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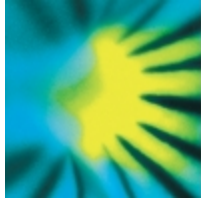
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# New Phytologist

## Lineage Functional Types (LFTs): Characterizing functional diversity to enhance the representation of ecological behavior in Land Surface Models

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29

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34

**35 Summary (200/200):**

36 Process-based vegetation models attempt to represent the wide range of trait variation in biomes by  
37 grouping ecologically similar species into plant functional types (PFTs). This approach has been  
38 successful in representing many aspects of plant physiology and biophysics, but struggles to capture  
39 biogeographic history and ecological dynamics that determine biome boundaries and plant distributions.  
40 Grass dominated ecosystems are broadly distributed across all vegetated continents and harbor large  
41 functional diversity, yet most Land Surface Models (LSMs) summarize grasses into two generic PFTs  
42 based primarily on differences between temperate C<sub>3</sub> grasses and (sub)tropical C<sub>4</sub> grasses. Incorporation  
43 of species-level trait variation is an active area of research to enhance the ecological realism of PFTs,  
44 which form the basis for vegetation processes and dynamics in LSMs. Using reported measurements, we  
45 developed grass functional trait values (physiological, structural, biochemical, anatomical, phenological,  
46 and disturbance-related) of dominant lineages to improve LSM representations. Our method is  
47 fundamentally different from previous efforts, as it uses phylogenetic relatedness to create lineage-based  
48 functional types (LFTs), situated between species-level trait data and PFT-level abstractions, thus  
49 providing a realistic representation of functional diversity and opening the door to the development of  
50 new vegetation models.

51

52 **Keywords:** C<sub>4</sub> photosynthesis, earth system models, land surface models, evolution, grass biogeography,  
53 plant functional types, vegetation models

54

**55 Main body:**

56

**57 Introduction**

58 Functional trait variation within biomes arises from evolutionary histories that vary biogeographically,  
59 leading to plant taxa with differing ecological behavior and differences in ecosystem structure and  
60 function across continents (Lehmann *et al.*, 2014; Higgins *et al.*, 2016; Griffith *et al.* 2019). Land  
61 Surface Models (LSMs), fundamental components of Earth System Models, typically apply abstracted  
62 plant functional types (PFTs; but see Pavlick *et al.*, 2013; Scheiter *et al.*, 2013; Medlyn *et al.*, 2016) to  
63 represent physical, biological, and chemical processes crucial for soil and climate-related decision making  
64 and policy. However, PFTs must generalize across species, and inevitably encapsulate a wide range of  
65 plant strategies and vegetation dynamics, a demand that contrasts with efforts to investigate nuanced and  
66 species specific ecological behavior (Cramer *et al.*, 2001; Bonan, 2008; Sitch *et al.*, 2008; Kattge *et al.*,  
67 2011). Furthermore, PFTs account for only a modest degree of variation in a wide array of functional  
68 traits, ranging from seed mass to leaf lifespan (LL), in the TRY database (Kattge *et al.*, 2011). For

69 example, standard PFTs may not generally capture key drought responses in tree species (Anderegg,  
70 2015), although models with a hydraulics module can be specifically applied for this purpose (e.g.,  
71 *ecosys*; Grant *et al.*, 1995). Oversimplification of the physiognomic characteristics of PFTs can have  
72 major unintended consequences when simulating ecosystem function (Griffith *et al.*, 2017), such as highly  
73 biodiverse savanna ecosystems (Searchinger *et al.*, 2015). However, studies that explicitly incorporate  
74 species-level trait variation into vegetation models (e.g., Grant *et al.*, 1995; Sakschewski *et al.*, 2016; Lu  
75 *et al.*, 2017; Grant *et al.*, 2019; Mekonnen *et al.*, 2019) have demonstrated improvements in model  
76 performance. Selecting trait data from multi-variate trait distributions for model parameterization (Wang  
77 *et al.*, 2012; Pappas *et al.*, 2016) is very challenging for global modeling applications, particularly in  
78 hyper-diverse regions like the tropics, and may not be feasible for areas with biased or limited data. Until  
79 these data-gaps are filled, a finer-grained representation of the functional diversity among species might  
80 be achieved by reorganizing PFTs based on tradeoffs and evolutionary relatedness.

