- (Cope, 1982)

*Eleusine indica*

"Pantropics and subtropics, origin paleotropics. Annual or short-lived perennial... generally unpalatable to stock, eaten when young, when mature foliage is very tough, cyanogenic or HCN toxic, can be poisonous to stock, has been recorded as causing the deaths of calves and sheep, culms used for hats, can withstand flood inundation for limited periods, a very polymorphic species, suitable for stabilizing sandy soils, similar to and confused with Leptochloa digitata (R.Br.) Domin, a common aggressive noxious weeds of lawns and playing fields, common in bare disturbed areas, lowlands, low hills, sandy soils, compacted soils, in ordinary garden soil, yards, sandy riverbanks, garden weeds and arable land, cultivated areas, waste places, and along roadsides, hill forest, on rocky roadside and gravel, wet plains, farm tracks, on floodplains and shores, thickets, damp pasture, areas exposed to trampling...”- (Quattrocchi, 2006)

“Annual...widespread in Delta Amacuro, Bolívar, and Amazonas. Widespread elsewhere in Venezuela and worldwide in tropical and warm-teperate regions.”- (Davidse et al., 2004)

“In open, treeless areas. On flat, disturbed areas near villages or hamlets, where nitrogenous waste accumulates. Often on poorly drained, red-brown or black clay soil. In sparse clumps, associated with Sprobolus diander. Its compact form enables it to withstand trampling by buffalo.”- (Hodd and Hodd, 1982)

“The common pantropical weed, E. indica, occurs in Southeast Asia in altitudes <2000 m, in an extremely wide range of coastal and inland, often moist habitats. It colonizes disturbed ground and provides useful cover on denuded soils susceptible to erosion.”- (Lazarides, 1980)

*Elymus mutabilis-*

“Tufted perennial without rhizomes...Distribution: Gilgit; Arctic Eurasia and North America; the Caucasus and the mountains of Central Asia.”- (Cope, 1982)

“Sparse forests, forest margins and glades, among shrubs, mountain slopes, meadows, pebbles...This species is a good forage grass.”- (Flora of China vol. 22)

*Elymus tibeticus-*

"Forests, mountain slopes, valleys, roadsides; ca. 2500m. Xizang, Yunnan [Bhutan]"- (Flora of China vol. 22)

*Enneapogon scoparius-*

"Southern tropical Africa, Yemen. Perennial...rhizomatous...moderately to very palatable, low grazing value, weed species used for broom-making, growing on open grassland, dry situations, under trees in disturbed veld, arid sweet bushveld, on sand, dry grasslands, on well-drained stony hills, limestone, on stony slopes, among rocks, stony hills, shallow soils, closely related to Enneapogon cenchroides..."- (Quattrocchi, 2006)

"... prefers to grow in the shade under trees. It is also associated with dolomitic soils. Its small stature makes it ideal for landscaping. Bottlebrush grass is very hardy and is ideal to plant where soil has to stabilized against erosion."- (Wentzel, 2020)

"Mostly in Colophosperumum mopane woodland, but also in scrub and open grassland, growing in arid conditions, amongst limestone pebbles, on basaltic soil, also on sandy hill-slopes and along roads..."- (Flora Zambesiaca)

*Eragrostis airoides-*

"The Caribbean to Argentina, Brazil, Paraguay. Perennial, caespitose....forming colonies, sandy areas, savannah, seasonally inundated areas, disturbed places."- (Quattrocchi, 2006)

"...a South American species that, in the Manual region, is known from roadsides and disturbed sites in Brazos County, Texas and Lamar County, Alabama."- (Barkworth et al., 2007)

*Eragrostis mexicana-*

> “North and South America, US, Mexico, Argentina, Brazil, Paraguay. Annual...fodder, a weed of urban areas, ballast, disturbed open areas, slopes, near cultivated fields, on waste ground, muddy soil, edge of river, hard ground, trampled, soil, along roadsides...”- (Quattrocchi, 2006)

> “...grows along roadsides, near cultivated fields, and in disturbed open areas, at 100-3000m. It is native to the Americas its native range extending from the southwestern United States through Mexico, Central and northern South America, to Argentina.”- (Barkworth et al., 2007)

> “...grows best in sandy soils and may be found on the edges of cultivated fields, roadsides, and open disturbed areas. It has little value as forage for livestock or wildlife. It is found in the southwestern Great Plains and southwestern United States, on the West Coast, and in Mexico, Central America, and South America.”- (Stubbendieck et al., 2017)

*Eragrostis papposa-*

> “Ethiopia, Kenya, Sudan, Uganda, Tanzania, Yemen, India, Nepal. Short-lived perennial....weed of cultivation, useful for erosion control, found in shallow soil, rocky places, open stony hillsides, sandy and gravelly soil, dry alluvial plains, sandy loam basic soil...”- (Quattrocchi, 2006)

> “Tufted perennial, often short-lived...A very distinctive species...Nothing seems to be known of its economic uses.”- (Cope, 1982)

*Eragrostis superba-*

"Southern and tropical Africa. Perennial bunchgrass...heavy seeder, escaped from cultivation, large seedheads rather ornamental, very to fairly palatable, utilized as hay, forage, cultivated fodder, gives a high yield, weed of cultivation, native pasture species, stemmy and unpalatable at maturity, quick growing, dense undergrowth provides a habitat for wildlife, useful for erosion control and stabilization of bare soils, used for reseeding denude land in dry areas, good drought tolerance, high tolerance to salinity and alkalinity, grows on poor sandy soils, plains, omiramba, slopes, stony soils, sandy clay loam brushland, coastal bushland, in arid and semiarid land, in wooded grassland, disturbed sandy clay, disturbed sandy roadside, on dry sandy beach, disturbed rocky roadside, red sandy soil, clay loams and clays, shallow rocky clay, clay loam grassland, gravelly grassland, alluvial sand and irrigated orchards, black clay soil , drainage furrows..."- (Quattrocchi, 2006)

"...native to Africa, where it is grown for hay, being fairly palatable and drought resistant. It is also used for erosion control and revegation. In the Manual region, it grows on rocky slopes, in sandy flats, and along roadsides, at 480-1650 m, often with Acacia, Prosopsis, Fouquieria splendens, Juniperus, and Quercus."- (Barkworth et al., 2007)

"Perennial up to 1m tall...This grass if found from the Free State and Kwazulu-Natal northwards to the Sudan usually on sandy or gravel soils occasionally on clay. Found mainly in disturbed places in the veld and roadsides, also grows on termitaria. It has been introduced to India, Australia and the USA.... a plalatable grass especially in spring and is fairly drought-resistant and because of this has been cultivated as a pasture in some countries. As it grows in disturbed places, it has been used in erosion control and re-vegetation projects."- (PlantZAfrica, 2000)

"Deciduous woodlands, wooded grassland and floodplain grasslands, in sandy soils, on dry Kalahari Sands, in shallow pan-like depressions and in black clay alluvium, sometimes on rocky outcrops and termitaria; also in cultivated or disturbed ground at roadsides 0–1400 m."- (Flora Zambesiaca)

*Eragrostis tef*-

"Northeast Afria, Ethiopia. Annual bunchgrass...famine crop possibly derived from Eragrostis pilosa (L.) P. Beauv., edible seeds, one of the faster growing hay crops known, food and fodder, straw used in brick manufacture, cultivated cereal, high grazing value, extremely palatable and very well grazed, valuable hay and pasture grass suitable for all kinds of stack, widely grown for hay, seed eaten by wildlife and cattle, cultivated by the ancient Egyptians, a staple cereal in Ethiopia, grain crop species, good for erosion control, in Ethiopia grains ground to flour and used for making unleavened bread and a pancake (injera), susceptible to frost, tolerant of drought, common sandy loams or black soils, flood channels, weedy places, gardens, cultivated lands, disturbed veld, heavy loams, waste ground, along roadsides..."- (Quattrocchi, 2006)

"This plant is native of Ethipioa, where, according to Bor (Grasses Ind. Burm. & Ceyl. 513. 1960) it is used as food grain. But in other parts of the world it is used as a hay fodder."- (Sherif and Siddiqi, 1988)

"In Ethiopia, tef grows where annual rainfall ranges between 950-1500 mm, with about 450-550 mm during the growing season (Tefera et al., 2006). Tef cannot withstand more than 2500 mm rainfall. However, tef can adapt to growing conditions ranging from drought to waterlogging, and is able to withstand wet conditions, perhaps better than any cereal other than rice."- (Feedipedia)

*Eragrostis variabilis*-

“Hawaii. Bunchgrass, found in coastal dry grassland, basalt cliffs, rock crevices on steep basalt sea cliffs, rocky sites, in coastal dry or mesic forest, wetland...”- (Quattrocchi, 2006)

“...known to occur on sand dunes, grasslands, open sites in dry forest, and exposed slopes and ridges or cliffs. On the main islands and the Northwest Islands of Kure Atoll, Midway Attol, Pearl & Hermes Reef, Lisianski, Laysan, and ihoa, kawelu is often a main component of native bird habitat.”- (Native Plants Hawai’i)

“Kawelu is one of the dominant species on Laysan and Lisianski islands and Pearl and Hermes Atoll where it is widely used by seabirds for nesting and foraging.... endemic that occurs in the Hawaiian Island on sand dunes, grasslands, open sites in dry forests, and exposed slopes and ridges or cliffs from sea level to approximately 3,700 feet...grows naturally in areas that receive approximately 40 to 100 inches of rainfall annually....distinct difference in growth habit between plants from the Northwestern Hawaiian Islands and those found on the main islands.”- (USDA, NRCS National Plant Data Team, 2020)

*Eriachne aristidea-*

“South Australia, Western Australia, Northern Territory, Queensland, New South Wales. Annual or short-lived perennial...usually not very palatable, readily grazed when green, usually trampled or blown away, an inland species, stabilizer of loose sandy soils, an indicator of poor range condition, grows on loose sandy soils, sand dunes...”- (Quattrocchi, 2006)

“Endemic in SA and NSW, and predominantly south of 20°S in WA, NT and Qld. A characteristic species of the arid interior, but extending into semi-arid areas in Qld and NSW. A common species of sand dunes, sand plains and sand hills; also of seasonally flooded, alluvial sandy or loamy flood plains, levees and swales; sometimes also in shallow, stony soils on sandstone and quartzite outcrops and ridges.”- (Mallett et al., 2005)

“Widespread; occurring mainly on clayey sands of sand plains and dune fields association with spinifex grasslands, but also on coarse alluvial soils and sandy red earths with bloodwood, ironwood, and mulga. Distribution is sparse, though locally dense stands occur in depressions and disturbed sites. Plains flower mainly in the summer months, though with favourable rainfall growth continues until September.”- (The Grasses of Central Australia)

*Festuca arundinacea-*

“Europe, temperate Asia, northwest Africa. Long-lived perennial bunchgrass...short-rhizomatous or without rhizomes, rarely stoloniferous...planted as a pasture grass, cultivated for hay and fodder, turf, forage, palatable when young and succulent, coarse and tough when mature, noxious and invasive weed widely naturalized elsewhere, potential seed contaminant, ornamental, sometimes poisonous due to phytotoxins, drought-resistant, resistant to trampling, tolerant of poor drainage and seasonal flooding, ground cover, excellent soil improver, colonizes bare soil, useful in rehabilitation and watershed protection, suitable for reclamation of surface mines and for erosion control, usually found on both wet and dry sites, marshes, in grazed woods, bottomlands, meadows, eroded patches, open habitats, ditches, in fallow and abandoned fields, damp hollows, disturbed areas, along roadsides, railroad tracks, on heavy clay soils or on deep loam, fields and open grounds, swampy verges...”- (Quattrocchi, 2006)

“...native of C and N Asia and Europe, widely introduced as a pasture grass and naturalized in other temperate countries....Valleys, under shrubs, along forest margins; 700-1200m.”- (Flora of China vol. 22)

“...adapted to cool and humid climates and most soils with a pH of 5.5 to 7.0. Tall fescue will grow fairly well on soils low in fertility, but it is better adapted to fertile conditions.”- (USDA, NRCS National Plant Data Team, 2020)

“...Eurasian species that is grown in all but the coldest and most arid regions of the Manual region for forage, soil stabilization, and coarse turf, and often escapes. It is frequently infected with the endophytic fungi *Neotyphodium coenophialum*, which confers insect and drought resistance to the plant, as well as producing ergot alkaloids that are toxic to livestock.”- (Barkworth et al., 2007)

“...most common in deep, fertile, silty to clayey loams. It grows in moist soils of lawns, fields, pastures, meadows, woods, roadsides, waste areas, and disturbed sites. It is tolerant of drought and high water tables. It was introduced from Eurasia for turf and forage. The forage is coarse, palatable when young, and rated as fair for livestock and poor to fair for wildlife. Plants may contain an endophytic fungus that causes fescue foot, a serious disease affecting cattle, horses, and sheep.”- (Stubbendieck et al., 2017)

*Heteropogon contortus*-

“Warm temperate regions, throughout tropics and subtropics. Perennial bunchgrass or rarely annual...shortly rhizomatous...needle-sharp penetrative callus, fruits can become entangled n the wool of sheep and puncture their skin, an increaser species, seldom cultivated, rarely sown, native pasture species, low to medium palatability early palatable, good and nutritious only when young, coarse and unpalatable when old, valuable as fodder or hay, forage grass for cattle, eaten by mountain zebra and waterbuck, tillers eaten by baboons, noxious weed species, invasive, does not persist in semiarid areas, does not tolerate flooding and high levels of salinity, fairly tolerant of short-term droughts, useful in soil erosion control, used in India for making coarse mats, very good grass for thatching or roofing, suitable for paper manufacture...widespread in tropical open forest and woodland, savannah, Acacia scrub, dry woodland forest, field margins, open places in forest, cliff slopes, sandy alluvial soil, on poor soils, on sandy loams, coarse sand, in loose dry sand, open sandy soils, lawn, roadsides, moist ground, sandy linght-orange soil, on well drained and stony soils, disturbed sites and flatwoods, hillsides, infertile and shallow soils, grassland, bushveld areas, on rocky slopes and canyons, rocky ground in open places...”- (Quattrocchi, 2006)

“...grows best in sandy soils but will grow in other soil textures in open, dry, rocky prairies, hills, and canyons. It is most abundant in heavily grazed pastures. It provides fair to good forage for cattle and horses during the growing season but then becomes coarse and unpalatable. Its coarseness makes it of little value to sheep or wildlife. The awns may be troublesome to the eyes and mouths of grazing animals, especially sheep.”- (Stubbendieck et al., 2017)

“...grows on rocky hills and canyons in the southern United States into Mexico, and worldwide in subtropical and tropical areas, occupying a variety of different habitats, including disturbed habitats. It is probably native to the Eastern Hemisphere but is now found in tropical and subtropical areas throughout the world. It is considered a weed, being able to establish itself in newly disturbed and poor soils.”- (Barkworth et al., 2007)

“Savannas, 50-200 m...pantropics”- (Davidse et al., 2004)

“On treeless, open areas throughout the Gir Forest. On flat areas to steeply sloping hillsides having sandy red or rocky=red soil. In dense pure stands or in clumps associated with Aristida redacta, Hackelochloa granularis and Sehima nervosum. The annual variety is much commoner than the perennial variety, probably because it can readily recolonise overgrazed areas. The perennial form responds to grazing by becoming compact and rosette-like. In Devalia protected areas the perennial form is gradually invading, dominating all other grass species. Preferentially grazed by buffalo after the injurious awns are shed."- (Hodd and Hodd, 1982)

"In Southeast Asia, as in other parts of its distribution, it occurs in a very wide range of habitats on hill slopes and plains, often forming extensive gregarious stands. Suitable habitats include disturbed and waste places, the beds and banks of streams, and sandy coastal foreshores; while associated communities include grassland, eucalypt savannah, open scrub and deciduous or dipterocarp and other evergreen forests. Though more common in the lowlands, H. contortus extends to at least 1500 m altitude. Particularly when young, the grass is widely considered to be excellent fodder as pasture or hay. However, the mature long-awned, spear-like spikelets fall in entagled masses and may penetrate the hides of animals, at times injuring sheep and cattle."- (Lazarides, 1980)

"...good forage grass for the southwestern United States, and does not develop sharp awns if it is consistently grazed. It is palatable to most livestock during the growing season, but as it matures, it becomes coarser, and loses palatability...high degree of adaptability that has allowed it to survive in locations around the world...In Texas, it is found in sandy prairies, the coastal regions, the Trans-Pecos Mountains, and persists in well-managed pastures, although it was once a common grass in the coastal prairies. In Hawaii, tanglehead occurs naturally on all the major islands at sea level to about 2,000 feet elevation and favors dry habitats and rocky cliffs close to the ocean."- (USDA, NRCS National Plant Data Team, 2020)

"Spear grass is native to the tropics and subtropics of Africa, Southern Asia, Northern Australia and Oceania and is naturalized in tropical and subtropical areas of America, East Asia and the Pacific Region. Spear grass is a summer-growing grass, highly resistant to grass fires. It is a species of savannahs and open forests (*Combretum-Terminalia*) (Cook et al., 2005). *Heteropogon contortus* is seldom cultivated and usually found wherever grasslands are periodically burned. Spear grass mainly grows from 30°N to

30°S and from sea level up to an altitude of 3800 m (Cook et al., 2005; Göhl, 1982). It is found from sub-humid to semi-arid areas in the tropics and subtropics where annual rainfall is comprised between 600 and 1000 mm, but it can grow under rainfall lower than 210 mm (Soromessa, 2011). It is tolerant of frost but does not grow during winter (FAO, 2012). Spear grass does not withstand waterlogging but may bear short periods of flooding. *Heteropogon contortus* can grow on a wide range of well-drained soils provided they are neither too infertile nor too saline. Optimal pH for spear grass ranges from 5 to 6. It has some tolerance of light shade (Cook et al., 2005)."- (Feedipedia)

"...rhizomatous perennial, growing from 200 to 1000mm high...prefers tropical and warm temperate regions around the world. It is very widespread in South Africa, occurring in the North-West, Limpopo, Mpumalanga, Gauteng, KwaZulu-Natal, Eastern Cape and the Western and Northern Cape. It also occurs in Namibia, Botswana, Swaziland and Lesotho. This species thrives on poor soils. However, it prefers growing in sandy to clayey loam, well-drained soils, usually on hillsides and among rocks. It is resistant to grass fires...often grows naturally in Savanna grasslands. Seasonal fire disturbances play a vital role in clearing up an area..."- (PlantZAfrica, 2000)

*Homopholis proluta-*

"Queensland, New South Wales. Perennial, rare species, tufted, spreading, rhizomatous or stoloniferous...useful for pasture, ornamental, not invasive on heavy soils, poor soils, dry woodland..."- (Quattrocchi, 2006)

*Hordeum spontaneum-*

"Africa, Asia temperate and tropical, Europe. Annual, wild form of barley, progenitor of cultivated barley, brittle rachis, husked grains..."- (Quattrocchi, 2006)

"Annual; culms up to 70 cm high...ancestor of two-rowed barley. It is considered poor fodder and can become a serious weed of cereal crops. It is not always easy to distinguish it from two-rowed barley, particularly when the latter is self sown in ruderal sites."- (Cope, 1982)

"Annual. Stems 30-70 cm, fasciculate....Quercus forests, scrub, rocky limestone slopes, marly banks, waste places and cultivated land, 30-1650 m."