81  
82 Importantly, in seeking approaches to restructure PFTs, numerous observations over the last decade have  
83 shown that both plant traits and biome-occupancy are commonly phylogenetically conserved, with closely  
84 related species having similar traits and niches (e.g., Cavender-Bares *et al.*, 2009, 2016; Crisp *et al.*, 2009;  
85 Liu *et al.*, 2012; Donoghue & Edwards, 2014; Coelho de Souza *et al.*, 2016). The existence of strong  
86 evolutionary constraints on plant functioning and distribution suggests that, as an alternative, vegetation  
87 types should be organized in a manner consistent with phylogeny. Eco-evolutionary models have  
88 increased our mechanistic understanding of ecological patterns in fields ranging from community ecology  
89 (e.g., Webb *et al.*, 2002; Cavender-Bares *et al.*, 2009) to global biogeography (e.g., the Latitudinal  
90 Diversity Gradient; Pontarp *et al.*, 2019; Visser *et al.* 2014). We advocate for explicit inclusion of  
91 evolutionary history and a consistent framework for integrating traits into global vegetation models. This  
92 approach brings a testable method for defining vegetation types, enables the functional traits of  
93 uncharacterized species to be inferred from relatives, and allows evolutionary history to be explicitly  
94 considered in studies of biome history. Here, we illustrate this approach for grasses and grass-dominated  
95 ecosystems, where we use our framework to aggregate species into Lineage-based Functional Types  
96 (LFTs) to capture the species-level trait diversity in a tractable manner for large-scale vegetation process  
97 models used in LSMs. Capturing the evolutionary history of woody plants is also critical to understanding  
98 variation in ecosystems function in savannas (Lehmann *et al.*, 2014; Osborne *et al.*, 2018), and in general  
99 we are advocating for the development of LFTs in other vegetation types and in other ecosystems.  
100 Grasses provide a tractable demonstration for the utility of LFTs; we also discuss the potential to  
101 significantly improve ecological and biogeographical representations of other plants in LSMs.

102

103 Grasses are one of the most ecologically successful plant types on earth (Linder *et al.*, 2018) and provide  
104 great opportunity for increasing understanding of plant functional diversity. Ecosystems containing or  
105 dominated by grasses (i.e., temperate, tropical, and subtropical grasslands and savannas) account for  
106 a>40% of global land area and productivity, and are a staple for humanity's sustenance (Tilman *et al.*,  
107 2002; Still *et al.*, 2003; Asner *et al.*, 2004; Gibson, 2009). The photosynthetic pathway composition (C<sub>3</sub> or  
108 C<sub>4</sub>) of grass species is a fundamental aspect of grassland and savanna function, ecology, and  
109 biogeography. Of the ~11,000 grass species on Earth, some ~4,500 use the C<sub>4</sub> photosynthetic pathway  
110 (Osborne *et al.*, 2014). Although they account for less than 2% of all vascular plant species (Kellogg,  
111 2001), C<sub>4</sub> grasses are estimated to account for 20-25% of terrestrial productivity (Still *et al.*, 2003),  
112 having risen to such prominence only in the last 8 million years (Edwards *et al.*, 2010). Dominance by  
113 C<sub>4</sub> versus C<sub>3</sub> grasses has major influences on gross primary productivity and ecosystem structure and  
114 function (Still *et al.*, 2003) and strongly influences interannual variability of the global carbon cycle, due  
115 to a combination of ecological and climatic factors (Poulter *et al.*, 2014; Griffith *et al.*, 2015). Dynamic  
116 vegetation models largely fail to reproduce spatial patterns of grass cover —both past and present—  
117 and productivity at regional to continental scales, limiting ability to predict future plant community  
118 changes (Fox *et al.*, 2018; Still *et al.*, 2018). As a consequence, LSMs require significant improvement to  
119 adequately represent vegetation responses to increasing CO<sub>2</sub> (Smith *et al.* 2016; De Kauwe *et al.*, 2016).  
120 Many models also miss key transitions between biome states (e.g., Still *et al.*, 2018) that exist as a result  
121 of disturbance or biogeographic history (e.g., Staver *et al.*, 2011; Dexter *et al.*, 2018).

122  
123 Most LSMs classify grasses into two PFTs based on differences between temperate C<sub>3</sub> grasses and sub-  
124 tropical and tropical C<sub>4</sub> grasses. However, grass ecological adaptations and physiological properties are  
125 highly diverse, ranging from cold-specialized to fire- and herbivore-dependent species. While grasses are  
126 often equated functionally, in reality they exhibit a high degree of variation in hydraulic, leaf economic,  
127 and phenological traits (Taylor *et al.*, 2010; Liu *et al.*, 2012) that likely explains their broad geographic  
128 dominance in different regions (Edwards *et al.*, 2010; Visser *et al.*, 2014). These differences include  
129 economically important forest-forming grasses such as bamboos, although here we focus on globally  
130 dominant herbaceous lineages. Grasses exhibit strong phylogenetic diversity in leaf economics variation  
131 and associations with disturbance (Taylor *et al.*, 2010; Liu *et al.*, 2012; Simpson *et al.*, 2016).

132 Disturbances such as fire and herbivory have large impacts on ecosystem function and distributions, and  
133 PFT based approaches are unlikely to capture these differences among lineages. At broad phylogenetic  
134 and spatial scales, niche and biome conservatism of major plant lineages is common (Crisp *et al.*, 2009;  
135 Cornwell *et al.*, 2014; Donoghue & Edwards, 2014), and we therefore argue that evolution and  
136 biogeography provide a framework for aggregating species (across ecosystems and strata) into LFTs that

137 capture species-level trait diversity in a way that can be feasibly incorporated for use in global vegetation  
138 models, and that will improve PFT-based modeling approaches. Focusing on grasses, we developed this  
139 approach by collecting grass traits from databases (e.g., Osborne *et al.*, 2011) and literature (e.g.,  
140 Atkinson *et al.*, 2016; Supplemental Appendix S1), for five key categories (physiology, structure,  
141 biochemistry, phenology, and disturbance). We summarize these species traits at the lineage level and  
142 relate these functional types to their observed global distributions.

143

#### 144 ***Methods for establishing lineage-based functional types (LFTs) for grasses***

145 There are 26 monophyletic C<sub>4</sub> lineages described in the Poaceae family, yet only two (the Andropogoneae  
146 and Chloridoideae) account for most of the areal abundance of C<sub>4</sub> grasses globally (Lehmann *et al.*, 2019  
147 ; Fig 1.) (Edwards & Still, 2008; Edwards *et al.*, 2010; Grass Phylogeny Working Group II, 2012).

148 Among C<sub>3</sub> grasses, only the Pooideae are globally dominant today. The Pooideae occupy cooler climates  
149 than the C<sub>4</sub> Andropogoneae and Chloridoideae, which dominate in warm and wetter and drier climates,  
150 respectively. Therefore, we focused on collecting species-level trait data from the literature and from  
151 databases for grass species from these three lineages. The term ‘trait’ is defined differently across  
152 research disciplines (Violle *et al.*, 2007). Our aims necessitate a collection of broad trait space beyond  
153 that typically used for the leaf economic spectrum to include morphological and physiological  
154 determinants of plant hydraulics, physicochemical controls of photosynthesis, allocation to reproduction,  
155 and spectral reflectance. Many traits are highly correlated, reflecting plant functional strategies. Further, a  
156 single trait can relate to multiple forms of plant fitness. Here, traits were assigned to groups (Table 1)  
157 based on their use in models and how they might be used in future applications (e.g., hyperspectral remote  
158 sensing of LFTs, or modeling of fire). We present median and variation in trait values among-species for  
159 three major grass lineages (LFTs) as per Figure 1, and compare these with commonly used values for C<sub>3</sub>  
160 and C<sub>4</sub> PFTs (Table 1).