"Thickets, stony screes, pebbles, roadsides, waste places, often as a weed in cultivated fields of Hordeum and other crops; 3500-4000m."- (Flora of China vol. 22)

*Ischaemum rugosum-*

"Tropical and temperate Asia. Annual or perennial...sometimes the grain is used as food, native pasture species, valued for grazing, animal food, good forage and fodder, eaten buy cattle and horses when young and fresh, also used as hay, invasive plant, potential seed contaminant, naturalized, in Malaysia infests rubber and vegetables, bad and noxious weed of ricefields and irrigation ditches, young plants very similar in appearance to rice, growing in water, moist and wet habitats, low-lying black soil, in open and wet grasslands, tank margins, in damp places along stream banks and marshy areas, in roadside ditch, roadside gravel, edge of road, drainage ditches, at field edge, areas permanently flooded with water..."- (Quattrocchi, 2006)

"...an erect or ascending perennial or sometimes annual plant, which grows in lowlands <300m altitude in open, wet or periodically flooded sites. Though sometimes used as a cereal and producing the younger stages nutritious fodder for cattle and horses, it can be a troublesome weed of ricefields where flooding provides optimum growing conditions."- (Lazarides, 1980)

"Weedy annual 25-70 cm tall. Secondary , weedy vegetation, especially in open, seasonally wet sites..."- (Davidse et al., 2004)

“Marshy fields, ditch banks, river banks, other wet often slightly saline grassy places; 100-1800m...This native of tropical Asia is now widespread as a weed in tropical parts of the world, especially as a weed of rice fields.”- (Flora of China vol. 22)

“...opportunistic and effective colonizer of open, disturbed or newly cleared areas. Although it is a sun-loving plant, it can persist in sites receiving only 30-35% of full sunlight. It occurs at altitudes of up to 2400 m in the Philippines. It is particularly well adapted to wet sites and is often found in ricefields or low-lying areas that are periodically flooded.”- (CABI, 2020)

*Iseilema macratherum-*

“Queensland, Northern Territory, Western Australia. Annual...useful for erosion control, generally not grazed when young...usually on cracking clay soils and medium-textured red earths, palatable to stock when sufficient bulk has grown...”- (Quattrocchi, 2006)

“...grows in a wide variety of habitats from – to 650 m asl, over nine ecoregions of northern Australia. This annual usually occurs on cracking clay soils and medium textured red earths, often on river flats, in swamps and other riparian habitats...palatable to stock when sufficient bulk has grown, and is generally not grazed when young...”- (IUCN)

“Bull Flinders is similar in distribution to red Flinders [Red Flinders description: ‘confined entirely to cracking clay soils and medium-textured red earths. These are alluvial in origin or developed on calcareous rocks, and usually red-brown or grey. It is commonly localized to drainage lines and other depressions, and occurs with Mitchell grasses, gidgee, coolibah, or saltbush and bluebush.’], but apparently less common and restricted to the far northern part of the area.”- (The Grasses of Central Australia)

*Iseilema membranaceum-*

"Australia, South Australia, Queensland, Northern Territory, Western Australia, New South Wales. Annual, ephemeral, variable...grain borne among the small leaves, very palatable when young, high forage value, excellent and nutritious hay, spreads rapidly by seed, will tolerate temporary flooding, it does not stand heavy stocking, grows on heavy cracking clays, dry parts, gray clay, open grassland..."- (Quattrocchi, 2006)

"Sparsely distributed throughout the area; almost wholly confined to cracking clays and medium-textured red earths in association with short grasses and forbs, Mitchell and neverfail grasses and gidgee. It is also known to occur on sand dunes and probably in gilgais in saltbush-bluebush country."- (Grasses of Central Australia)

*Leersia drepanothrix-*

"Tropical Africa. Annual or perennial, loosely tufted, shortly rhizomatous, wet places, marshy areas..."- (Quattrocchi, 2006)

"Up to 1 m, high, erect from a short rhizome; marshy places." - (Hutchinson et al., 1972)

open- (personal communication M. Vorontsova, 2019)

*Leptochloa panicoides-*

"North America, US, South America. Annual...forage, troublesome weed in water-seeded rice, found in wetlands, shallow canals, marshes and wet habitats, moist open sandy areas."- (Quattrocchi, 2006)

“...native from the central Mississippi and Ohio river drainages south through Mesoamerica to Brazil. It usually grows in somewhat mesic habitats.”- (Barkworth et al., 2007)

“From central Mississippi and Ohio River drainages in the United States south through Mesoamerica to Brazil; generally in mesic sites.”- (Snow et al., 2008)

*Leptochloa virgata-*

“Southern US to Argentina, Mexico, Brazil, Paraguay. Perennial or annual...caespitose...weed speceies, may infest rice fields, growing on wet sandy soils, mud, disturbed areas, open ground, savannah, edge of river, cultivations, grasslands, tropical lowland, dry slopes...”- (Quattrocchi, 2006)

“...common neotropical species that extends from the southern United States through the West Indies to Argentina.”- (Barkworth et al., 2007)

“Caespitose perennial 50-100 cm tall...Savannas, disturbed areas, 100-1200m...Widespread elsewhere in Venezuela and throughout tropical and warm temperate America.”- (Davidse et al., 2004)

“From southern Texas, southern Florida, and the West Indies through Mesoamerica and South America (excluding Chile) and locally in Papua New Guinea and Papua Province, Indonesia (formerly Iryan Jaya); occurring in numerous vegetation and soil types, but mostly in more mesic climates.”- (Snow et al., 2008)

*Leymus karelinii-*

“Russia, Asia temperate. Perennial, natural pasture, useful for erosion control, found in disturbed sites, along roadsides and river drainage, rocky areas, sandy soils...”- (Quattrocchi, 2006)

“Grassy places on mountains; 1600-2100m. Xinjiang [Kazakhstan, Kyrgyzstan, Russia, Turkmenistan, Uzbekistan]. This species is used for forage.”- (Flora of China vol. 22)

*Lolium multiflorum*-

“Mediterranean, Europe, exact native range obscure. Annual or biennial to short-living perennial...ornamental grass widely naturalized in temperate regions, a successful invader of post-agricultural succession in the Inland Pampa grasslands in Argentina, cultivated and occasionally escaped, soil improver, quick ground cover, hay, useful for fodder and for erosion control, palatable and highly nutritious, a valuable pasture grass, dry or very wet soils are not suitable, sensitive to summer drought, requires mild or warm climates, shade intolerant, very sensitive to winter cold and winter flooding, if well established can survive short periods of flooding, weed species of roadsides and waste places, disturbed sites, open habitats, fields, pastures and gardens, along edge of road...”- (Quattrocchi, 2006)

“...a European species, now grows in most of the Manual region. It is planted as a cover crop, as a temporary lawn grass, for roadside restoration, and for soil or forage enrichment; it often escapes from cultivation, becoming established in disturbed sites.”- (Barkworth et al., 2007)

“Al-Abiad, cultivated ground near water course...Most of Europe (incl. SW Russia). N Africa and temperate Asia; introduced into China, Japan, S Africa, S America, N America and Australia.”- (Sherif and Siddiqi, 1988)

“Weedy places...A most valuable grass, known as Italian rye grass. Unfortunately, Italian rye grass is subject to freezing in the USSR, and can be grown successfully only along the Black Sea coast and in the southwest of the Ukrainian SSR.”- (Komarov et al. (1963))

“Pakistan (Baluchistan & NWFP); Central and Southern Europe, Northwest Africa and Southwest Asia; introduced into most temperate countries. Italian Rye-Grass readily hybridizes with L. perene and species of Festuca. It is a valuable fodder grass.”- (Cope, 1982)

“Europe, Mediterranean area, Transcaucasia, Iraq, Iran, Palestine, Egyp; introduced in N & S America, Australia, Japan and China. A valuable, high yielding fodder grass (Italian Rye-grass), much cultivated for pasture or hay. Perhaps only naturalized in most of its Turkish localities.”- (Davis et al. 1985)

“Grasslands, introduced. Anhi, Fujian, Guizhou, Hebei, Henan, Hunan, Jianngxi, Nei Mongol, Shaanxi, Sichuan, Taiwan, Xinjiang, Yunnan [N Africa, SW Asia, C and S Europe]. This species is widely grown in temperate regions of the world for pasture and forage...”- (Flora of China vol. 22)

“...very widespread non-native grass found in fields, roadsides and disturbed areas across much of the temperate world. It has been widely planted as a cover crop, forage, and lawns...Anthropogenic (man-made or disturbed habitats), meadows and fields...Occurs most often in non-wetlands, but rarely in wetlands.”- (Go Botany)

“wide range of adaptability to soils, but thrive on dark rich soils in regions having mild climates. They do not withstand hot, dry weather or severe winters. They will stand fairly wet soils with reasonably good surface drainage.”- (USDA, NRCS National Plant Data Team, 2020)

“*L. multiflorum* is able to invade a number of habitats, particularly where ground cover is discontinuous or where there is regular disturbance. It is grown as a forage species throughout its range and frequently occurs as a weed of arable land, or as an invasive species on waste ground, farm tracks and around farm buildings. It has also been reported as an invasive species on natural species-rich grassland and as a riparian weed species. It performs best in areas with relatively high rainfall and on fertile soils. Severe frost, drought, excessive moisture or infertile soils do not favour the establishment and development of *L. multiflorum*, and growth is best on soils ranging from pH 6 to 7, with 8 as maximum."- (CABI, 2020)

*Loudetia phragmitoides-*

"Tropical Africa. Perennial...awn not deciduous...found in marshy places, swamps, moist bottomlands, open savannah, wet savannah..."- (Quattrocchi, 2006)

"A pampas-like perennial up to 4.5m high, forming dense tussocks on marshy ground."- (Hutchinson et al., 1972)

"Marshy places 650-1300 m."- (Flora Zambesiaca)

*Loudetia simplex-*

"Tropical Africa, South Africa, Kalahari. Perennial, very variable...weed species, thatching grass, low palatability or unpalatable when mature and dry, grazed when young, useful for erosion control, not very tolerant of drought, common on red clay soil, edges of vleis, deciduous bushland, on seasonally flooded grasslands, stony slopes, red earth, open grassland, sands plain, poor veld, hillsides and rocky hillsides, poor shallow sandy soils, wet sands, in shade of trees, poorly drained sandy soils, on riverine plains..."- (Quattrocchi, 2006)

"In rocky places in open woodland but also in waterlogged soils."- (Hyde et al., 2020)

"Wooded grassland, on both stony and seasonally waterlogged soils 1000-2500 m."- (Flora Zambesiaca)

*Loudetiopsis kerstingii-*

"Africa"- (Quattrocchi, 2006)

"Up to 1m high; panicles erect, peduncles straight or stiffly flexuous; shallow soils over ironstone."- (Hutchinson et al., 1972)

"Saltlick with clay."- (Naturalis Biodiversity Center WAG. 1584243)

"At police post just E of Bobo Dioullasso. Dune sand and rocks."- (Naturalis Biodiversity Center L. 3882055)

"Erect herb, growing in savanna."- (Naturalis Biodiversity Center WAG. 1452759)

*Lygeum spartum-*

"Mediterranean. Perennial, herbaceous, much used for papermaking...rhizomatous with scaly rhizomes...useful for erosion control, used for paper and making rope, food plant for *Melanargia occitanica*, growing in dry open places, dry salt marshes, salt steppes, sandy soils..."- (CRC World Dictionary of Grasse)

"...plant of arid places in the Mediterranean region. It is extremely unlikely that it is native in Kashmir."- (Cope, 1982)

"Habitat: Sand, Desert. Salt Resistance: glycophyte. Synanthrop: obligate natural"- (Danin and Fragman-Sapir, 2016)

*Microstegium vimineum*-

"Asia, temperate and tropical, China, India, Japan. Annual or perennial, slender, branched, decumbent, sprawling habit, growing in colonies, forming dense monotypic stands...cleistogamous and chasmogamous conditions...reproduction from seed, shade tolerant or shade adapted, damp places, moist woodlands, wet meadow, thickets, roadside ditches, lawns, in open to shady locations, disturbed shady areas, disturbed understory habitats, mesic understory habitats, along stream banks, river bluffs, floodplains, aggressive weed species, a pest, adapted to low light conditions, potential seed contaminant, invasive, naturalized..."- (Quattrocchi, 2006)

"Distributed from Northeastern India to South-eastern Asia, China and Japan...This is a common grass growing along ditches and hillsides."- (Gramineae in Flora of Taiwan)

"Forest margins, moist grassy places."- (Flora of China vol. 22)

"...introduced to Tennessee from Asia...now established in much of the eastern United States. Although often associated with forested and wetland areas, it also does well in many disturbed areas. In suitable habitats it quickly spreads by rooting from its prostrate culms, forming dense, unispecific stands."- (Barkworth et al., 2007)

"...mostly associated with forest edges, wetlands, and disturbed areas throughout its US distribution. Shade, low elevation, and mesic soils are important for successful Japanese stiltgrass invasion, with overstory type apparently less important in determining Japanese stiltgrass presence or absence...In its native range, Japanese stiltgrass grows mostly in riparian and mesic areas, being common along shady riverbanks in broadleaved forests...common in disturbed areas including roadsides, shorelines, floodplains, and ‘waste places’. It is most common on disturbed soils at low to middle elevations and prefers moist, continental climates. Japanese stiltgrass is strongly associated with disturbed forest sites, especially roads.”- (Fire Effects Information System)

*Muhlenbergia porteri-*

“US Perennial...forming clumps, good forage, palatable, found along roadsides...”- (Quattrocchi, 2006)

“...most abundant in calcareous soils of dry mesas, hills, canyons, deserts, arroyos, and desert flats. It is excellent for all classes of livestock, deer, and pronghorn. It remains green year-round if moisture is adequate, which makes it palatable in winter and early spring before other grasses begin growth. Once abundant, it now occurs in the protection of shrubs and often ascends through the shrubs.”- (Stubbendieck et al., 2017)

“...grows among boulders on rocky slopes and on cliffs, and in dry arroyos, desert flats, and grasslands, frequently in the protection of shrubs, at elevation of 600-1700m.”- (Barkworth et al., 2007)

“Among boulders or shrubs, rocky slopes, cliffs...”- (Jepson eFlora)

“...occurs in desert grasslands, desert shrub, within and above interior chaparral, and as an understory component of the Madrean evergreen woodland in central Arizona. It occurs mainly along drainages in the Great Basin...readily eaten by livestock throughout the year when available; however, it is usually not abundant enough to provide much forage. It is grazed heavily in winter when other species become scarce. Because of its branching habit, it is extrememly susceptible to heavy grazing...ranges from average to highly palatability to all classes of livestock, depending on season and precipitation. With sufficient moisture, bush muhly may remain green throughout the year and is especially palatable in the winter and prior to summer rains when other grasses are dry."- (Fire Effects Information System)

*Muhlenbergia rigens*-

"...grows in sandy washes, gravelly canyon bottoms, rocky drainages, and moist, sandy slopes, often along small streams, at elevations of 90-2500 m."- (Barkworth et al., 2007)

"US, California, Mexico. Perennial bunchgrass, caespitose...found in dry or damp places, grassland, riparian, meadow..."- (Quattrocchi, 2006)

"...most abundant in sandy or gravelly well-drained soils. It cannot tolerate poorly drained soils, but it does tolerate shade and drought. It occurs in canyons, washes, rocky drainages, slopes, meadows, and near streams. Immature herbage is grazed by deer, horses, and cattle. Palatability rapidly decreases with maturity, but it may remain palatable if continually grazed."- (Stubbendieck et al., 2017)

"Sandy to gravelly places, canyons, stream bottoms..."- (Jepson eFlora)

*Muhlenbergia rigida*-

"...grows on rocky slopes, ravines, and sandy gravelly slopes derived from granitic and calcareous substrates, at elevations of 1200-2200 m, in two disjunct areas: the southwestern United States south to Chiapas, Mexico, and in Ecuador, Peru, Bolivia, and Argentina. It is often a common upland bunchgrass, and is also grown as an ornamental."- (Barkworth et al., 2007)

"Mexico to Argentina. Perennial bunchgrass...rhizomatous...forming dense clumps more or less large to small, fodder, handicrafts, slopes, dry places, roadbanks, rocky places, gravel..."- (Quattrocchi, 2006)

"drypuna, humidpuna, yungas, dryvalleys...altiplano, andes."- (Bolivia Checklist)

*Nassella pubiflora*-

"Chile, Argentina, Ecuador, Peru, Bolivia. Perennial, caespitose...rhizomatous...dense ground cover, grazed, found in sheltered arroyo, slopes, mountain, open areas, moist places along roadsides..."- (Quattrocchi, 2006)

Gutiérrez et al. (1997) lists *N. pubiflora* as a component of a study site described as follows:

> "This 10000-ha park contains semiarid thorn scrub vegetation, and isolated fog forests (on coastal mountain ridges), which have been protected from grazing and disturbance since 1941. The climate is semi arid Mediterranean with 90% of the mean 85 mm annual precipitation falling in winter months (May-September); summer months are warm and dry...The plant community of the study area (Quebrada de las Vacas, 240 m elevation) is characterized by spiny drought-deciduous and evergreen shrubs 2-3 m in height, with an herbaceous understory, and generally unvegetated sandy areas between shrubs."