161

#### 162 ***LFTs for grasses differ drastically in key functional traits***

163 Our LFTs demonstrate both the importance of considering lineage to explain ecological patterning, and  
164 the need for modification of current LSM PFT approaches. For instance, C<sub>4</sub> plants typically have lower  
165 RuBisCO activity ( $V_{\text{cmax}}$ ) but higher electron transport capacity ( $J_{\text{max}}$ ) than C<sub>3</sub> plants, reflecting both the  
166 additional energetic cost of C<sub>4</sub> physiology and the greater efficiency of RuBisCO in higher CO<sub>2</sub>  
167 environments (Collatz *et al.*, 1998). The Chloridoideae (C<sub>4</sub>) grasses have intermediate  $V_{\text{cmax}}$  and  $J_{\text{max}}$   
168 compared to the Andropogoneae (C<sub>4</sub>) and the Pooideae (C<sub>3</sub>) (Table 1). Furthermore, the Pooideae have  
169 evolved to tolerate much colder conditions (reflected in Trange; Sandve & Fjellheim, 2010; Vigeland *et*  
170 *al.*, 2013; McKeown *et al.*, 2016), and our results suggest that C<sub>4</sub> lineages may differ in their thermal

171 tolerances (Watcharamongkol *et al.*, 2018). These differences suggest that macroecological synthesis  
172 studies with global implications (e.g., Walker *et al.*, 2014; Heskell *et al.*, 2016) should, at minimum,  
173 include more grass species in their datasets, ideally organized as LFTs.

174

175 Trade-offs among adaptations and tolerances in natural systems promote coexistence among plant species  
176 (Tilman, 1988; Tilman & Pacala, 1993; Kneitel & Chase, 2004). Specific leaf area (SLA) measures the  
177 cost of constructing a leaf, which represents a tradeoff between acquisitive (high relative growth rate) and  
178 conservative (high leaf lifespan) plant strategies (Westoby, 1998; Westoby *et al.*, 2002; Wright *et al.*,  
179 2004). Model simulations of growth are highly dependent on the value of SLA used (Korner, 1991; Sitch  
180 *et al.*, 2003; Bonan, 2008). However, in most of these LSMs, C<sub>3</sub> grass PFTs have higher or similar SLA  
181 values as C<sub>4</sub> PFTs likely biasing predictions. In contrast, we found that the C<sub>4</sub> LFTs had higher SLA than  
182 the C<sub>3</sub> LFT, but SLA did not differ between the two dominant C<sub>4</sub> grass lineages (Atkinson *et al.* 2016).  
183 SLA can be highly variable within lineages in grasses, likely due to the importance of herbivore pressure  
184 as a competing demand on leaf economics (Anderson *et al.*, 2011; Griffith *et al.*, 2017) as well as  
185 intraspecific variation. As a result, SLA highlights that some traits are harder to generalize than others  
186 using the LFT approach, and suggests that a range of values may be appropriate than a single value for  
187 constraining LFT parameters. The phylogenetic signal among grass lineages is stronger for stature (Taylor  
188 *et al.*, 2010; Liu *et al.*, 2012), with the Andropogoneae being considerably taller on average than the  
189 Chloridoideae. This difference suggests that not all traits are oriented along a fast-slow axis at broad  
190 taxonomic scales across C<sub>3</sub> and C<sub>4</sub> grass lineages (Reich, 2014; Díaz *et al.*, 2016; Archibald *et al.* 2019).  
191 Furthermore, the C<sub>3</sub>- and eudicot-centric approach in the current leaf economics framework suggests that  
192 a higher SLA should also correlate with a higher specific leaf nitrogen content, yet the evolution of C<sub>4</sub>  
193 photosynthesis allows for a significant reduction in RuBisCO content, and hence plant nitrogen  
194 requirements (Taylor *et al.*, 2010). Thus, grass lineages differ in numerous leaf traits which have  
195 consequences that extend from palatability and flammability to hydrological differences.

196

197 Physiological and morphological leaf vascular traits underlie variation in SLA, constrain the hydrology of  
198 plants (e.g., Blonder *et al.*, 2014; Sack *et al.*, 2014), and are key traits related to the evolution of C<sub>4</sub>  
199 photosynthesis (Sage, 2004; Ueno, 2006). We describe next key hydraulic differences between the two  
200 dominant C<sub>4</sub> lineages, which correspond to the C<sub>4</sub> biochemical subtypes (Ueno, 2006; Liu & Osborne,  
201 2015). The Chloridoideae have low conductance and high embolism resistance hydraulic traits (Table 1),  
202 and tend to inhabit drier sites (Fig. 1). Some Andropogoneae have been described as “water spenders”  
203 (Williams *et al.*, 1998), and their hydraulic traits help to explain their affinity with higher rainfall habitats  
204 where they rapidly expend available soil water (Taub, 2000) and promote fire after curing. These



205 hydraulic differences should have large effects in models, especially those that consider tree-grass  
206 coexistence (Higgins *et al.*, 2000) and explicit representation of plant hydraulics (Grant *et al.*, 1995;  
207 Mekonnen *et al.*, 2019).

208  
209 Lineages also differ in biogeochemical traits that influence nutrient turnover rates and the reflectance and  
210 absorbance properties of vegetation. For example, Andropogoneae have higher C:N than Chloridoideae  
211 grasses, likely a result of growth rate differences and the frequent association of Andropogoneae grasses  
212 with fire. Similarly, a greater proportion of N in Chloridoideae leaves is allocated to RuBisCO, which is  
213 related to  $V_{\text{max}}$  (Ghannoum *et al.* 2012). Finally,  $C_3$  and  $C_4$  grasses are distinguishable spectrally at the  
214 leaf, canopy, and landscape level based on differences between the functional types in chlorophyll a/b  
215 ratio, canopy structure, and seasonality (Foody & Dash, 2007; Siebke & Ball, 2009; Irisarri *et al.*, 2009).  
216  $C_3$  and  $C_4$  grasses are typically given many of the same optical properties in vegetation models, but we  
217 show here that Chloridoideae might have considerably higher near infra-red (NIR) reflectance than other  
218 lineages, possibly producing interesting optical variation and affecting the surface energy balance and  
219 albedo (Ustin & Gamon, 2010)(Table 1). Foliar spectral traits are also correlated with morphological and  
220 chemical traits related to nutrient cycling and plant physiology (Dahlin *et al.*, 2013; Serbin *et al.*, 2014).

221  
222 Grass lineages also show key differences in reproductive traits and the timing of related biological events  
223 (e.g., leaf-out times) that should be captured in models, especially those that include demographic  
224 predictions (Davis *et al.*, 2010). Chloridoideae grasses have seeds with lower mass than other lineages  
225 (Liu *et al.*, 2012; Bergmann *et al.*, 2017), and this may represent a life-history trade-off with higher seed  
226 production and other ‘fast’ growth strategies (Adler *et al.*, 2014). Wind versus animal dispersal strategies  
227 might also affect diaspore size in a way not directly related to disturbance (e.g., Westoby 1998; Bergmann  
228 *et al.*, 2017), whereas some reproductive traits may also indicate fire and disturbance-related adaptations.  
229 Phenological traits, such as flowering and leaf-out times and their cues (which can include disturbance  
230 factors) exhibit conservatism across many plant lineages (Davies *et al.*, 2013). Fire and herbivory are two  
231 globally important and contrasting disturbances for grass-dominated vegetation (Archibald & Hempson,  
232 2016; Archibald *et al.*, 2019) and adaptations to both can be characterized by phenological and  
233 reproductive traits in addition to physiological and leaf traits. It is less clear how herbivory effects can be  
234 captured in such models, given that many herbivore-related traits vary greatly in grasses (Anderson *et al.*,  
235 2011). Many fire-related traits show patterns of phylogenetic conservatism, with high flammability  
236 clustering into particular lineages such as the Andropogoneae (Simpson *et al.*, 2016). Large-scale  
237 vegetation models that have simulated grass fires in Africa have attributed faster curing (becoming dry

238 fuel) rates to C<sub>4</sub> vegetation (Scheiter *et al.*, 2012), and this behavior appears to be due largely to dominant  
239 Andropogoneae grasses.

240

241 We have identified large differences among LFTs, across six trait categories, that are not captured by the  
242 standard PFT approach. Many of these trait data have very low sample sizes (from 1 to 1365) and come  
243 from non-overlapping species, highlighting the need for systematic data collection for grasses. Such a  
244 data collection effort would be an excellent opportunity to test for coordination among trait axes in a  
245 phylogenetic context, which has rarely been done in other systems despite the likelihood that relatedness  
246 drives patterns of trait covariation (e.g., Salguero-Gómez *et al.*, 2016; Griffith *et al.*, 2016). Furthermore,  
247 intra-group (whether PFTs or LFTs) trait variation deserves to be properly estimated (only some traits in  
248 Table 1 have enough data to estimate variability) as convergence and adaptation produce meaningful trait  
249 variation that should be incorporated into models.