*Oryza barthii*-

"Tropical Africa, Nigeria, West Africa, Parc national de Waza Yaéré floodplains, Yaoundé. Annual wild floating rice species, robust, rare...among the worst weed in West Africa and Sahel, wild ancestor species of *Oryza glaberrima* Steud., seeds eaten by humans, these plants are harvested by the people as food, spontaneously growing in a deep-water area in African savannah, forming weedy hybrids with cultivated rice, good grazing for all stock when young or before flowering, found in mopane or savannah woodlands, ponds, in deep or shallow water, seasonally flooded lands, rivers, streams, swamps, stagnant water and slowly flowing water or pools, depressions...”- (Quattrocchi, 2006)

“Growing in water, often as a weed in rice fields.”- (Hutchinson et al., 1972)

“...grows in stagnant water, slowly flowing water or pools, shallow ponds, seasonally flooded land, rice fields and similar habitats, often forming pure dominant stands but usually scattered with other aquatic grasses, up to 1500 m altitude. It is also found in mopane or savanna woodland, savanna, or fadama...”- (CABI, 2020)

*Oryza glaberrima-*

“West Africa, Nigeria, Sierra Leone. Annual, highly variable species...dryland types and floating types...competes better with weeds, its grains ted to split, removing the husk is laborious, high nutritional quality, a carbohydrate source, baby foods, rice beer, gruel made from the seeds, Mandingo and Susu people use rice flour and honey to make sweet tasting bread, genetic interaction between African rice’s wild and cultivated races, root eaten raw for diarrhea, usually found in swampy and wet sites...”- (Quattrocchi, 2006)

“An indigenous cultivated rice, grown on flood-plains from Senegal to L. Chad.”- (Hutchinson et al., 1972)

“Cultivated, in flooded fields. Hainan, Yunnan [domesticated in W tropical Africa].”- (Flora of China vol. 22)

*Panicum aequinerve*

"South Africa, Uganda, Ethiopia, Madagascar, Malawi. Short-lived perennial or annual...found in damp places, fields, forest margins, open grasslands, clay or sandy soil..."- (Quattrocchi, 2006)

"Forest margins and rocky mountain grasslands 1000-2700 m."- (Flora Zambesiaca)

"Flowering September and January to June. Clay or sand on shallow soils of forest margins or open grasslands, mainly in damp places and around boulders. Infrequent to locally common. Biome: Grassland and Forest. Northwards to Uganda, Ethiopia and in Madagascar. Shows much variation in the inflorescence shape and spikelet size."- (Russell et al., 1990)

*Panicum amarum*

"Belize, Cuba, Bahamas, Mexico, Honduras, US, Texas, Florida. Perennial...vigorously rhizomatous, excellent for sand trapping, occurring on coastal dunes and sea beaches, useful for coastal dune erosion control and for stabilizing sand dunes."- (Quattrocchi, 2006)

"...grows in the coastal dunes, wet sandy soils, and the margins of swamps, along the Atlantic Ocean and the Gulf of Mexico from Connecticut to northeastern Mexico."- (Barkworth et al., 2007)

"...adapted to very dry sterile sites. It can withstand periods of extended drought and is somewhat winter hardy."- (USDA, NRCS National Plant Data Team, 2020)

"...inhabits beaches, dunes and sandy roadsides along the coast...Anthropogenic (man-made or disturbed habitats), coastal beaches (sea beaches), dunes...Usually occurs in non-wetlands, but occasionally in wetlands."- (Go Botany)

*Panicum bisulcatum-*

> "Southeast Asia, China, India, Indonesia, Japan, Australia, Queensland, new South Wales, Victoria. Annual or biennial or short-lived perennial...aquatic or semiaquatic grass, useful for erosion control, stabilizing stream banks and reduce the erosion of mud and stream banks, swamps, banks of dams and ponds, wet sandy banks, seasonally flooded ground..."- (Quattrocchi, 2006)

> "In tropical heaths, tropical and subtropical wet sclerophyll forests, temperate wet sclerophyll forests, and dry sclerophyll forests."- (Simon and Alfonso, 2020)

*Panicum dregeanum-*

> "Tropical Africa. Perennial...attractive ornamental, pasture, high grazing value, good forage, grazed when young, grows on red clay soil, marshes, grassland, moist soils, wet places, vleis, alluvial and sandy soils, hillsides, lowlands, savannah, seasonally damp soil."- (Quattrocchi, 2006)

> "...erect, 60-90 cm. high; seasonally moist soils....throughout tropical and S. Africa."- (Hutchinson et al., 1972)

> "In damp grassland. 300-2000 m. Throughout tropical Africa."- (Hyde et al., 2020)

> "Damp grassland 330-2000 m."- (Flora Zambesiaca)

*Panicum laetum*

"West Africa. Annual...grazed by stock, grain eaten in time of scarcity, seeds shattering, in wet places, damp soil, overgrazed pastures."- (CRC World Handbook of Grasses)

"30-60 cm. high; moist soils. Also in the Sudan, Ethipia and Eritrea."- (Hutchinson et al., 1972)

*Panicum rigidulum-*

"US, Florida, Guatemala, Mexico. Perennial...growing in wet ditches, wet meadows, wet prairies, damp woods, in roadside ditches, along streams and around ponds and lakes.."- (Quattrocchi, 2006)

"...most abundant in medium-to fine-textured, moist to wet soils of marshes, drainage ditches, pine savannas, woodlands, floodplain forests, and shores of rivers and lakes. It is tolerant of drought and moderate salinity. It provides fair forage for livestock and good forage for wildlife but is not an important forage resource. It is found in the southeastern Great Plains, southeastern United states, eastern United States and adjacent Canada, and south to Mexico and Central America."- (Stubbendieck et al., 2017)

"...grows in swamps, wet woodlands, floodplain forests, wet pine savannah, marshy shores of rivers, ponds, and lakes,  drainage ditches, and other similar wet to moist places; it is rarely found in dry sites. Its range extends from southern Canada to Mexico, Guatemala, and the Antilles."- (Barkworth et al., 2007)

*Panicum trichanthum-*

“Brazil, Peru, Mexico, Argentina, Paraguay, Colombia, Belize. Annual...rhizomes are aromatic, emmolient and dieuretic, sometimes used as excitant, weed, found in open and disturbed site at river’s edges, damp places, roadsides.”- (Quattrocchi, 2006)

“Damp thickets, swamps, river banks, and along trails in forests from sea level to about 500 metres.”- (Swallen and McLure, 1955)

*Paspalidium desertorum-*

“Ethiopia, Kenya, Sudan, Arabian Peninsula. Perennial...sometimes decumbent, sometimes soloniferous, spreading by rhizomes and hard stiff stolons...pasture grass, well grazed by cattle, excellent drought tolerance, prefers loams and alluvial silts, grows in the dry areas, dry open bushland, sandy fields, alluvial plains, seasonally floodplain, dry river beds, margins and banks around cultivation, seasonally flooded grassland, grassland plains, cultivated fields...”- (Quattrocchi, 2006)

“...in north-eastern tropical and subtropical Africa including Northern Kenya, Sudan, Ethiopia and Somalia. It is also found in the Arabian Peninsula and in India...highly drought-tolerant grass, requires 375 mm rainfall and grows in semi-arid and arid areas, but in seasonally wet sites. It prefers alluvial silts or loams and avoids heavy clays and sandy soils. In the annual grass zone of Northern Kenya, Paspalidum desertorum is one of the few perennial grasses to be able to survive long dry seasons...need for a rainy season may limit its usefulness.”- (Feedipedia)

*Paspalum distichum-*

“Cosmopolitan, tropics and subtropics. Perennial, water-loving, wiry, spreading by rhizomes and stolons...economic plant, now widely distributed and naturalized in warm temperate regions and throughout the tropics, a common weed of wet places and cultivated land, a serious weed in irrigation channels, very difficult to eradicate, crop diseases and pest, harmful organism host, potential seed contaminant, useful for erosion control and stabilizing salt marsh, beach protection and coastal sand binder, a soil binder along streams, a very good lawn grass where only salty water is available, quite palatable, a good and important forage grass and valuable duck food, good fodder grass, relished by water buffaloes, readily grazed by sheep, l=tolerant of water logged conditions and periodic flooding in salt swamps and by tidal waters, withstands heavy grazing, a littoral species growing in an near fresh water, found along fresh and brackish marshes, in saline soils and swamps, in wetlands and freshwater wetlands, vleis, salt seepage areas, wet grasslands, warm coasts and coastal salt marshes, wet places at low altitudes, freshwater-marsh habitats, paddy fields and marshy meadows, ponds, canals and ditches, shorelines, beaches and dunes, in sand and mud near the seashore, along pan edges in muddy soil...”- (Quattrocchi, 2006)

“...grows on the edges of lakes, ponds, rice fields, and wet roadside ditches. It is native in warm regions throughout the world, being most abundant in humid areas. In the Western Hemisphere it grows from the United States to Argentina and Chile.”- (Barkworth et al., 2007)

“...grows in moist to wet places along streams, canals, ditches, rice fields, ponds, and lakes. It tolerates moderate salinity and standing water. While actively growing, it provides good forage for livestock and fair forage for wildlife. Palatability rapidly decreases as the plants mature, and the forage is nearly worthless during the dormant season.”- (Stubbendieck et al., 2017)

“Fields, roadsides, ditches and other disturbed places, mostly on moist fertile soils...[tropical and warm-temperate regions of the world].”- (Flora of China vol. 22)

“The tropics and subtropics of the world. Taiman, in roadsides, dampy places and along ditches.”- (Gramineae in Flora of Taiwan)

“...can provide valuable forage for livestock, especially in areas of high salinity...can tolerate a waterlogged environment which allows it to be used in the restoration of wetlands, marshes, beaches, and stream banks...found in both wet and well-drained areas. Common locations to find knotgrass are meadows, marshes, and ditches, but it can also be found growing in cultivated and disturbed areas. Knotgrass is also adapted to areas with high salinity.”- (USDA, NRCS National Plant Data Team, 2020)

“seashores, near the beach or on tidal flats.”- (Hutchinson et al., 1972, under *P. vaginatum*)

“...fast-growing rhizomatous grass of wet areas...almost world-wide distribution in tropical and subtropical regions...generally accepted that it is native in N and S America and introduce to Europe and most of Asia...found in wasteland areas, rotation crops, perennial crops and aquatic habitats, but not too frequently on grassland... a non-submerged aquatic plant commonly occurring in streams and alluvial flatlands in the tropics and subtropics, and throughout the world. It populates still or moving water to a depth of one metre or more; it may also be a problem in merely irrigated conditions. It is a $C_4$ plant adapted to semi-aquatic environments and is not cold tolerant...can proliferate in drier conditions provided abundant water is present for at least part of the growth cycle.”- (CABI, 2020)

*Paspalum fimbriatum*-

“Central America, west Indies, Brazil. Annual...a prolific seeder, spring up immediately after rains, economic plant of some value as early forage grass, spikelets cling to clothing and fur, weed species on sunny and shady places, moist disturbed ground, disturbed coastal areas, lawns, along roadsides, open regions, grassy roadside, cultivated areas...”- (Quattrocchi, 2006)

“Sunny, moist disturbed areas up to 300m elevation.”- (Pacific Island Ecosystems at Risk, 2008)

*Paspalum hartwegianum-*

“South America, Paraguay, Argentina, Mexico, US, Texas. Perennial desert grass, erect bunchgrass, stoloniferous...growing in poorly drained site, alkaline meadows...”- (Quattrocchi, 2006)

“...grows in wet prairies, ditches, and swales from southern Texas through Mexico and Central America to Paraguay and Argentina.”- (Barkworth et al., 2007)

*Paspalum haumanii-*

“Culms erect; robust, 250-300 cm long...”- (Clayton et al., 2016)

“Moist sand along a little stream”- (MNHN P01780831)

“...forming more or less pure colonies in the semi-permanent swamps (“Malezales”) on low land with clayey, impenetrable subsoil.”- (MNHN P01905419)

“...Uruguay, Brazil, Argentina. Useful for erosion control...”- (Quattrocchi, 2006) from *P. exaltatum*:

> "Uruguay, sothern Brazil to Argentina...in wet places, marshy and swampy habitats..."- (Quattrocchi, 2006)

"Rosengurtt et al. (1970) indican que es un forraje apetecido cuando joven y productivo. Sur de Brasil, Paraguay, la Argentina y Uruguay. Habita en bordes de arroyos, ríos o bañados, en suélos húmedos."- (Zuloaga et al., 2012)

"A tall, vigourous grass, forming more or less pure colonies in the semi-permanent swamps ("Malezales") on low land with clayey, impenetrable subsoil."- (Naturalis Biodiversity Center U.1520911)

Isotype: "matas densas y altas (2,5 meters) raias en pajonal formado por el Paspalum No B699 plantas recubertas por una sustancia gusàcea"- (US 1722609)

*Paspalum malacophyllum-*

"Argentina, Colombia to Paraguay, Bolivia, Puerto Rico. Perennial...rhizomatous...resistant to the disease ergot, growing in forest margins, on wet banks along ditch..."- (Quattrocchi, 2006)

"...native from Mexico to Bolivia and Argentina. It was introduced to the southern United States for forage and soil conservation, and is now established in the southeastern United States, growing in disturbed sites at scattered locations."- (Barkworth et al., 2007)

"yungas, dryvalleys, rain, chiquitano, drychaqueo"- (Bolivia Checklist)

*Paspalum notatum-*

“Central and southern America. Perennial bunchgrass...rhizomatous, short and stout rhizomes and stolons...usually a prolific seed producer, propagation by seeds and woody runners, ornamental weed species highly invasive, does not grow well in shade, naturalized in the wild, potential seed contaminant, rapidly growing when established, quickly colonizes large areas, native pasture species, fair grazing for livestock, rather unpalatable to cattle, poor grazing for wildlife, economic plant, cultivated as lawn grass and fodder grass, once established can be grazed heavily, ground cover useful for erosion control, recommended for protection against erosion on sloping ground, often used to stabilize terraces, sometimes susceptible to paspalum ergot, excellent drought resistance, tolerant of flooding and salinity, best in poor conditions and in sandy soil, a weed of roadsides and lawns, found on coastal sands and other sandy soils in areas with moderate to high rainfall and a short dry season, disturbed places, damp grassland...”- (Quattrocchi, 2006)

“...native from Mexico through the Caribbean and Central America to Brazil and northern Argentina. It was introduce to the United States for forage, turf, and erosion control. It is now established, generally being found in disturbed areas and at the edges of forests in the southeastern United States. A number of cultivars have been developed for use as turf grasses.”- (Barkworth et al., 2007)

“...grows in sandy to sandy loam soils on the edges of forests, roadsides, and disturbed areas. It was introduced from Mexico and South America for forage, turf, and erosion control. Occasionally, when abundant, it provides fair forage for livestock and poor forage for wildlife. Hay quality is fair. It is sometimes considered to be a weed. It grows in the southeastern Great Plains, southeastern United States, East Coast, Mexico, Central America, and South America.”- (Stubbendieck et al., 2017)

“rain, ssavannas, campos, chiquitano”- (Bolivia Checklist)

“...deep-rooted perennial adapted to a wide range of soils. It is low-growing and spreads with stolons and stout, scaly rhizomes.”- (USDA, NRCS National Plant Data Team, 2020)

“...native to Mexico, the Caribbean and Soth America. It is widespread in North America and in some areas of Africa, Asia (Indonesia, Thailand and Vietnam) and Australia. It grows from sea level to an altitude of 2000 m, and in regions with annual rainfall from 750 mm to 2000 mm. Optimal mean temperature is 20 C. It is very tolerant to drought and to a lesser extent to salinity when well established. It is known to survive 20 to 3 days of flooding.”- (Feedipedia)

“Introduced for grazing and erosion control. It is found as an occasional escape of disturbed places, often found in lawns and on road sides, mainly in and around urban areas.”- (Hyde et al., 2020)

“...commonly found on sandy or light textured soils over its native and naturalized range, and sometimes extends onto clays...Rainfall in its native habitat mostly ranges from 700-1,500 mm year. It is generally sown in areas with a well-distributed annual rainfall from about 900-1,500 mm, but can be used at up to 2,500 mm. It is very drought tolerant by virtue of its deep root system, and is fairly tolerant of flooding, surviving over 30 days of inundation...moderately tolerant of reduced light, but is not as shade tolerant as Paspalum malacophyllum or P wettsteinii. It may persist better under sustained grazing in shaded situations than these other species...It can tolerate light to moderate fire, but stands can be diminished by fire if there is an abundance of dry fuel...Feeding value varies greatly with age of regrowth, genotype and fertility of soil...Palatability varies with age, genotype and soil fertility. Although young growth is readily eaten, the species generally, and ‘Pensacola’ in particular, are increasingly poorly eaten with age. It is essential to maintain grazing pressure to avoid this decline in palatability.”- (Cook et al., 2005)

*Paspalum unispicatum-*

"Central America, Mexico, Honduras...shortly rhizomatous...along roadsides..."- (Quattrocchi, 2006)

"...grows in sandy soil in the coastal plain of Texas and extends southward through Mexico and Central America to Cuba and Paraguay, Uruguay, and Argentina."- (Barkworth et al., 2007)

*Pennisetum clandestinum-*

"East Africa highlands, North Africa, tropical Africa. Perennial, ...rhizomatous and stoloniferous...cultivated nutritious fodder widely naturalized in tropics and subtropics, drought resistant and palatable, nutritious fodder grass if cut before flowering, very high grazing value, a pasture plant in tropical and subtropical areas, grown for pastures and lawns, playing fields, invasive, invades under heavy grazing, excellent colonizer, tolerates flooding well, useful for soil conservation and for erosion control, a serious noxious weed in turf and waste places, a troublesome weed of highland crops, can be a nitrate-toxic, prefers sandy soils, common on flat areas and banks along roads, arable land, in moist places around dams, in dry and mesic habitats, grassy areas, on alluvial soils and on moist sandy soils, irrigation channels, lakeshores, disturbed areas, in the high rainfall regions, well-drained and fertile soil, gardens and roadsides, forest clearings..."- (Quattrocchi, 2006)

"...native to Africa. It now grows in many parts of the world, often as a forage or lawn grass. The US Department of Agriculture considers it a noxious weed. In parts of the Manual region, it is well-established in lawns."- (Barkworth et al., 2007)

“Upland grassland on fertile soils subject to grazing, probably introduced. Cultivate for pasture, soil stabilization and lawns under the name Kikuyu grass 1300-2500 m.”- (Flora Zambesiaca)