250

#### 251 ***Potential for lineage-based functional types in other vegetation types***

252 Many current PFTs implicitly represent groupings of closely related lineages (e.g., pinaceous conifers,  
253 grasses). However, even in these cases biogeographic distributions, and the coarseness of the  
254 phylogenetic unit, generates a lack of useful resolution. Currently, there are efforts to incorporate species-  
255 level trait data and methods such as those proposed by Cornwell *et al.*, (2014) could be employed to  
256 cluster species into prominent lineage-based groupings representing unique trait combinations.

257 Phylogenies are hierarchical by nature and allow the LFT approach to be scalable and adjustable to the  
258 research question being addressed. While many technical challenges still remain, the ability to remotely  
259 sense plant lineages adds potential for rapidly developing LFTs from spectral data (e.g., Cavender-Bares  
260 *et al.*, 2016). LFTs would be valuable for a wide range of systems. For example, trees in Eurasian boreal  
261 forests suppress canopy fires through the structure of their canopies, whereas North American boreal trees  
262 enable greater intensity canopy fires (Rogers *et al.*, 2015). These distinctions lead to major differences in  
263 CO<sub>2</sub> emissions and function (Rogers *et al.*, 2015) that might be captured in an LFT framework. The  
264 boreal tree example is challenging because these communities are comprised of closely related species  
265 that are ecologically different, potentially requiring species level parameterization or being better  
266 represented by fire-based PFTs. Secondly, LFTs for savanna tree communities could better represent  
267 differing climatic responses that are driven by unique evolutionary and biogeographic histories (Lehmann  
268 *et al.*, 2014; Osborne *et al.*, 2018). Finally, tropical ecosystems such as the dipterocarp forests in  
269 Southeast Asia would be well suited to LFTs which might better represent carbon storage (Brearley *et al.*,  
270 2016).

271

272 Potential challenges with a lineage-based functional approach include the fact that many plant traits do  
273 not show strong phylogenetic conservatism (Cadotte *et al.*, 2017), with several being labile. There are  
274 likely spatial and phylogenetic scales at which the LFT approach will be most appropriate; for example, at  
275 large scales (regional to continental), lineage conservatism is common (Crisp *et al.*, 2009). In contrast, at  
276 the scale of local communities, we might expect character displacement and limiting similarity (processes  
277 that lead to reduced trait similarity of coexisting species) could obscure phylogenetic patterns and limit  
278 the utility of LFTs as proposed here (Webb *et al.*, 2002; Cavender-Bares *et al.*, 2009; HilleRisLambers *et al.*,  
279 *et al.*, 2012). However, in grassy ecosystems, there is evidence that the patterns of spatial ecological sorting  
280 of lineages would be captured with LFTs also at landscape scales (e.g., within Serengeti National Park,  
281 Anderson *et al.*, 2011; Forrestel *et al.*, 2017). Finally, we focus on extant lineages that are functionally  
282 important today, but their past interactions with other clades may have shaped the biomes they inhabit  
283 (Edwards *et al.*, 2010).

284

### 285 **Conclusions**

286 We conclude that an LFT perspective captures important variation in functional diversity for grasses  
287 (Table 1). Our analysis of current knowledge of grass functional diversity (in terms of physiology,  
288 structure, biochemistry, phenology, and disturbance), distributions, and phylogeny indicates that to  
289 represent grass ecological behavior, division of today's ecologically dominant grasses into at least two  $C_4$   
290 and at least one  $C_3$  LFT could potentially improve representation in LSMland models. These proposed  
291 LFTs capture key evolutionary differences in physiological, structural, biogeochemical, anatomical,  
292 phenological, and disturbance-related traits. We also highlight the need for systematic trait data collection  
293 for grasses, which we show are vastly underrepresented in trait databases, despite their ecological and  
294 economic importance. More broadly, we outline the LFT framework which is highly flexible and has the  
295 potential for use in a wide range of applications. Here, we speak to incorporating LFTs as groupings in  
296 vegetation models, but we also suggest that trait-based models might capture important biogeographic  
297 variation (e.g., due to historical contingency) through the inclusion of phylogenetic conservatism. We  
298 advocate for the use of phylogeny as a way to help guide and constrain the inclusion of burgeoning plant  
299 trait data to expand the range of functional types considered by global vegetation models.