“...aggressive perennial plant, spreading by rhizomes below ground, especially by long runners above ground, and it also sets seed...originates in the highlands of East Africa....widely introduced into other parts of the world, usually deliberately, for use as a pasture grass and/or to prevent soil erosion...tropical and sub-tropical grass, used in managed grasslands, urban areas and recreational areas (such as golf courses) as a turf grass, but commonly invades natural and managed forests, plantation crops and agricultural areas, as well as coastal areas, roadsides, etc...Little information is available on seed biology, but longevity is at least 10 years and seeds are viable after passage through cattle, thus being spread in dung...occurs predominantly at high altitudes in tropical regions, generally where rainfall is high, though it is able to survive dry spells. It has been introduced to lower altitudes around the world and survives a wide range of conditions between 35N and S, though not severe frost. It requires high nitrogen levels to grow rapidly. It is fire-resistant and tolerates moderate shade but is gradually suppressed as canopy cover increases.”- (CABI, 2020)

“Introduced in 1948, and now naturalized; native in the E. African highlands, and widely introduced to upland regions throughout the tropics.”- (Hutchinson et al., 1972)

“...originates from areas with an annual rainfall of 1,000-1,600 mm. Although this native environment mostly does not have a pronounced dry season, the grass has become naturalized in areas of summer or winter rainfall with a distinct 5 month dry season. Where soils are suitable, it has become naturalized in areas with rainfall up to 3,000 mm and down to 800 mm/yr, and performing well under irrigation in lower rainfall areas. It is moderately drought tolerant, because of deep root system...Moderate shade tolerance but does not grow well in heavy shade...Rarely burn but recovers from even severe fire by virtue of rhizomes...Young growth is very soft and palatable, but older growth is not relished by most animals. The presence of a legume in the sward increases utilization of the kikuyu."- (Cook et al., 2005)

*Pennisetum lanatum-*

"China, India, Himalayan region. Fodder grass, useful soil binder, growing in subtropical subhumid zones, in mountain meadows..."- (Quattrocchi, 2006)

"Tufted perennial with tough extensive rhizomes; culms 30-150 cm high, erect...Pakistan; Afghanistan, Tibet and the Western Himalayas. Reported to be abundant and valuable fodder grass above 2000m."- (Cope, 1982)

"Dry mountain slopes; above 1500m...This is a distinctive species on account of its long, scaly rhizomes and branched bristles in the inflorescence."- (Flora of China vol. 22)

*Piptochaetium avenaceum-*

"Northern America, US, Mexico. Perennial, weed, rocky places, woods..."- (Quattrocchi, 2006)

"...grows in open oak and pine woods, often on sandy soils, primarily in the southeastern United States."- (Barkworth et al., 2007)

"...inhabits sandy or rocky woodlands in Connecticut, Massachusetts and Rhode Island. Cliffs, balds, or ledges, ridges or ledges, woodlands" (Go Botany)

"...grows in sandy soils in open oak and pine woodlands, oak-hickory forests, grasslands, and rocky outcrops. It provides good to excellent forage for livestock and fair to poor forage for wildlife in spring and summer. Rarely is it abundant enough to be important forage."- (Stubbendieck et al., 2017)

*Poa annua-*

"Europe, large climate range. Annual, sometimes biennial...ornamental, palatable, very low grazing value, grazed by livestock and horses, noxious weed species, found in turf, herb fields, in stream, wetlands, damp places, in muddy soil along river, sandy soil, moist alluvial soils, cultivated ground and disturbed sites, moist disturbed areas, in disturbed soil near creek, gardens, lawns, fallow fields, open habitats, open woods, shaded forest edge, in sandy clay over loam, in wet soils, on rich soils, along roadsides, waste places, flood deposit..."- (Quattrocchi, 2006)

"...grows best in moist soils and is found in a wide range of soil textures. It occurs in full sunlight to shady areas in disturbed areas of pastures, roadsides, lawns, gardens, waste places, ditches, openings in woods, and fields. It starts growth early and provides a small amount of forage for livestock during this period. Because of its low stature, sheep utilize the herbage to a greater extent than cattle. This annual weedy species was introduced from Eurasia. It grows throughout the Great Plains and North America. It is one of the most widespread weeds in the world."- (Stubbendieck et al., 2017)

"Tufted annual or short-lived perennial; culms 5-30cm high...very common weedy species found in a variety of habitats. 1400-4300m..." (Cope, 1982)

"Sandy, grassy and waste places, often in irrigated areas, s.l.-2200m." (Davis et al. 1985)

"Meadows, fields, weedy places, and roads...occurs everywhere, except polar and alpine regions and deserts."- (Komarov et al. (1963))

"Weed of disturbed, often moist and shady ground; near sea level to 4800 m..."- (Flora of China vol. 22)

"...can be found from Arctic to the Antarctic regions in practically all terrestrial ecosystems...native to temperate areas of Eurasia...adaptability of this species makes ecological generalizations difficult and often meaningless..."- (CABI, 2020)

*Poa arida*-

"North America, US, Canada. Perennial...mildly rhizomatous to nearly rhizomatous...drought and dry soils tolerant, useful for erosion control, palatable, low-value forage, growing on moist banks, on disturbed sites, pastures, meadows and wet-meadows, prairies, shores and seepage areas, piedmont valleys, saline soils, foothills and alpine sites, plains, wet sandy soils, alkaline meadows..."- (Quattrocchi, 2006)

"...grows best in damp, sandy loam soil, but it tolerates dry soils. It is found in meadows, riparian areas, disturbed sites, plains, and prairies. It is palatable to livestock and wildlife and has some grazing value because it begins growth earlier than many other species."- (Stubbendieck et al., 2017)

"...grows mainly on the eastern slope of the Rocky Mountins and in the northern Great Plains, primarily in riparian habitats of varying salinity or alkalinity..."- (Barkworth et al., 2007)

"...minor species in most plant communities and is generally not important as forage. It has some value in early spring because it greens up before most associated grass species...palatable to domestic and wild ungulates, small mammals and birds, and upland game birds...occurs on disturbed sites, pastures, meadows, prairies, piedmont valleys, foothills, ad alpine sites. Soils with plains bluegrass are often alkaline and/or sandy...Unlike most bluegrasses (Poa spp.), plains bluegrass tolerates dry soils. Soil moisture is highly variable, however; plains bluegrass occurs on arid, well-drained soils and on wet, sometimes poorly drained soil. At the northern edge of its range in extreme northern Alberta, plains bluegrass occurs only on well-drained south-facing slopes."- (Fire Effects Information System)

*Poa compressa-*

"Eurasia. Perennial...rhizomatous with wiry and slender rhizomes...cultivated fodder, good forage, palatable and nutritious, pioneer and colonizer of disturbed soils, useful for erosion control and pasture, suitable for revegetation of mined areas, resistant to grazing, does not withstand heavy grazing, drought-tolerant, found in waste places, gardens, most disturbed habitats, relatively moist disturbed sites, open habitats, open woods, dry soils, moist to dry prairies, dry woods, on rocky-stony hillside, sandy areas, dam sites, along roadsides and horse trails, waste places, disturbed ground, under dry conditions, in meadow habitats, shores, stream banks, fields and rock outcrops, wet banks of creek, foothill woodland, meadows, clearings and around edge of woods, chaparral, pastures..."- (Quattrocchi, 2006)

"...grows on moist to dry soils with low fertility and poor drainage. It is found in wet meadows, bottomland pastures, open timber, roadsides, riparian areas, cultivated fields, waste places, and disturbed ground. It was introduced from Europe for forage and is moderately drought tolerant and tolerant of salinity. It is not shade tolerant. It provides good forage for cattle, horses, and sheep, but low productivity keeps it from being an important forage species. The culms remain green after the leaves have senesced, providing autumn grazing."- (Stubbendieck et al., 2107)

"Stony and sandy places, disturbed ground, fields, poolsides, nr s.l.-1400 m."- (Davis et al. 1985)

"Clay, stony and sandy slopes, and roadsides."- (Komarov et al. (1963))

“Moist grassy places in forests.”- (Flora of China vol. 22)

“...naturalized throughout much of North America since its introduction into Canada in the late 1700s. It is found on wet sites, open meadows, and in open deciduous and coniferous forests as well as waste areas...adapted to wet sites but thrives on moderately acidic, and droughty soils with poor fertility...best adapted to areas receiving at least 18 inches annual precipitation.”- (USDA, NRCS National Plant Data Team, 2020)

“...unable to compete with other grasses on good soils and generally develops best on soils of low fertility or poor drainage. It has moderate drought and salinity tolerances but is not shade tolerant. In the UK, Hubbard (1959) records it as occurring in poor, thin grassland, on dry banks, on waste ground, mostly on shallow, well-drained soils; also on old walls and ruins.”- (CABI, 2020)

“...unable to compete with other grasses on good soils and generally develops best on soils of low fertility or poor drainage. It has moderate drought and salinity tolerances but is not shade tolerant. It grows about anywhere Kentucky bluegrass grows but only achieves dominance on soils that are too acid, droughty, or nutrient-deficient for Kentucky bluegrass dominance.”- (Fire Effects Information System)

*Polypogon fugax*-

“Himalayan region, Nepal, Somalia. Annual or perennial bunchgrass...grazed by cattle, a weed of wheat and rice, irrigation ditches, damp wasteland, plains and hills, swampy ground, banks of streams, sand flats, along roadsides...”- (Quattrocchi, 2006)

“Annual...Pakistan (Baluchistan, Punjab, NWFP & Kashmir); Iraq eastwards to Burma, mainly in the Himalayas Usually in wet ground beside lakes and streams or in marshes. Of little value for fodder. 600-2400 m.”- (Cope, 1982)

"Moist places, near farmlands; 100-3600 m."- (Flora of China vol. 22)

"Distributed in Japan, Korea, China, India and Africa. This is a very common grass growing on the plain and lowland regions in Taiwan."- (Gramineae in Flora of Taiwan)

*Puccinellia distans-*

"Europe. Perennial bunchgrass, halophytic...pastures, weeds, ornamental grass widely naturalized in temperate regions, salt tolerant, grows in saline sites, mudflats, shores, salt flats and along lakeshores in the lowland to montane zones, salt pans, in wet alkali spot, wet disturbed places, in mountain meadows, swamps, springs, ballast, in salty marshes and on sandy grounds, along irrigation ditches, muddy estuaries, roadsides, waste ground, poorly drained saline areas..."- (Quattrocchi, 2006)

"Wet solonets sites."- (Komarov et al. (1963))

"Saline soil at edge of streams, salt lakes and Limonium salt steppe, 670-1350 m."- (Davis et al. 1985)

"...grows in medium- to fine-textured soils and is tolerant of saline and alkaline soils. It is found in moist habitats in pastures, fields, lawns, disturbed sites, and waste areas. It grows on roadsides where salt is used on the roads. It was introduced from Eurasia for pasture, but palatability is only fair."- (Subbendieck et al., 2017)

"...Eurasian native, reportedly introduced in North America, where it is widespread, particularly as a weed in non-littoral environments, including the margins of salted roads. It is also found occasionally in coastal environments."- (Barkworth et al., 2007)

"Anthropogenic (man-made or disturbed habitats)...Usually occurs in wetlands, but occasionally in non-wetlands."- (Go Botany)

"Saline meadows, flats..."- (Jepson eFlora)

*Rostraria cristata-*

"Arabian Peninsula, Mediterranean, Sudan, Pakistan, north-west India. Annual...weed of disturbed places, growing in wet site, coastal areas..."- (Quattrocchi, 2006)

"Waste or open places, sandy plots, forested foothills, mountain slopes, s.l.-1200 m."- (Davis et al. 1985)

"Pakistan (Baluchistan, Punjab, NWFP & Kashmir); Northwest India to the Mediterranean region; introduced in South Africa, North America etc...widespread and variable species, often occurring as a garden weed, but where it grows in quantity it has been recommended for fodder."- (Cope, 1982)

*Sacciolepis striata-*

"US, Florida. Perennial or annual, aquatic or semiaquatic...stoloniferous with creeping stolons...food for waterfowl, weed species, growing in large stands or colonies on wet shores and in marshes, wet savannahs, freshwater marshes, around ponds and lakes, on muck of seasonal ponds, emergent fresh marsh habitat, coastal marshes, swamps and ditches in the coastal plains, ditches, wetlands, sloughs, margins of bayous and streams, pools, littoral beds along the river channel, adapted to deep water with high flows and varying water levels..."- (Quattrocchi, 2006)

“...native to the southeastern United States and the West Indies, and from the Guianas to Venezuela and Amapá, Brazil. It grows along and in ponds, lakes, streams, and ditches, and flowers in late summer to fall.”- (Barkworth et al., 2007)

“Anthropogenic (man-made or disturbed habitats), shores of rivers or lakes...Occurs only in wetlands.”- (Go Botany)

*Setaria barbata-*

“Tropical Africa and Southeast Asia, India, the Philippines, Indonesia, Uganda, Nigeria, Sudan, Mali, Tanzania, Ghana, Guinea, Madagascar, Mauritius. Perennial or annual...weed species widely naturalized in tropics, forage, fodder for all stock, growing in high rainfall areas, deep and well-fertilized soils, savannahs, in shade or light shade, open scrub, waste places, around irrigated plantations and cultivated fields, disturbed lands...”- (Quattrocchi, 2006)

“A weed on disturbed land.”- (Hutchinson et al., 1972)

“Western Africa; with a few isolated records elsewhere in Africa; tropical Asia; introduced to the West Indies. A shade-loving weed of disturbed land.” (Flora Zambesiaca)

*Setaria leucopila-*

“Mexico, US, Arizona, Texas. Perennial bunchgrass...basal leaves highly palatable....good forage value, good range grass and seed producer for dove and quail, fair grazing for wildlife, not very resistant to grazing, grows in open dry ground and under the protection of brush in overgrazed areas, common on rocky slopes and along washes and canyons, often in partial shade of shrubs and trees, often in the open shade of low trees or clumps of brush, abundant on dry plains, in sandy to sandy loam soils and on extremely dry sites, open disturbed soil, along roadsides, useful for erosion control and in revegetation of eroded range sites, abandoned cropland and highway construction sites..."- (Quattrocchi, 2006)

"...most abundant in well-drained alkaline soils along gullies or streams or in alluvial basins or other areas with occasional abundant moisture. It may be found growing in partial shade of brush and small trees where it is protected from livestock. It is an important forage species and rated as good for cattle and horses and fair for sheep and wildlife. It cannot withstand heavy grazing and usually does not occur in dense stands."- (Stubbendieck et al., 2017)

"...grows in the southwestern United States and northern Mexico. It is the most common of the perennial "Plains bristlegrasses."- (Barkworth et al., 2007)

"...provides fair to good forage for livestock and wildlife. It is a good seed producer, and its seeds can provide a source of food for upland-bird habitats...generally found in the dry rangelands of Texas to Arizona with annual rainfall of 10 to 26 inches. In the west it occurs at elevations of 3,000 to 7,000 feet. It is located on bottomlands and alluvial flats as well as well-drained, dry, open sites. However, it predominates on loamy bottomland, clay flat, and saline clay range sites."- (USDA, NRCS National Plant Data Team, 2020)

*Setaria parviflora*-

"Tropical America, Mexico, US, Brazil, Bolivia, Guatemala, Peru, Uruguay, Venezuela, Paraguay, Argentina. Perennial or annual, polymorphic...useful grass naturalized elsewhere, fodder, pasture grass, weed species, used by waterfowl, growing on roadsides and roadbanks, gardens, lawns, crops, fields, freshwater and brackish marshes, coastal swales, wetlands, flatwoods, salt marsh boarders, hillsides, hammocks waste places and disturbed areas, mossy banks in primary forests, among roadside weeds in a single clump...”- (Quattrocchi, 2006)

“Pastures and other disturbed open areas, savannas, 100-900 m; widespread in Delta Amacuro, Bolívar, and Amazonas.”- (Davidse et al., 2004)

“...common, native species of moist ground. It is most frequent along the Atlantic and Gulf coasts, but it also grows from the Central Valley of California east through the central United States and southward through Mexico to Central America, as well as in the West Indies.”- (Barkworth et al., 2007)

“...grows best on moist sandy loam to clay loam soils. It is tolerant of saline soils and is found in salt marshes, ditches, and wet prairies. It provides fair forage for livestock and wildlife. It is found in the southern and southeastern Great Plains as well as on the East Coast and in the southeastern and Midwestern states.”- (Stubbendieck et al., 2017)

“...grazed moderately by livestock, usually during the spring and summer. It becomes unpalatable in the fall and provides poor forage after maturity...Birds readily eat the seeds...grows best on moist or wet sites. In Florida, it grows on wet sandy soils, sloughs, and acid flatwoods. In Texas and Louisiana, it grows well on salty prairie sites; also grows on salt marshes if water level is relatively low.”- (USDA, NRCS National Plant Data Team, 2020)

“Anthropogenic (man-made or disturbed habitats), marshes, wetland margins (edges of wetlands)...Occurs in wetlands or non-wetlands.”- (Go Botany)

“Usually described as native to the USA, Central America and parts of South America, it may be an ancient introduction from Asia...Able to colonize wet sites, S. parviflora is regarded as a facultative wetland plant, and is common in wet savannas, salt marshes, and flooded areas. This belies its ability to withstand drought and fire. It is a relatively recent naturalization in parts of Europe where it is found in waste places, lawns and parks...Habitat of S. parviflora in its native range includes open ground, pastures, cultivated soil, salt marshes, and moist ground along the coast. Elsewhere it occurs in waste places, cultivated soils, lawns, concrete margins, mountain slopes, roadsides, and forest margins. IN Hawaii it occurs in wet, mesic and dry sites, and in clearly arid low lying sites."- (CABI, 2020)

*Setaria verticillata-*

"Origin paleotropics. Annual...one of the weeds of coffee plantations and many crops, palatable, low grazing value, grazed by cattle when young, suitable for hay-making, seeds eaten by small birds, grain used for an alcoholic drink, a source of food and vegetable salt, inflorescence sticking, seed can attach itself to clothing and to animals, usually found in places seasonally wet or irrigated, in gardens and greenhouses, grasslands, shrublands, irrigation canals, in open dry areas, orchards, moist shaded ground, along stream banks, arable land and waste places, as well as in disturbed and cultivated areas, on road- and trailsides, on nitrogen-rich disturbed soils, irrigation ditches, wadi beds..."- (Quattrocchi, 2006)

"In the open beside river banks in Dry Teak Forest. Grows on silty soil. Responds to grazing by becoming compact and rosette-like in form."- (Hodd and Hodd, 1982)

"...widespread, annual plant...occurs in low elevations <300 m by streams in mixed deciduous forests, though more often as a weed and ruderal in waste places, temple grounds, cultivation, plantations and on roadsides. The retrorsely scabrous bristles of the fruiting panicle, which readily adhere to the coats of animas, ensure wide dispersal of the seed."- (Lazarides, 1980)

"...tropical and warm temperate regions generally...It is eaten by cattle when young, but avoided once the spikes appear."- (Cope, 1982)

“Disturbed ground, irrigated fields and gardens, ditches, s.l.-800 m.”- (Davis et al. 1985)

“Tropical and temperate regions of the Old World. Taiwan, common in open and waste places.”- (Gramineae in Flora of Taiwan)

“Roadsides, open weedy places; 300 – 1000 m. Nei Mongol, Taiwan, Yunnan [tropical and warm-temperate regions of the Old World; introduced in America].”- (Flora of China vol. 22)

“Ascending annual up to 1 m high; weedy places.”- (Hutchinson et al., 1972)

“...species is ruderal in disturbed areas, such as cultivated fields, cattle kraals and along paths; often in damp soil, shady places. It is a common and persistent weed in gardens and in cultivated lands that can spread uncontrollably...fruiting panicle of S. verticillata attaches itself to the fur of passing animals by means of the retrorsely-barbed bristles and thereby achieves wide distribution of the seeds.”- (PlantZAfrica, 2000)

“Tropical and warm temperate regions generally...Pathsides, old farmland and weedy places, with some preference for damp or shady sites 850-1600 m.” (Flora Zambesiaca)

“...can also become dominant in grassland. The combination of ready dispersal by its ‘sticky’ seed and seed-heads, and its $C_4$ physiology and rapid growth make it an extremely successful invader...plant of disturbed areas, especially in annual and perennial crops, but also along roadsides and in waste places over a wide ecological range between northern and southern temperate areas including the sub-tropics and tropics, where it also occurs at high altitude, e.g., in East Africa. It is a species mainly of disturbed ground and is not reported as a problem in natural vegetation. While it has been reported to prefer shady damp sites, it is rarely found in wetlands...Although the seeds eventually separate from the inflorescence, dispersal is very often assisted by the complete inflorescence being carried on animal fur, or even on hairy insects such as the cetoniid beetle...”- (CABI, 2020)

"...adapted to a wide range of soil types and is found in abused pastures, waste places, gardens, fields, roadsides, and disturbed areas. This aggressive annual weed was introduced from Europe and thrives with irrigation but does not withstand standing water. It has little value as forage for livestock or wildlife."- (Stubbendieck et al., 2017)

"Good fodder for livestock in young state; later it coarsens considerably. The seeds are used for food, for feeding poultry, and for distillation of alcohol."- (Komarov et al. (1963))

*Setaria viridis*-

"Disturbed ground, gardens, s.l.-2300 m...Temperate and subtropical regions of the Old World; introduced elsewhere, absent from most of SW Asia."- (Davis et al. 1985)

"Temperate regions. Annual, variable...sometimes cultivated as a forage grass, small grains used in the same ways as rice or millet, fodder for cattle when young, drought resistant, the plant crushed and mixed with water used as an external application for bruises, seed diuretic and febrifuge, a weed of disturbed and cultivated land, weed in soybean and corn, roadsides, railroads, plains, waste places, gravelly soil..."- (Quattrocchi, 2006)

"grows in all soil textures and is most common in well-drained, fertile soils, it is found in fields, canyons, disturbed areas, lawns, gardens, roadsides, abused pastures, and waste places. It was introduced from Eurasia and can be an aggressive weed. It is moderately palatable when actively growing and is considered to be fair forage. It rapidly becomes unplatable with inflorescence emergence and is not an important forage species."- (Stubbendieck et al., 2017)

“In fields, in weedy places, along stream borders, and on rocky and stony slopes.”- (Komarov et al. (1963))

“Hill slopes, roadsides, grassy waste places.”- (Flora of China vol. 22)

“Anthropogenic (man-made or disturbed habitats), meadows and fields.”- (Go Botany)

“...primarily a weed of the temperate zone, and is rarely present in the tropics, other than at high altitudes. It grows mainly in cultivated fields and gardens, but also in waste places, disturbed areas and along roads...no specialized mechanism for seed dispersal, but long-distance spread is known to have occurred through contaminated crop seed. Seeds are able to survive passage through the digestive systems of livestock and transmission with irrigation or flood water.”- (CABI, 2020)

*Sorghum angustum*-

“Australia, Queensland. Erect or ascending, green...”- (Quattrocchi, 2006)

“...endemic to northern Australia. The taxon is reported to occur in Queensland and the Northern Territory...an annual to 1 m tall, which grows in a wide variety of habitats within tropical savanna, from 0 to 500 m asl, over five ecoregions of northeastern Australia. The taxon has been collected in bloodwood savanna-forest, on low/moist sandy ridges near coast, low open woodland, on sand flats, in drainage area, in dune scrub, on slopes of steep granite hills and littoral vine woodland on sand plain.”- (IUCN)

*Sorghum ecarinatum*-

“Australia, Western Australia.”- (Quattrocchi, 2006)

"Annual, grass-like or herb, (0.8-)1.2-2.5 m high. Fl. Brown, Apr to Jun. Grey-brown sand. Beach dunes."- (FloraBase the Western Australian Flora)

*Sorghum propinquum-*

"Tropical Asia, India, the Philippines. Perennial, solid, long stolons...rhizomatous...grain used as famine food, whole plant used as a forage, usually not cultivated, found growing on waste grounds, lowlands, grasslands, forests, disturbed places, riverbanks, along roadsides, open hill slopes..."- (Quattrocchi, 2006)

"...a robust, cane-like, rhizomatous perennial attaining almost 3 m in height. It occurs in lowlands <c. 1000 m altitude on river banks, roadsides, and open hill slopes in grassland and primary or secondary forest. Because of its sporadic occurrence and stout habit, it is of limited value as fodder."- (Lazarides, 1980)

"Distributed in the Malay Peninsula, China and the Philippines. Cultivated in Taiwan."- (Gramineae in Flora of Taiwan)

"Streamsides, moist places...sometimes used for fodder."- (Flora of China vol. 22)

*Sorghum timorense-*

"Asia topical, Indonesia, Western Australia, Northern Territory, Queensland. Annual or perennial...native fodder, growth promoted by burning, grazed when young, annual food plant for Aborigines..."- (Quattrocchi, 2006)

"Tufted annual, grass-like or herb, 0.3-3(-4) m high. Fl. Brown, Mar to Jun. Clay, black sand, red loam."- (FloraBase the Western Australian Flora)

Full sun- (personal communication D. Lewis, 2019)

“Perennial tussock to 2m high; Eucalyptus alba open woodland; steep slope; clay soil...”- (Naturalis Biodiversity Center L. 1336814)

“...sandstone talus slope with grasses and scattered trees.”- ((Naturalis Biodiversity Center L. 1336771)

“...roadside vegetation on black soil.”- ((Naturalis Biodiversity Center L. 1342078)

“Blue grass-browntop downs with scattered E. pruinosa forming a fringe around pure grassy areas.”- ((Naturalis Biodiversity Center L. 1342077)

“Inrequent (sic) in stabilized coastal dune deep sand.”- ((Naturalis Biodiversity Center L. 1335981)

“Common by roadside on Tipara clay soil”- ((Naturalis Biodiversity Center L. 1342079)

“Dominant under Terminalia sp. And Bauhinia cunninghamii on grey cracking clay soil developed on volcanic rocks.”- (Naturalis Biodiversity Center L. 1342075)

“...common as a ruderal, wayside, scattered in pasture. Especially abundant around Kupang, where it is cut for fodder even when dry.”- (Naturalis Biodiversity Center L. 1336757).

“On open somewhat gravelly downs with Astrebla squarrosa”- (Naturalis Biodiversity Center L. 1336773)

“seacoast”- (Naturalis Biodiversity Center L. 1336768)

*Spartina pectinata-*

"Northern America. Perennial...ornamental, native pasture species, adaptable species, useful for erosion control, open soil, prairies, grasslands, salt marshes, freshwater swamps, moist soils..."- (Quattrocchi, 2006)

"...native to Canada and the United States, but it has been introduced at scattered locations on other continents. On the Atlantic coast, it grows in marshes, sloughs, and flood plains, being a common constituent of ice-scoured zones of the northeast and growing equally well in salt and fresh water habitats. In western North America, it grows in both wet and dry soils, including dry prairie habitats and along roads and railroads."- (Barkworth et al., 2007)

"...grows in wet and dry soils of prairies, meadows, marshes, ditches, sloughs, floodplains, and along streams. Its herbage is coarse and furnishes poor to fair forage for cattle and poor forage for wildlife. It becomes unpalatable with maturity. It produces fair hay if cut while immature."- (Stubbendieck et al., 2017)

"...forms thick stands around marshes, providing good cover for game birds, song birds and small mammals...The seed typically matures within a week or two of frost and is flat, paper-like with barbed awns that attach firmly to fur or fabric. There are 197,000 seeds per pound...typically found on lower, poorly drained soils along roadsides, ditches, streams, marshes and potholes. It also occurs in floodplains, wet meadows and back dune areas. Prairie cordgrass frows well on seasonally dry sites, tolerates alkaline conditions and high water tables but is intolerant of prolonged flooding. Seedlings are not shade tolerant."- (USDA, NRCS National Plant Data Team, 2020)

"Anthropogenic (man-made or disturbed habitats), brackish or salt marshes and flats, fresh tidal marshes or flats, marshes, meadows and fields, shores of rivers or lakes, wetland margins..."- (Go Botany)

"...codominant with bulejoint reedgrass (Calamagrostis Canadensis) on wet and prairies and alkaline fens in Indiana. The wet prairie is highly productive for agriculture, and remnants are uncommon today. Alkaline fens are more common on the eastern prairies of Ohio and Indiana than on prairies to the west...provides fair to poor forage for livestock and wildlife. It is seldom grazed because of the large amount of standing litter produced and the boggy areas in which it grows. If grazed, it is usually during the spring before the stems become coarse and woody, or in the fall after other forage has dried. Early spring growth is the most palatable...most abundant grass of low floodplains and wetlands in Indiana. It is a facultative wetland species, meaning it is usually found in wetlands (67 to 99 percent of the time) but is occasionally found in nonwetlands. It occurs on most soil textures from fine clays to silt loams and is somewhat tolerant of alkaline conditions. It is tolerant of high water tables but intolerant of prolong flooding...grows on wet banks of sluggish streams and around ponds...Sites where praire cordgrass has been reported include: lower, poorly drained soils and alkaline fens of moraines, till plains, and floodplains, pothole borders, and around pairie marshes and along drainage ways through the tall and mixed-grass pairies."- (Fire Effects Information System)

*Sporobolus fimbriatus*-

"South Africa, Botswana, Kenya, Ugnda, Sudan and Somalia, Tanzania, Namibia. Perennial bunchgrass...short oblique rhizome...famine food, tillers, planted pasture, very high grazing value, palatable food fodder, grains and seed head eaten by baboons, grains pounded and eaten as porridge, useful for erosion control, xerophytic, drought-tolerant, growing in shallow rocky red clay, open deciduous bushland or grassland, heavy soils, well-drained soils, sandy well-drained loam, in shady spots, near water, near rivers or along river courses, moist conditions, semiarid grassvelds, along highways and roadsides, ungrazed sites, under trees, disturbed sites..."- (Quattrocchi, 2006)

"Sudan; Somalia, and southwards to South Africa. In miombo woodland often on termitaria, mopane woodlands and pans in mopane woodland, in riverine woodland and grasslands, and in shallow rainwater pans in dry sandveld, sometimes on rocky hill-sides 0-1220 m."- (Flora Zambesiaca)

"...commonly found up to 2000 m altitude in open woodland and grassland, often in shallow rainwater pans, sometimes on rocky hillsides, also in disturbed or shady locations."- (Plant Resources of Tropical Africa)

*Sporobolus indicus*-

"India, Himalaya, southern US to Paraguay. Perennial bunchgrass...it stands drought, pasture, handicrafts, smutgrass plants generally unpalatable to cattle, green fodder, when old becomes tough and unpalatable, widespread in tropic and warm temperate regions, weed species of disturbed ground and pastoral areas, cultivated soils, lawns, in hot areas, clay soils, cool moist areas, rich moist bottoms, rocky stream margins, on roadsides and yards, waste places..."- (Quattrocchi, 2006)

"...grows in sandy to clayey soils in pastures, roadsides, disturbed areas, and lakeshores. This weedy species can be either an annual or a perennial. It provides poor forage for livestock and wildlife. It is often infected with a fungus (Bipolaris spp.) that cover the foliage and inflorescence with a black "smut." It is pantropical in distribution..."- (Stubbendieck et al., 2017)

"...pantropical species. It commonly grows in disturbed places and open areas such as roadsides, pastures, and lake shores. In the Manual region, it is found on sandy or clay soils and is associated with many plant communities."- (Barkworth et al., 2007)

"Arabia; Ascension Island; Cameroon; Easter Island; Hawaii; Sri Lanka; Ethiopia, and southwards to South Africa. Floodplain and swampy grasslands; also in montane grassland and margins of evergreen forest 100-2300 m."- (Flora Zambesiaca)

“...often grows in disturbed and open areas, such as roadsides, pastures and lake shores.”- (Feedipedia)

*Stipa capensis-*

“North Africa, Algeria, South Africa, Middle East. Annual, toxic, persistent awn bent and twisted...useful for erosion control, found in open veld, disturbed places...”- (Quattrocchi, 2006)

“Pakistan (Baluchistan, Punjab, NWFP & Kashmir); Mediterranean region eastwards to Northwest India; South Africa. This, the only annual species of Stipa found locally is characteristic of dry stony hillsides and deserts.”- (Cope, 1982)

“Dry sandy places, s.l.-400 m.”- (Davis et al. 1985)

“Open dry sandy habitats (deserts or semi-deserts) and on hard soil on the floor of pans...”- (Flora Zambesiaca)

“Desert, Shrub-steppes”- (Flora of Israel Online)

*Stipagrostis ciliata-*

“Algeria, Sudan, Namibia, Yemen, Pakistan. Perennial...young growth more or less palatable, high nutritive value, useful for erosion control, a sandbinder, extremely drought-resistant, growing on open hillsides, dry areas, on steep stony slopes, red sandy soil, sandy soils with lime substratum...”- (Quattrocchi, 2006)

“...south-western and North Africa, eastwards to Sinai, Arabia and Afghanistan. Usually in open grassland on dry sandy soils in hilly areas...”- (Flora Zambesiaca)

“Sand...Saharo-Arabian...”- (Danin and Fragman-Sapir, 2016)

*Stipagrostis hirtigluma-*

“Ethiopia, Angola, tropical and southern Africa, Namibia. Annual or short-lived perennial...palatable fodder before flowering or seeding, camel grass, weed of plantations, escarpment foothills, semidesert grasslands, dry stony Acacia-Commiphora bushland, coarse sandy soils, poor dry sandy soil, water courses, sandy riverbeds, arid waste places...”- (Quattrocchi, 2006)

*Stipagrostis obtusa-*

“Kuwait, South Africa, Namibia, Egypt, Tunisia. Perennial...very drought resistant, pasture, palatable, very high grazing value, good sand binder, useful for erosion control, occurs in dry areas, semidesert, stony and sandy soils in dry areas, along roadsides, on loose sandy soil, in sand at base of outcrop...”- (Quattrocchi, 2006)

“Cape Province; eastern Pakistan; Iraq; North Africa; Orange Free State; Sinai Peninsula; south-western Africa; Open dry sandy habitats (deserts or semi-deserts) and on hard soil on the floor of pans)”- (Flora Zambesiaca)

“Shrub-steppes, Deserts, Semi-steppe shrublands...Sand, Saharo-Arabian-Sudanian...”- (Danin and Fragman-Sapir, 2016)

“...very palatable forage for the grazing animals. The arid and sandy habitat of this species makes it an important plant to be exploited as a forage.”- (Sherif and Siddiqi, 1988)

*Stipagrostis plumosa-*

"North Africa."- (Quattrocchi, 2006)

"A desert grass of great value not only as a fodder but also by virtue of its ability to act as a sand-binder."- (Cope, 1982)

*Stipagrostis uniplumis-*

"Tropical and South Africa, Arabia, India, Pakistan. Perennial, often short-lived...grazed by cattle, useful for erosion control, growing on sandy soils, arid areas, Acacia bushland, open grasslands, riverbanks, semidesert scrub..."- (Quattrocchi, 2006)

*Tribolium echinatum-*

"South Africa. Annual, vigorous...weed, useful for erosion control, along roadsides, in dry river bed, in disturbed clay soil, on loose roadside soil, in roadside depression, sandysoils..."- (Quattrocchi, 2006)

"Flowering August to Novermber. Sandy soils and roadsides. Locally common. Biome: Fynbos and Succulent Karoo. Endemic."- (Russell et al., 1990)

GENUS: "11 species. South Africa. Mesophytic to xerophytic (winter rainfall); in open habitats (Fynbos and Karoo): glycophytic. Cape Province. 11 indigenous species"- (Russell et al., 1990)

*Triraphis schinzii-*

"South Africa, Mozambique, Tanzania, Namibia, Zimbabwe, Kalahari. Perennial...shortly rhizomatous...palatable, ornamental, growing in sandy soil, deep sand, riverbanks, dunes, bushveld, grassland..."- (Quattrocchi, 2006)

"Namibia; South Africa; Tanzania; In dry open woodland and scrub, on Kalahari Sand and on basic sandy soils 0-1480 m."- (Flora Zambesiaca)

GENUS: "Tropical and southern Africa, Australia. Mesophytic to xerophytic; in open habitats (savanna, in sandy or rocky soil); glycophytic. Namibia, Botswana, Transvaal, Orange Free State, Natal, and Cape Province. 5 indigenous species."- (Russell et al., 1990)

"Flowering November to April. Sandy grassland or bushveld, deep sand on dunes or riverbanks and on forest margins. Common. Biome: Savanna and Grassland, Tanganyika. Closely related to T. andropogonoides, which has a very well developed rhizome ad the central awn of the lemma shorter than the lemma."- (Russell et al., 1990)

*Tristachya superba-*

"Tropical Africa, Malawi, Mali, Zambia, Angola. Perennial...pasture, roots used as an aphrodisiac, common in sandy soil, in low-lying areas, moist meadows, rocky sites."- (Quattrocchi, 2006)

"Tropical Africa; Deciduous woodland 450-1900 m."- (Flora Zambesiaca)

GENUS: "About 20 species. Tropical and southern Africa, Madagascar, tropical America. Helophytic to xerophytic; in shade and in open habitats (grassland and savanna, woodland and floodplains, wet to dry soils); glycophytic."- (Russell et al., 1990)