300

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310

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593 **Table 1.** Common PFT parameters from LSM models, and median LFT parameters (IQR; interquartile  
 594 range in parentheses, where calculable) for three dominant grass lineages, taken from the literature and  
 595 trait databases. Lineage assignments are based on Osborne *et al.* (2014). The table shows a subset of  
 596 common parameters, with up to five parameters from each of six major categories. Blank values in the  
 597 PFT/LFT columns signify parameters that are not typically included in LSM models but are  
 598 potentially important for accounting for the ecological behavior of grasses. Bolded numbers with letters  
 599 (i.e., a compact letter display; sharing a letter [a, b, c] indicates no difference) indicate significant  
 600 differences with a Tukey's test from simple linear model fits when all three lineages had at least three  
 601 data points. Sources are in table footer.  
 602

Category	Parameter	PFT			LFT*		
		C <sub>4</sub>	C <sub>3</sub>	Source	Andropogoneae	Chloridoideae	Pooideae
Physiological	Vcmax ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ )	39	90	1, 2	38	45.6 (4.4)	63.6 (28)
	Jmax ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ )	400	100	3	180	108.1 (43)	128.8 (45)
	Rd ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ )	0.8	1.1	1, 2	<b>0.9a (0.2)</b>	<b>2a (1.4)</b>	<b>0.9a (0.7)</b>
	Phi ( $\mu\text{mol } \mu\text{mol}^{-1}$ )	0.06	0.085	4, 5	0.06	0.06	0.09
	Trange ( $^{\circ}\text{C}$ )	< 15.5	> 15.5	6	> 5**	> - 5**	> -30 <sub>5</sub> and <
Structural	SLA ( $\text{m}^2\text{kg}^{-1}$ )	16	33	7	<b>33b (11)</b>	<b>29b (14)</b>	<b>25a (12)</b>
	LDMC ( $g\text{g}^{-1}$ )	-	-		-	-	-
	SRL ( $\text{m g}^{-1}$ )	-	-		-	-	-
	Culm Height ( <i>cm</i> )	-	-		<b>150c (150)</b>	<b>80b (50)</b>	<b>60a (60)</b>
	R:S ( $g\text{g}^{-1}$ )	2	2	7	<b>0.4b (0.07)</b>	<b>0.3a (0.07)</b>	<b>0.4b (0.1)</b>
Biogeochemical/ spectral	C:N ( $g\text{g}^{-1}$ )	10	17	7	<b>66.1b (14.7)</b>	<b>39.9a (22.2)</b>	<b>55.7ab (10)</b>
	Nrubisco ( <i>proportion</i> )	0.09	0.137	7	0.05 (0.01)	0.08 (0.03)	0.2
	Reflectance (300–2500 nm)	-	-		-	-	-
	e.g., rNIR (reflectance)	0.35	0.35	7	0.4	0.5	0.3
Anatomical/ Hydraulic	IVD ( $\mu\text{m}$ )	-	-		<b>85.7a (25.2)</b>	<b>136.8b (40)</b>	<b>242.1c (58)</b>
Hydraulic	Xylem dia. ( $\mu\text{m}$ )	-	-	7	<b>21.4b (12.2)</b>	<b>16.8a (10.7)</b>	<b>19.3a (6.7)</b>
	<i>K<sub>leaf</sub></i>	-	-		-	-	-
	Vein Hierarchy ( <i>Primary vein secondary vein</i> )	-	-		<b>0.11a (0.09)</b>	<b>0.29b (0.2)</b>	<b>0.58c (0.6)</b>
	Leaf Width:Length	-	-		<b>0.04b (0.05)</b>	<b>0.03a (0.04)</b>	<b>0.03a (0.02)</b>
Life History	LL ( <i>months</i> )	1.68	12	7	2 (0.4)	1.1	2 (1.8)
	1000-seed mass ( <i>g</i> )	-	-	7	<b>1.4b (2.4)</b>	<b>0.2a (0.4)</b>	<b>1.4b (3.8)</b>
	Life History (% <i>annual</i> )	-	-	7	0.25	0.28	0.15
Disturbance	Curing rate (%)	80	20	8	80	50**	20
	Bud Bank	-	-		-	-	-
	Flammability ( $g\text{s}^{-1}$ )	-	-		-	-	-