“Flowering February to August. Granite sandveld and Kalahari sands. Locally common (sandy areas, widespread). Biome: Savanna. Tropical Africa. Domestic use (culms used as drinking straws by Bushmen), or pasture (roots eaten by warthogs).”- (Russell et al., 1990)

*Triticum dicoccoides*-

“Dry mountain slopes, between 1,200 and 1,700 m alt., on brown serozems with salt efflorescence on the surface.”- (Komarov et al. (1963))

“Wild emmer is distributed over the Near East Fertile Crescent...In this area, T. dococcoides grows as an annual component in several steppe-like herbaceous formations and in the Quercus ithaburensis or in the Q. brantii park-forest belts.”- (Nevo et al., 1982)

*Urochloa mosambicensis*-

“Tropical East Africa, South Africa. Perennial, often short-lived...shortly stoloniferous...economic plant, cultivated pasture, forage, weed and fodder, grazing of good nutritive value even when dry, palatable, grazed heavily by wild animals, grains and tillers eaten by baboons, seeds boiled and eaten in times of famine, grows quickly, heavy seed production, drought resistant, poor frost tolerance, it does not tolerate soils subject to flooding or badly drained sites, useful for erosion control and revegetation, naturalized in tropics, grows in disturbed places, along roadsides, wooded grassland, over-grazed trampled veld, sandy soil and red sandy soil, coarse sand, in open grassland, in sheltered disturbed places, red clay soil and disturbed red clay soils, deciduous bushland, hard red clay soil, brown clay loam, in fertile sand-loam soil and waste ground, stolons and broad leaves protect the soil effectively against rain, wind and sun...”- (Quattrocchi, 2006)

“In savanna woodland and wooded grassland, often spreading by stolons through disturbed areas.”- (Hyde et al., 2020)

“Usually found in wooded grassland and deciduous bushland, or on disturbed sites, especially where the soil is fertile...From 360-1,300 (mean 710) mm rainfall environments, usually on well-drained soils and does not tolerate flooding or waterlogging...Tolerant of light shade...Recovers well from fire.”- (Cook et al., 2005)

“...occurs from KwaZulu-Natal northwards to east Africa. It is planted in Australia as a cultivated pasture. Bushveld signal grass is a ruderal, common on disturbed areas such as roadsides, fallow lands and trampled ground, especially where the soil is fertile. In central Africa it is usually an open savanna or woodland species, whereas in South Africa it favours grassland...grows on a variety of soil types, mostly fertile sand-loam and usually in sheltered disturbed places. It often grows in light shade. Pollination is by wind, seed dispersal by wind and water. It is a palatable grass with an average leaf production. It is an introduced forage crop in tropical countries and a good indicator of disturbed places.”- (PlantZAfrica, 2000)

“Uganda and Kenya to S. Africa; introduced to many other tropical countries as a forage plant. Savanna woodland and open grassland, often on seasonally flooded clays or disturbed sites 0-1600 m.”- (Flora Zambesiaca)

*Vulpia myuros*-

“Europe, Mediterranean, Eurasia, Africa. Annual...shade species, useful for erosion control and revegation of disturbed areas, open fields, weed of lawns and roadsides, roadside embankment, disturbed areas, waste places, dry fields, dry sand, moist sand, wet sand of stream, arid areas, fine sandy loam, in dry rocky or sandy habitats, damp bare soil, banks in sandy soil, along streams, moist gravel...”- (Quattrocchi, 2006)

“Dry slopes; often as a weed (among crops and in gardens).”- (Komarov et al. (1963))

“Quercus scrub, sand dunes, weed of fallow and cultivated fields, 20-1400 m.”- (Davis et al. 1985)

“...usually found as a weed of cultivation.”- (Cope, 1982)

“Mountain slopes, roadsides, especially in sandy places...This species is adventives in most temperate parts of the world.”- (Flora of China vol. 22)

“...introduced, short, aggressive, early maturing cool season annual grass with many fibrous roots. It has excellent seedling vigor and emerges in fall very soon after the first rain. It matures seed earlier than most annual grasses, assuring perpetuation. It can tolerate soil problems of acidity, serpentine, and low fertility. This species is native to Asia and Europe...drought tolerant grass that will persist and provide good erosion control cover with an annual precipitation of at least 25 cm. (10 in.), or on areas receiving extra run-in moisture, and on areas receiving some supplemental irrigation.”- (USDA, NRCS National Plant Data Team, 2020)

“Antrhopogenic (man-made or disturbed habitats), meadows and fields”- (Go Botany)

“Annual grass, native to much of Europe and parts of Asia, introduced to the USA, Australia and a number of other countries...outcompetes native species in grasslands of the western US and is a significant agricultural weed. It forms dense swards and its shallow roots suppress growth of native grasses and forbs...In its native range, V. myuros commonly grows in dry ruderal sites, on sand and gravel banks, roadsides and embankments, and in old fields, usually on acidic soils. In the West Coast states of the USA, V. myuros is an important component of annual grasslands; it is also reported from a wide range of habitats subjected to disturbance, for example fires, soil degredation, abandonment of cultivated fields and logging. It is an important groundlayer component in western hardwoods, especially in oak woodland, although it is most common in early successions, tends to decrease with canopy closure in woodlands, and does not persist in closed forests...sensitive to drought due to their shallow roots. It tolerates a wide range of soils, but not drought."- (CABI, 2020)

"...important component of California and Oregon grasslands, where it is often dominant or codominant in annual grasslands. It is mainly confined to disturbed sites in Washington....same perennials that historically dominated California and Oregon's native prairies once dominated the groundlayer vegetation of native deciduous woodlands. As with the pariries, native groundlayer vegetation of these hardwood ecosystems has been largely replaced by nonnative annuals....present to dominant in many western shrubland communities."- (Fire Effects Information System)

*Whiteochloa capillipes*-

"A genus of 5 species endemic in monsoonal Australia, with the exception of *W. capillipes* which extends to the Moluccas. The group, which is closely allied to *Panicum*, comprises annuals and short-lived perennials growing abundantly at low altitudes in deep, sandy soils in association with eucalypt savannah."- (Lazarides, 1980)

"Culms 60-105 cm long..."- (Clayton et al., 2016)

"Australia, Indonesia..."- (Quattrocchi, 2006)

"Extends to New Guinea and Malaysia. In tropical and subtropical sub-humid woodlands."- (Simon and Alfonso, 2020)

"Known only from the Northern Territory...The species is not yet known from Queensland or Western Australia despite the records by Hughes (1923)...Plants occur chiefyly on alluvial soils or sites related to watercourses, lagoons and similar depressions. Associated plants include Callitris, Pandanus, Chrysopogon latifolius ST Blake, Coelorachis rottboellioides (R. Br) A Camus and Tristania lactiflue F Muell. Essentially the species is a summer-growing, wet-season (Nov-April) annual, but individuals sometimes produce short rhizomes and probably behave as short-lived perennials."- (Lazarides, 1977)

*Zea mays-*

"New World, Mexico, Central America. Annual...cultivated as a food crop plant for humans and domesticated animals, palatability excellent for all green matter, ground as flour, alcohol production, the main use of the whole plant is as silage, corn may accumulate free nitrates, dry weather at pollination time seriously affects pollination, period of lowering and to maturity varies greatly, maze is subject to many diseases, maize has no tolerance to flooding, crops are very susceptible to erosion, seed is diuretic and a mild stimulant, a glue is made from the starch in the seed, dried cobs used as a fuel, pith of the stems used as a packing material, a decoction of the leaves and roots is used in the treatment of strangury, dysuria and gravel, numerous cultivars are available throughout the world, cultivated in field, requires a well-drained and fertile soil, fairly drought tolerant, very susceptible to frosts, stigmas are diuretic and anti-hypertensive..."- (Quattrocchi, 2006)

*Zoysia japonica-*

"China, Korea, Japan, Taiwan. Perennial or annual, light green, erect, coarse and tough...ornamental lawn grass cultivated and naturalized elsewhere, hard and unpalatable to livestock, usually drought resistant, useful for erosion control, used on golf course greens, playing fields, found along sea cliffs, open places, near dams, moderately wet areas, under shade of trees, on heavy soils, grassy hillsides..."- (Quattrocchi, 2006)

"Coastal areas, grassy hillsides, open places...a good lawn grass."- (Flora of China vol. 22)

**Methods S3: Ancestral State Estimation**

When fitting different models of character evolution, internal nodes were placed into one of two evolutionary regimes based upon ancestral state estimates of photosynthetic pathway and habitat type. Ancestral state estimation (ASE) was completed via stochastic mapping (Nielsen, 2002; Huelsenbeck et al., 2003) in the R package phytools (v. 0.6.44; Revell, 2012). Models assumed equal rates (i.e., rates of change between states were equal in both directions) and were run for a total of 1,000 generations. The results of these tests are shown in Figures S1 and S2, for photosynthetic pathway and habitat, respectively. Each internal node was assigned to the evolutionary regime corresponding to the state with the highest posterior probability at that node. For photosynthetic pathway, the inferred ancestral state at interior nodes was unambiguous, with posterior probabilities for the favored state never falling below 95%. The sole exception to this trend was the root node, which was weakly supported as $C_3$. However, because our sampling favors $C_4$ over $C_3$ PACMAD taxa, the relatively high posterior probability of possession of $C_4$ photosynthesis at the root is clearly erroneous (e.g., Spriggs et al., 2014). In addition, it is clear that our sampling within the PACMAD clade favors a reconstruction of $C_4$ photosynthesis at many of the deeper nodes within this group, where a more comprehensive sampling would suggest $C_3$ photosynthesis (e.g., Bouchenak-Khelladi et al., 2009; Spriggs et al., 2014). As such, we manually placed seven nodes into the $C_3$ evolutionary regime, despite their reconstruction here as possessing $C_4$ photosynthesis (Fig. S1). These were the node at the base of the PACMAD grasses, the node representing the most recent common ancestor (MRCA) of the Aristidoideae, Chloridoideae, Micrairoideae, and Danthonioideae, the MRCA of the Chloridoideae, Micrairoideae, and Danthonioideae, and the MRCA of the Danthonioideae and Chloridoideae. The nodes at the base of the Panicoideae and Paniceae, as well as the MRCA of the Paniceae, Paspaleae, Andropogoneae, and Arundinareae were also placed in the $C_3$ evolutionary regime (Figure S1). Reclassification of these nodes followed the results of Spriggs et al. (2014). We elected to restrict our manual reclassification to these nodes because they were unambiguously $C_3$, judging that a more extensive reclassification would have required rectifying topological differences and differences in reconstructions at interior nodes between studies (e.g., Bouchenak-Khelladi et al., 2009; Spriggs et al., 2014). We additionally ran a preliminary analysis that strictly followed our ASE results and found we obtained only negligible differences.

In contrast, ASE for habitat type returned ambiguous results at most interior nodes (Fig. S2). This complicated assigning nodes to evolutionary regimes, and model fitting results may therefore be less reliable than those for photosynthetic pathway. We placed nodes into the evolutionary regime corresponding to the state with the highest posterior probability at that node, while additionally constraining the stem node of each subfamily to occupy a non-grassland habitat (Fig. S3). The latter decision was based upon the fact that multiple lines of evidence demonstrate that the twelve subfamilies diverged from one another, well before evidence for grass dominated ecosystems first appears in the fossil record (Prasad et al., 2005; Prasad et al., 2011; Strömberg, 2011; Palazzesi and Barreda, 2012; Strömberg et al., 2013; Dunn et al., 2015; ; Wu et al., 2017; Gallaher et al., 2019).

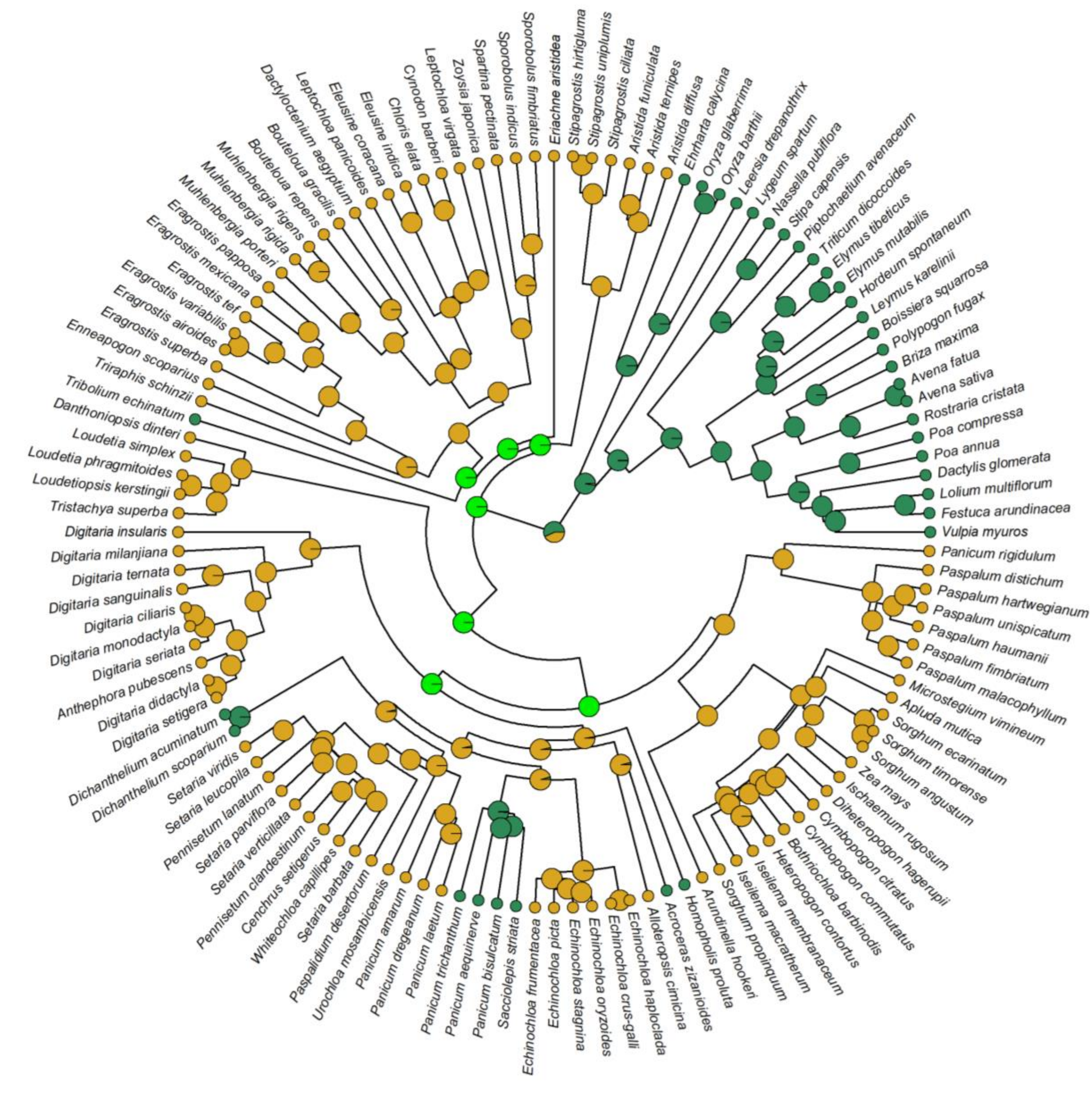



**Figure S1:** Results of our ASE of photosynthetic pathway. Colors represent ancestral states as follows: dark green – $C_3$, yellow – $C_4$, light green – nodes manually identified as $C_3$ (see discussion above).

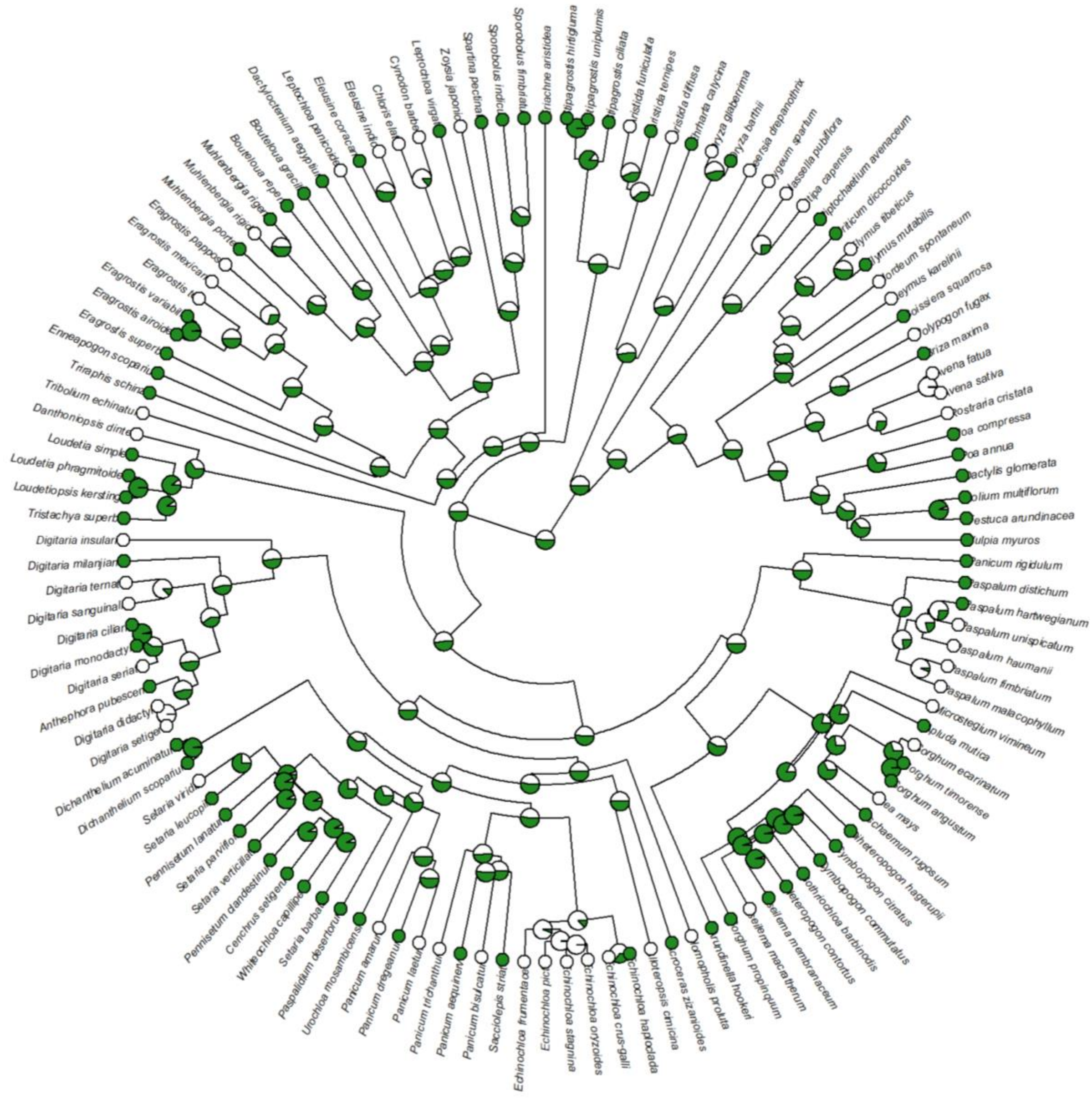



**Figure S2:** Results of our ASE of occupation of grassland/savanna type habitats. Colors represent ancestral states as follows: dark green – grassland/savanna, white – other.

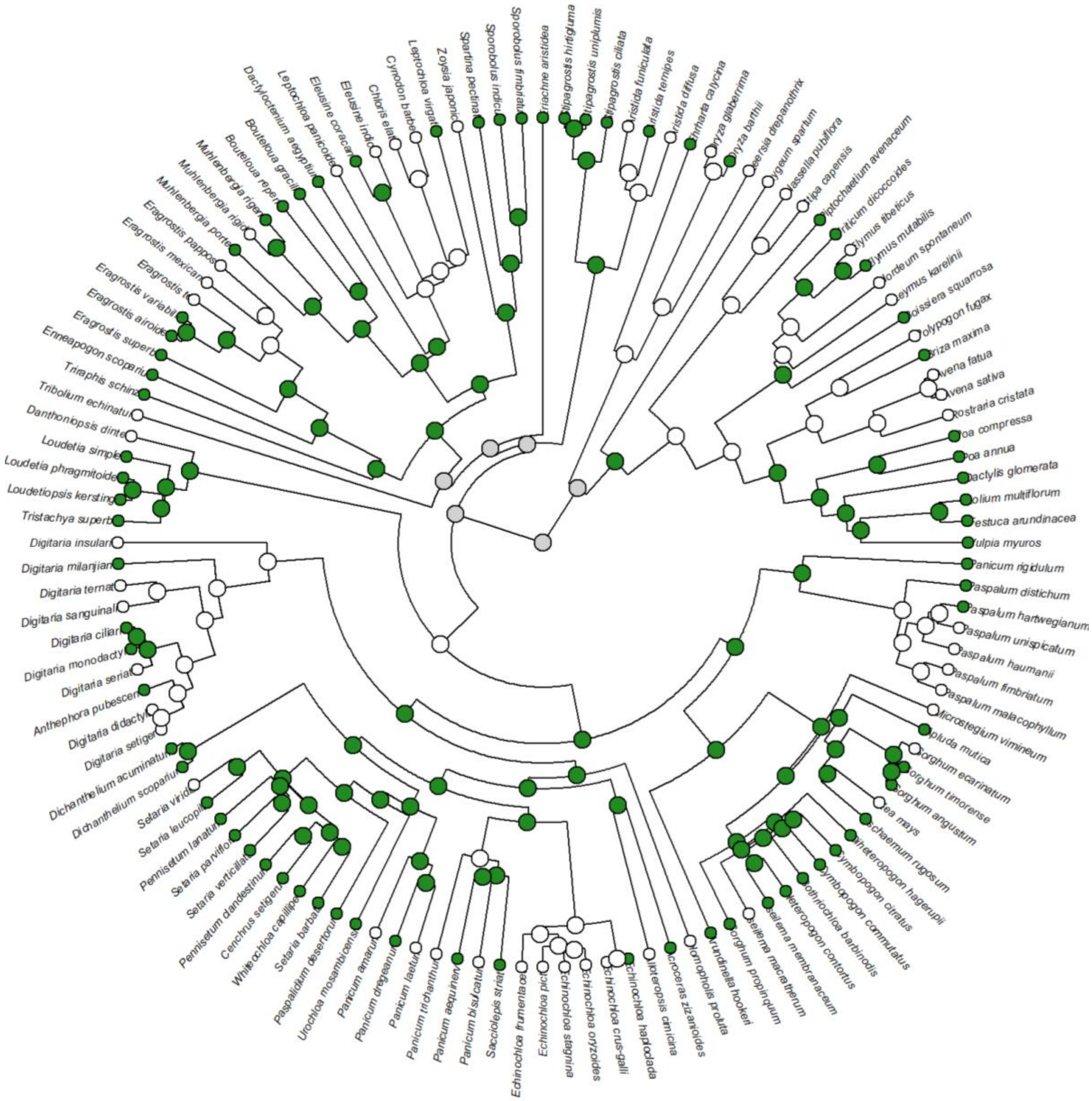
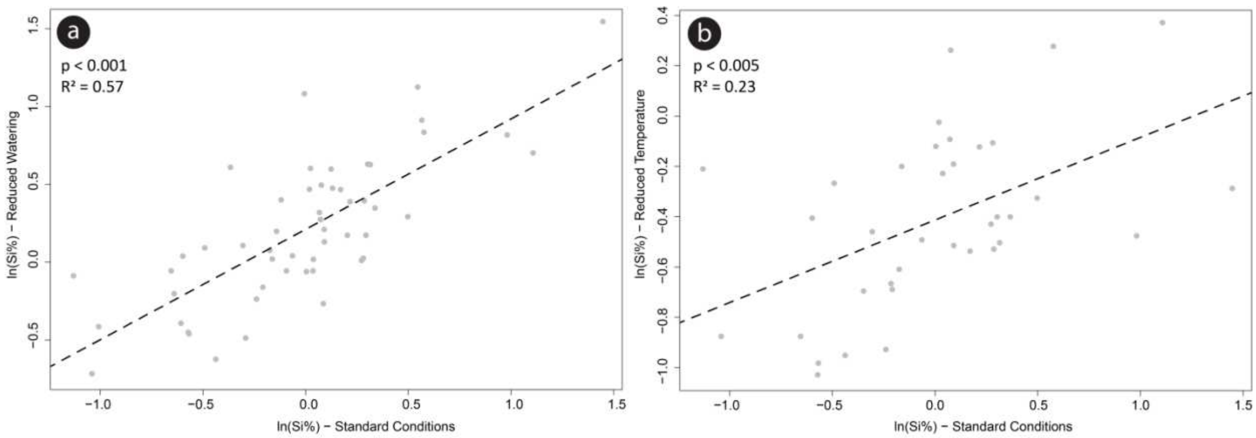


**Figure S3:** Phylogeny showing evolutionary regimes used during testing of OU models of the evolution of Si concentration in taxa of grassland/savanna, and all other habitats. Assignments were based upon the state with the highest posterior probability at each node (Fig. S2), with several of the deeper nodes manually assigned to the other category. Colors represent regimes as follows: dark green – grassland/savanna, white – other, grey – nodes manually identified as other (see discussion above). See Methods S3 for further explanation.

## Notes S1: Patterns of Si Concentration

For those taxa that were included in more than one of our three datasets, we looked at how well Si concentration under one set of conditions predicted concentration under another. To test this, we calculated average Si concentration to the species level and then ran linear regression for each of the three pairwise comparisons (Fig. S4). For all three, there was a significant correlation, though Si concentration in taxa grown under reduced temperature conditions appeared to be less representative of Si concentration in the other two datasets (Fig. S4).



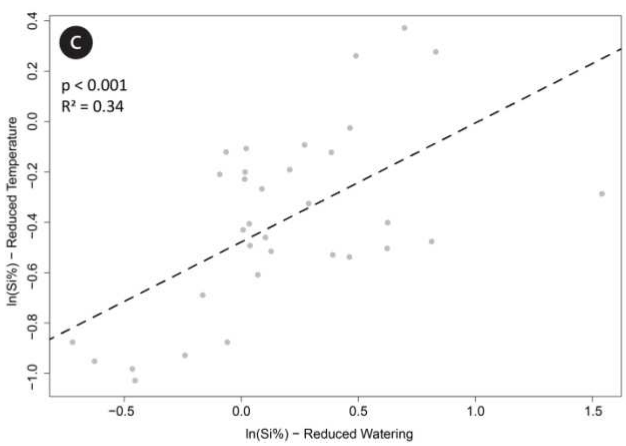




**Fig. S4:** Scatter plots showing relationship between species average Si concentration in (a) standard and reduced watering conditions, (b) standard and reduced temperature conditions, and (c) reduced watering and reduced temperature conditions.

## Notes S2: Intraspecific Variation

There are a number of potential limitations that complicate the study of intraspecific variation in Si deposition in this study. The first is the potential for measurement error to artificially inflate variation in species with low Si concentration values. This is potentially cause for concern because imprecision in measurements will have a relatively higher impact on measurements at the low end of the observed Si concentration spectrum, when compared with the upper end. It is therefore possible, that low Si species could be driving up the average levels of intraspecific variation within our dataset. To see if this was an issue in our data, we ran a linear regression with ln(Si concentration) as a predictor for coefficient of variation (CV). This suggested that low Si species did not have higher than average CVs, and our regression did not return significant results (Supporting Information Fig. S6; $F_{(1,85)}$= 0.08, $p$= 0.77, $R^2$< 0.001). We therefore concluded that this was unlikely to be a major issue in interpreting our results.

A second, and more systemic, issue is the possibility for the low sample sizes obtained for most species to skew our CV values. We used two separate approaches to evaluate this effect in our data. The first followed the same method as described above, but, this time using number of specimens as our predictor. We found a weak positive relationship between CV and the number of individuals per species (Supporting Information Fig. S7; $F_{(1,85)}$= 5.09, $p$= 0.03, $R^2$= 0.05). The second method was to simulate different sampling intensities from a hypothetical population of 10,000 individuals, where Si concentration followed a normal distribution with a mean of 10% and a standard deviation of 1.7 (i.e., the CV of the population is 17%, similar to the observed median value in our standard conditions dataset). We simulated 99 different sampling intensities from this population, starting with a sample size of two, and increasing the number of individuals per sample by one, up to a sample of 100 individuals. The CV was then calculated for each of these 99 samples, and the process repeated 1,000 times (Supporting Information Fig. S8). Consistent with our regression results, CV values at low sampling intensities tended to be lower than the true population value (i.e., 17%). For example, at a sample size of two, the median CV across 1,000 iterations was 11.4%, with only 30% of iterations returning CV values higher than the true population value (both were the lowest of any sample size). However, low sample sizes also showed the greatest amount of variation between runs, with the largest total range in CV values across all iterations (Supporting Information Fig. S8). Thus, the number of iterations returning values substantially higher, or lower, than the true value was highest at low sample sizes (i.e., at a sample size of two, 15% of iterations returned values more than 50% greater than the true value – the highest of our dataset). From these results, we draw two main conclusions. First, because of our small sample sizes, we must regard our highest observed intraspecific CV values with caution. Second, our median intraspecific CV values are unlikely to be biased upwards as a result of small sample sizes, and may, in fact, represent underestimates of the true levels of intraspecific variation. Even if we base our interpretations solely on our median CV values, it is clear that Si deposition in grasses is a trait with high levels of intraspecific variability.