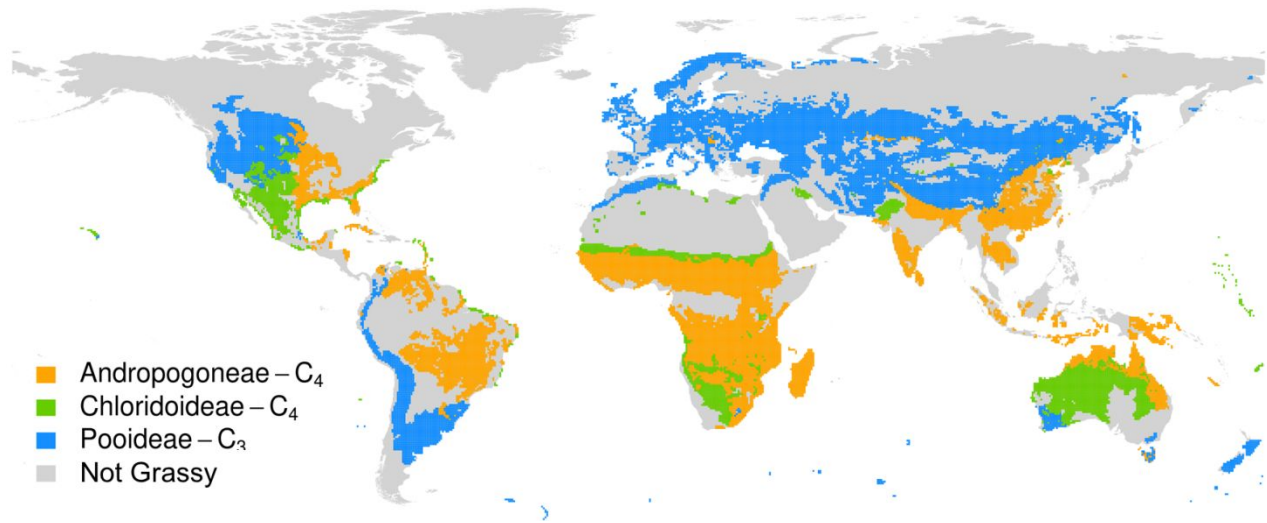
603

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605 1 - Farquhar *et al.* (1980), 2 - Collatz *et al.* (1992), 3 - von Caemmerer

606 (2000), 4 - Ehleringer *et al.* (1997), 5 - Collatz *et al.* (1998), 6 - Sitch *et al.* (2003), 7 - Oleson *et al.*  
607 (2013), 8 - Scheiter *et al.* (2012); Curing rate is the % cured 30 d after the end of the growing season as  
608 described in Scheiter *et al.* (2012); \*Published citations for LFT values can be found in Appendix S1.  
609 Anatomical data come from Gallaher *et al.* in prep. \*\*Estimated value. Abbreviations: Vcmax (maximum  
610 carboxylation rate), Jmax (light saturated rate of electron transport), Rd (dark Respiration), Phi (quantum  
611 efficiency), SLA (Specific Leaf Area), LDMC (Leaf Dry Matter Content), SRL (Specific Root Length),  
612 R:S (root to shoot ratio), C:N (Carbon to Nitrogen ratio), IVD (InterVeinal Distance), Kleaf (leaf  
613 hydraulic conductance), LL (Leaf Lifespan).  
614  
615

616 **Figures:**



617

618 **Figure 1.** Distributions of the three globally dominant grass lineages in the herbaceous layer. These data  
619 come from Lehmann et al (2019), and show where each lineage is more abundant than the other two  
620 lineages on a 0.5 degree grid.