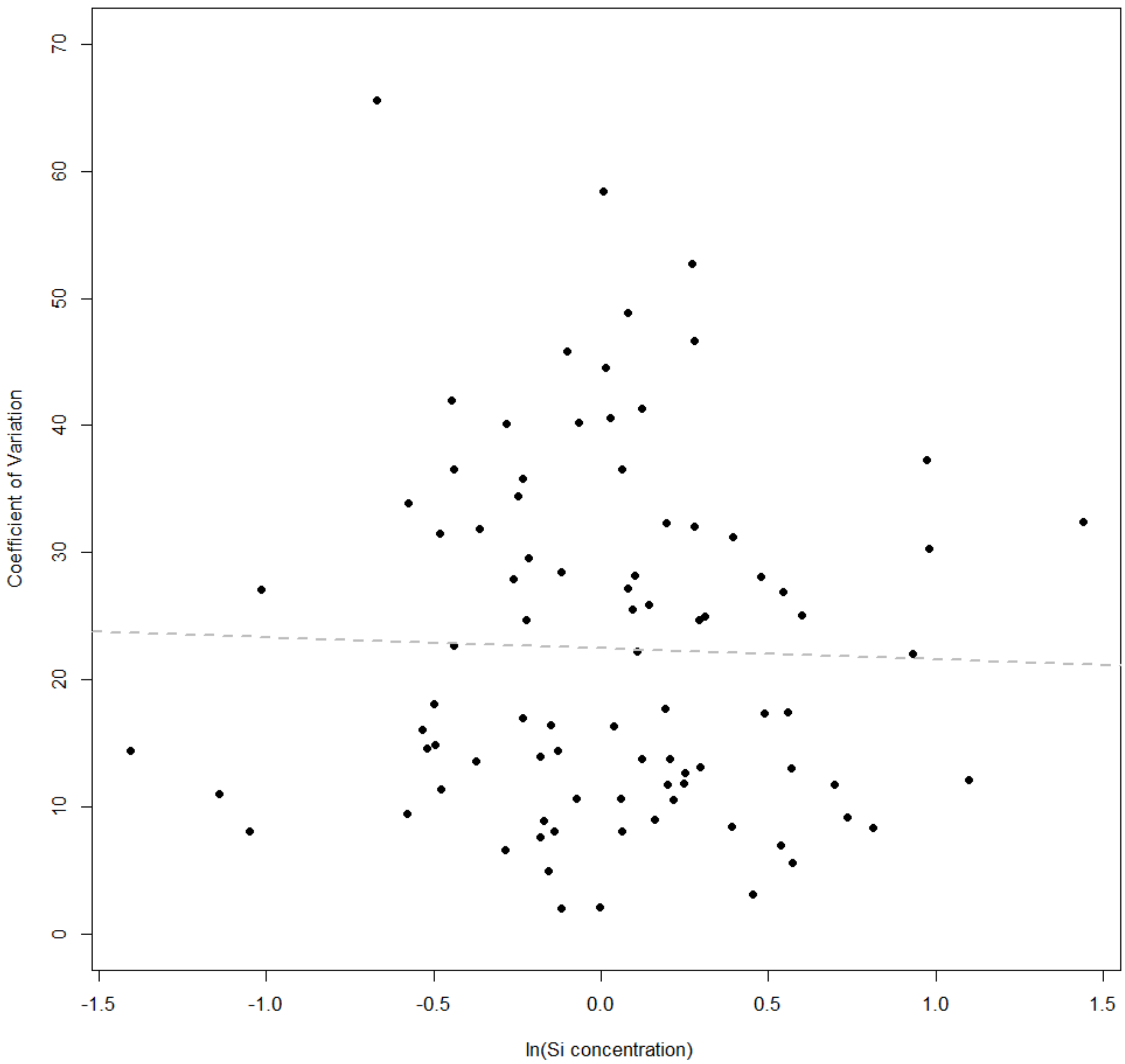



**Figure S5:** Relationship between species average Si concentration and intraspecific CV.

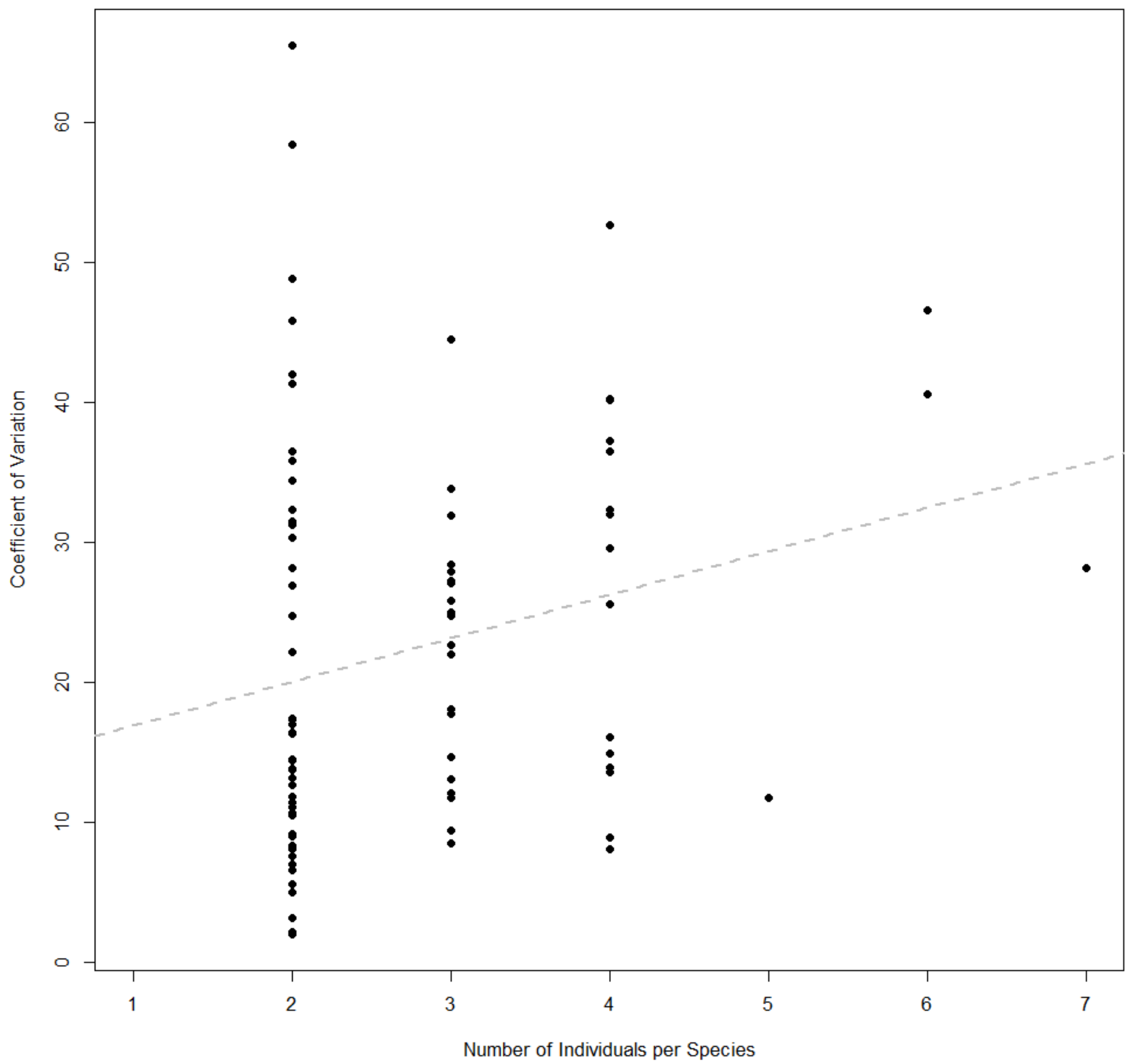



**Figure S6:** Relationship between number of individuals per species and intraspecific CV.

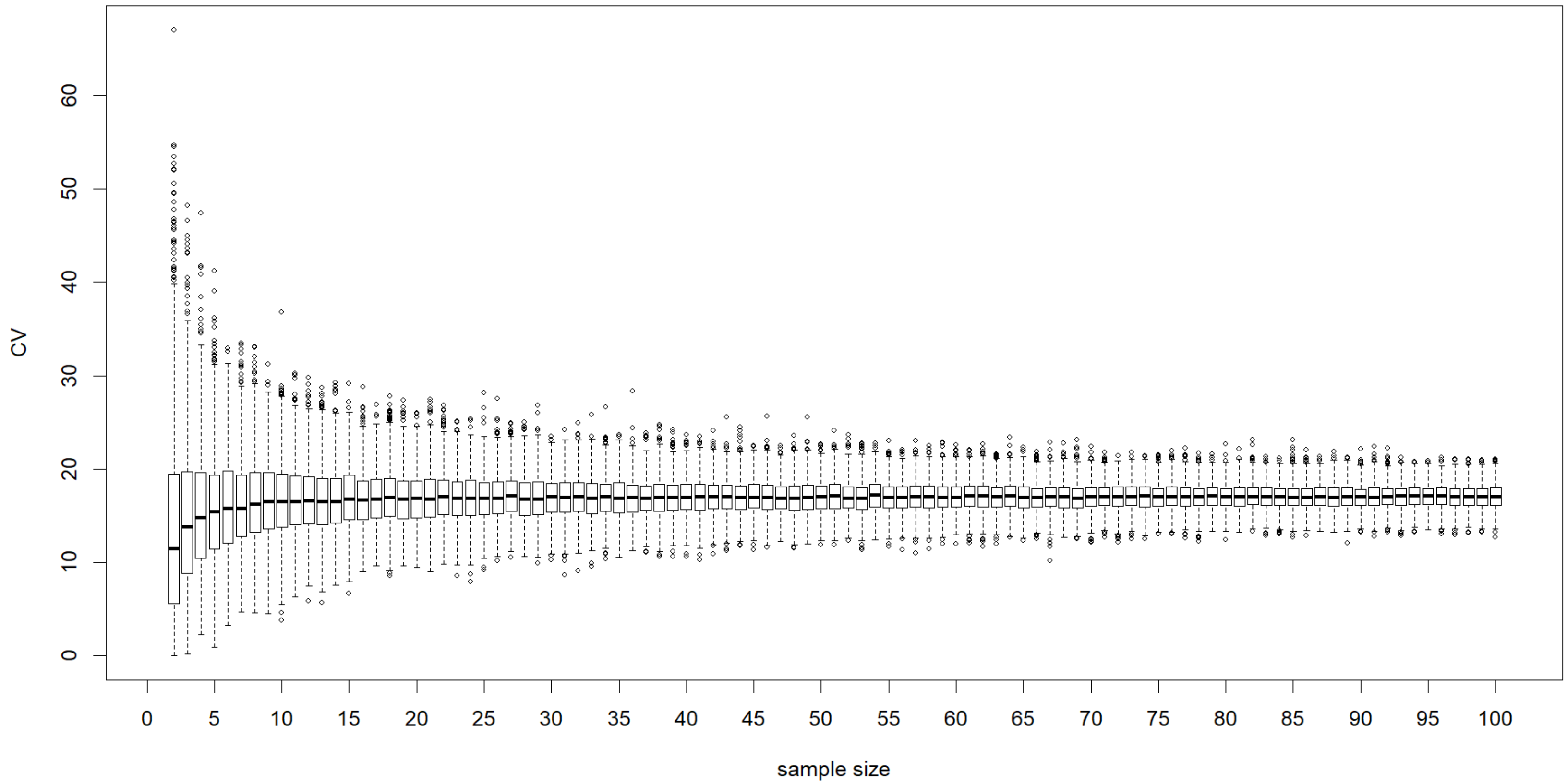



**Figure S7:** Results of simulated sampling of different intensities from a hypothetical population of 10,000 individuals possessing some normally distributed, quantitative trait with mean 10 and CV 17%.

**References:**


Arechavaleta, J. (1894). Flora Uruguaya. In *Las Gramineas Uruguayas*. Establecimiento Tipo-Litografico Oriental.

Atkinson, R. R. L., Mockford, E. J., Bennett, C., Christin, P. A., Spriggs, E. L., Freckleton, R. P., Thompson, K., Rees, M., & Osborne, C. P. (2016). $C_4$ photosynthesis boosts growth by altering physiology, allocation and size. *Nature Plants*, *2*(5), 1–5.

Barkworth, M. E., Anderton, L. K., Capels, K. M., Long, S., & Piep, M. B. (Eds.). (2007). *Manual of Grasses for North America*. Intermountain Herbarium and Utah State University Press.

*Bolivia Checklist*. (2008). EFloras. http://www.efloras.org/flora_page.aspx?flora_id=40

Bouchenak-Khelladi, Y., Verboom, G. A., Hodkinson, T. R., Salamin, N., Francois, O., Ní Chonghaile, G., & Savolainen, V. (2009). The origins and diversification of $C_4$ grasses and savanna-adapted ungulates. *Global Change Biology*, *15*(10), 2397–2417.

CABI. (2020). *Invasive Species Compendium*. CAB International. https://www.cabi.org/

Chamberlain, S., Oldoni, D., Barve, V., Desmet, P., Geffert, L., Mcglinn, D., & Ram, K. (2017). *rgbif: Interface to the Global "Biodiversity" Information Facility API*. https://cran.r-project.org/web/packages/rgbif/index.html

Cook, B., Pengelly, B., Brown, S., Donnelly, J., Eagles, D., Franco, A., Hanson, J., Mullen, B., Partridge, I., Peters, M., & Schultze-Kraft, R. (2005). *Tropical Forages: an interactive selection tool*. CSIRO, DPI&F(Qld), CIAT, and ILRI. http://www.tropicalforages.info/

Cooper, N., Thomas, G. H., Venditti, C., Meade, A., & Freckleton, R. P. (2016). A cautionary note on the use of Ornstein Uhlenbeck models in macroevolutionary studies. *Biological Journal of the Linnean Society*, *118*(1), 64–77.

Cope, T. A. (1982). Flora of Pakistan No. 143 Poaceae. In E. Nasir & S. I. Ali (Eds.), *No. 143 Poaceae*. University of Karachi.

Danin, A., & Fragman-Sapir, O. (2016). *Flora of Israel Online*. http://flora.org.il/en/plants/

Davidse, G., Judziewicz, E. J., & Zuloaga, F. O. (2004). Flora of the Venezuelan Guayana vol. 8 Poaceae - Rubiaceae. In P. E. Berry, K. Yatskievych, & B. K. Holst (Eds.), *vol. 8 Poaceae - Rubiaceae*. Missouri Botanical Garden Press.

de Melo, S. P., Monteiro, F. A., & de Bona, F. D. (2010). Silicon distribution and accumulation in shoot tissue of the tropical forage grass Brachiaria brizantha. *Plant and Soil*, *336*(1), 241–249.

Dunn, R. E., Strömberg, C. A. E., Madden, R. H., Kohn, M. J., & Carlini, A. A. (2015). Linked canopy, climate, and faunal change in the Cenozoic of Patagonia. *Science*, *347*(6219), 258–261.

*Feedipedia*. (n.d.). INRAE, CIRAD, AFZ, FAO. https://www.feedipedia.org/

Fick, S. E., & Hijmans, R. J. (2017). WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas. *International Journal of Climatology*, *37*(12), 4302–4315.

*Fire Effects Information System*. (n.d.). USDA. https://www.feis-crs.org/feis/#

Flora of Australia vol. 44A Poaceae 2. (2009). In A. Wilson, L. Jessup, P. Kodela, B. Kuchlmayr, B. Leditschke, K. Mallett, P. McCarthy, A. Monro, C. Moon, L. Randell, & H. Thomopson (Eds.), *vol. 44A Poaceae 2*. ABRS/CSIRO.

Flora of Australia vol. 44B Poaceae 3. (2005). In K. Mallett, B. Barnsley, J. Bleyerveen, D. Foreman, G. Garcon, B. Kuchlmayr, B. Leditschke, P. McCarthy, A. McCusker, A. Monro, J. Mowatt, J. Mowatt, H. Thompson, & A. Wilson (Eds.), *vol. 44B Poaceae 3*. ABRS/CSIRO.

*Flora of China vol. 22*. (2008). EFloras. http://www.efloras.org/volume_page.aspx?volume_id=2022&flora_id=2

Flora of the U.S.S.R. vol. II. (1963). In V. L. Komarov, R. Y. Rozhevits, & B. K. Shishkin (Eds.), *Vol. II*. Israel Program for Scientific Translations.

Flora of Turkey and the East Aegean Islands vol. 9. (1985). In P. H. Davis, R. R. Mill, & K. Tran (Eds.), *vol. 9*. Edinburgh University Press.

Flora Vascular de la Republica Argentina vol. 3. (2012). In F. O. Zuloaga, Z. E. R. de Agrasar, & A. M. R. Anton (Eds.), *vol. 3*. Instituto Multidisciplinario de Biologia Vegetal.

*Flora Zambesiaca*. (n.d.). Kew Royal Botanic Gardens. https://apps.kew.org/efloras/search.do

*FloraBase the Western Australian Flora*. (n.d.). Western Australian Herbarium, Department of Biodiversity, Conservatoin and Attractions. https://florabase.dpaw.wa.gov.au/

Gallaher, T. J., Adams, D. C., Attigala, L., Burke, S. V., Craine, J. M., Duvall, M. R., Klahs, P. C., Sherratt, E., Wysocki, W. P., & Clark, L. G. (2019). Leaf shape and size track habitat transitions across forest–grassland boundaries in the grass family (Poaceae). *Evolution*, *73*(5), 927–946.

*GBIF.org*. (2020).

*Go Botany*. (2020). Native Plant Trust. https://gobotany.nativeplanttrust.org/

*Gramineae (Poaceae) in Flora of Taiwan*. (2008). EFloras. http://www.efloras.org/flora_page.aspx?flora_id=1050

Gutiérrez, J. R., Meserve, P. L., Herrera, S., Contreras, L. C., & Jaksic, F. M. (1997). Effects of small mammals and vertebrate predators on vegetation in the Chilean semiarid zone. *Oecologia*, *109*(3), 398–406.

Hacker, J. B. (1984). Genetic Variation in Seed Dormancy in Digitaria milanjiana in Relation to Rainfall at the Collection Site. *British Ecological Society*, *21*(3), 947–959.

Hodd, T., & Hodd, P. (1982). *Grasses of Western India*. Bombay Natural History Society.

Hodson, M. J., White, P. J., Mead, A., & Broadley, M. R. (2005). Phylogenetic variation in the silicon composition of plants. *Annals of Botany*, *96*(6), 1027–1046.

Hodson, M. J., & Sangster, A. G. (1988). Observations on the distribution of mineral elements in the leaf of wheat (Triticum aestivum L.), with particular reference to silicon. *Annals of Botany*, *62*(5), 463–471.

Huelsenbeck, J. P., Nielsen, R., & Bollback, J. P. (2003). Stochastic mapping of morphological characters. *Systematic Biology*, *52*(2), 131–158.

Hutchinson, J., Dalziel, J. M., & Keay, R. W. J. (1972). *Flora of West Tropical Africa* (F. N. Hepper (Ed.); 2nd ed.). Crown Agents for Overseas Governments and Administrations.

Hyde, M. A., Wursten, B. T., Ballings, P., & Coates Palgrave, M. (2020). *Flora of Zimbabwe*. https://www.zimbabweflora.co.zw/

IUCN. (2020). *The IUCN Red List of Threatened Species*. https://www.iucnredlist.org/

*Jepson eFlora*. (2019). University of California, Berkeley Jepson Herbarium. https://ucjeps.berkeley.edu/eflora/

Lazarides, M. (1970). *The Grasses of Central Australia*. Australian National University Press.

Lazarides, M. (1977). The Genus Whiteochloa C.E. Hubbard (Poaceae, Paniceae). *Brunonia*, *1*(1).

Lazarides, M. (1980). *The Tropical Grasses of Southeast Asia (Excluding Bamboos)*. J. Cramer.

McInerney, F. A., Strömberg, C. A. E., & White, J. W. C. (2011). The Neogene transition from C 3 to C 4 grasslands in North America: stable carbon isotope ratios of fossil phytoliths . *Paleobiology*, *37*(1), 23–49.

Motomura, H., Mita, N., & Suzuki, M. (2002). Silica accumulation in long-lived leaves of Sasa veitchii (Carrière) rehder (Poaceae-Bambusoideae). *Annals of Botany*, *90*(1), 149–152.

*Native Plants Hawai'i*. (n.d.). Kapi'olani Community College, Leeward Community College. http://nativeplants.hawaii.edu/index/

Nevo, E., Golenberg, E., Beiles, A., Brown, A. H. D., & Zohary, D. (1982). Genetic Diversity and Environmental Associations of Wild Wheat, Triticum dicoccoides, in Israel. *Theoretical and Applied Genetics*, *62*(3).

Nielsen, R. (2002). Mapping mutations on phylogenies. *Systematic Biology*, *51*(5), 729–739.

O'Reagain, P. J., & Mentis, M. T. (1989). Leaf Silicification in Grasses - A Review. *Journal of the Grassland Society of Southern Africa*, *6*(1), 37–43.

Palazzesi, L., & Barreda, V. (2012). Fossil pollen records reveal a late rise of open-habitat ecosystems in Patagonia. *Nature Communications*, *3*, 1–6.

*Paspalum fimbriatum*. (2008). Pacific Island Ecosystems at Risk (PIER). http://www.hear.org/pier/species/paspalum_fimbriatum.htm

Peterson, P. M., Romaschenko, K., & Arrieta, Y. H. (2015). A molecular phylogeny and classification of the Eleusininae with a new genus, Micrachne (Poaceae: Chloridoideae: Cynodonteae). *Taxon*, *64*(3), 445–467.

*PLANTS Database*. (2020). USDA, NRCS National Plant Data Team. plants.usda.gov

*PlantZAfrica*. (2000). South African National Biodiversity Institute. http://pza.sanbi.org/

Prasad, V., Strömberg, C. A. E., Alimohammadian, H., & Sahni, A. (2005). Paleontology: Dinosaur coprolites and the early evolution of grasses and grazers. *Science*, *310*(5751), 1177–1180.

Prasad, V., Strömberg, C. A. E., Leaché, A. D., Samant, B., Patnaik, R., Tang, L., Mohabey, D. M., Ge, S., & Sahni, A. (2011). Late Cretaceous origin of the rice tribe provides evidence for early diversification in Poaceae. *Nature Communications*, *2*(1). https://doi.org/10.1038/ncomms1482

Quattrocchi, U. (2006). *CRC World Dictionary of Grasses*. CRC Press.

Reidinger, S., Ramsey, M. H., & Hartley, S. E. (2012). Rapid and accurate analyses of silicon and phosphorus in plants using a portable X-ray fluorescence spectrometer. *New Phytologist*, *195*(3), 699–706.

Revell, L. J. (2012). phytools: An R package for phylogenetic comparative biology (and other things). *Methods in Ecology and Evolution*, *3*(2), 217–223.

Russell, G. E. G., Watson, L., Koekemoer, M., Smook, L., Barker, N. P., Anderson, H. M., & Dallwitz, M. J. (1990). *Grasses of southern Africa* (O. A. Leistner (Ed.)). National Botanic Gardens.

Sangster, A. G. (1977). Characteristics of silica deposition in Digitaria sanguinalis (L.) scop. (Crabgrass). *Annals of Botany*, *41*(2), 341–350.

Sherif, A. S., & Siddiqi, M. A. (1988). Flora of Libya No. 145. In El-Gadi (Ed.), *145*. Al-Faateh University.

Simon, B. K., & Alfonso, Y. (n.d.). *AusGrass2 Grasses of Australia*. http://ausgrass2.myspecies.info/

Snow, N., Peterson, P., & Giraldo-Canas, D. (2008). Leptochloa (Poaceae: Chloridoideae) in Colombia. *Journal of the Botanical Research Institute of Texas*, *2*(2), 861–874.

*Sporobolus fimbriatus (Trin.) Nees*. (n.d.). Plant Resources of Tropical Africa. https://www.prota4u.org/database/

Spriggs, E. L., Christinb, P. A., & Edwards, E. J. (2014). $C_4$ photosynthesis promoted species diversification during the miocene grassland expansion. *PLoS ONE*, *9*(5).

Strömberg, C. A. E. (2011). Evolution of Grasses and Grassland Ecosystems. *Annual Review of Earth and Planetary Sciences*, *39*(1), 517–544.

Strömberg, C. A. E., Di Stilio, V. S., & Song, Z. (2016). Functions of phytoliths in vascular plants: an evolutionary perspective. *Functional Ecology*, *30*(8), 1286–1297.

Strömberg, C. A. E., Dunn, R. E., Madden, R. H., Kohn, M. J., & Carlini, A. A. (2013). Decoupling the spread of grasslands from the evolution of grazer-type herbivores in South America. *Nature Communications*, *4*(February 2016).

Stubbendieck, J., Hatch, S. L., & Dunn, C. D. (2017). *Grasses of the Great PLains* (First). Texas A&M University Press.

Swallen, J. R., & McClure, F. A. (1955). Flora of Guatemala vol. 24 Part II: Grasses of Guatemala. In *vol. 24 Part II: Grasses of Guatemala*. Chicago Natural History Museum.

Wentzel, J. (n.d.). *Enneapogon scoparius*. Wildflower Nursery Indigenous Plant Database. https://wildflowernursery.co.za/

Wu Y., You H-L., Li X-Q.(2017). Dinosaur-associated Poaceae epidermis and phytoliths from the Early Cretaceous of China. *National Science Review*, 5, 721-727.

Zizka, A., Silvestro, D., Andermann, T., Azevedo, J., Duarte Ritter, C., Edler, D., Farooq, H., Herdean, A., Ariza, M., Scharn, R., Svantesson, S., Wengström, N., Zizka, V., & Antonelli,

A. (2019). CoordinateCleaner: Standardized cleaning of occurrence records from biological collection databases. *Methods in Ecology and Evolution*, *10*(5), 744–751.