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1 Title page

2

3 **Savanna fire regimes depend on grass trait diversity**

4

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17

18

19 Keywords: Fire regimes, Flammability, Functional traits, Grasses, Poaceae, Savannas

20 **Highlights**

21

22 • Most fires on Earth occur in savannas, but vary considerably in their extent, frequency
23 and intensity. These patterns cannot fully be explained by climate or land management.

24 • An important ‘missing-piece’ in explaining the variation in savanna fire regimes is the
25 diversity of grasses that fuel fires and whose traits strongly influence fire behaviour.

26 The major differences in savanna fire behaviour across continents may lie in the
27 contrasting species and trait assemblages in savanna grass communities.

28 • Fire regimes change significantly when savanna grass communities or traits are altered
29 by the introduction of invasive species and climatic changes.

30 • Improved representation of grass trait diversity in fire models will be essential for
31 reliable forecasts of the behaviour and impacts of the majority of fires on Earth.

32 **Abstract**

33

34 Grasses fuel most fires on Earth and strongly influence local fire behaviour through traits which
35 determine how flammable they are. Therefore, grass communities that differ in their species
36 and trait compositions give rise to significant spatial variation in savanna fire regimes across
37 the world that cannot be otherwise explained. Likewise, fire regimes are continuously modified
38 by alterations to savanna grass community traits, through species introductions and climatic
39 changes. However, current representation of grassy fuels in global fire models misses important
40 variation and therefore limits predictive power. The inclusion of grass trait diversity in models,
41 using remotely-sensed trait proxies for example, will greatly improve our ability to understand
42 and project savanna fires and their roles in the Earth system.

43

44

45 **Main text**

46

47 Savanna fires in the Earth System

48 On average, 340 million hectares of the Earth's vegetated surface burns each year [1], but **fire**
49 **regime** (see **Glossary**) - the typical frequency, intensity and size of fires - varies hugely across
50 the land surface owing to complex interactions between climate, vegetation and land
51 management. For example, **fire return times** range from less than 1 year in tropical savannas
52 to hundreds of years in boreal forest, with human activity increasing return times in the latter
53 through suppression but reducing them in the former [2-3]. Understanding the factors that
54 influence fire regimes is increasingly important in the context of climate change, especially for
55 accurate predictions of how fire regimes will alter in the future, and therefore impact the
56 biosphere and atmosphere.

57

58 The vast majority of fires on Earth occur in tropical savannas. This biome, characterised by a
59 ground layer dominated by grasses (mainly using the C₄ photosynthetic pathway) and a low
60 density of trees or shrubs, covers 20% of the terrestrial surface [4] but annually accounts for
61 86% of the area burned [5] and 62% of greenhouse gas emissions from fires [6]. Savannas are
62 made highly flammable by the combination of a seasonally arid climate and a productive grass
63 layer that dries readily to provide low **fuel loads** of very fine vegetation. The high surface area
64 of grass biomass enables quick drying under warm conditions, and rapid and complete
65 combustion. The low fuel loads mean that savanna fires are cool-burning (<200°C) compared
66 with fires in shrublands or forests (~400°C) [7]. Consequently, most savanna grasses survive
67 fire and resprout quickly from basal buds [8-9]. This rapid regeneration of biomass after fire
68 [10] produces the most frequent fire regimes on Earth.

69

70 Despite commonalities in fire regimes among savannas when contrasted to those in forest or
71 shrubland ecosystems, savanna fire regimes are highly diverse. Fire return times in savannas
72 can range from sub-annual to decades [11], and there are large, unexplained differences among
73 continents in the extent, frequency and intensity of burning under similar environmental
74 conditions (Figure 1) [12-13]. Relationships in savannas between fire regime and climate are
75 well-characterised, with the most frequent fire associated with high rainfall and thus grass
76 productivity [14-16]. The impacts of human activity are similarly well-known, such that people
77 increase fire occurrence [2] but reduce fire extent [17]. However, considerable variation in
78 savanna fire regime (e.g. >30% variation in burned area; [14]) cannot be explained by climate
79 or human activity [18-19], highlighting the characteristics of the grassy vegetation itself as
80 being fundamental determinants of savanna fire regimes. Grass communities can vary hugely
81 across space, in both the species present and their traits, which in turn influence fuel properties.

82 We argue that grass trait diversity is the ‘missing-piece’ in explaining the variation in fire
83 regimes across the world’s savannas. Improved representation of grass trait diversity in fire
84 models is therefore essential to produce reliable predictions of the behaviour and impacts of
85 the majority of fires on Earth.

86

87 Grass traits influence savanna fire regimes

88 Fires are fuelled by vegetation, and it therefore follows that the **flammability** of that vegetation
89 strongly influences local fire behaviour [20]. Flammability itself arises from key **functional**
90 **traits** of plants relating to the quantity, quality, moisture content and aeration of plant biomass.
91 These traits together determine how easily biomass ignites, how long it burns, how much is
92 consumed, what temperatures are reached, the speed at which fire may spread, and therefore
93 the fire regime.

94

95 In woody plants, it is well-established that flammability varies significantly among and within
96 species [21-23] and it has been repeatedly demonstrated that small changes in woody species
97 composition may significantly alter vegetation flammability and fire regime [24-25]. However,
98 variation in the flammability of grass or other herbaceous species has only received attention
99 recently, despite its global importance [26-30]. This oversight likely originates with a historical
100 assumption that grasses vary little in their flammability, which has led to the diversity of grassy
101 fuels being reduced to one or few classes in fire behaviour modelling [31]. Overturning this
102 assumption, recent work has demonstrated that grass species vary in key functional traits
103 causing considerable differences in their flammability. Two traits that are especially important
104 for grass flammability are the amount of aboveground biomass and its moisture content (Box
105 1), since these dictate how much fuel is available and how easy fire ignites and spreads. Indeed,
106 these traits represent the two main limiting factors to savanna fire, whereby fire behaviour is

107 curbed by the amount of available grass biomass ('fuel build-up limited' *sensu* [19]), or by how
108 wet it is ('fuel-moisture limited'). In a comparison of African savanna grass species in peak
109 fire season, significant (20-fold) variation in flammability amongst species could be largely
110 explained by differences in these two traits [26].

111
112 Variation in grass flammability, combined with the strong influence this has on local fire
113 behaviour, are strikingly illustrated by the altered fire regimes arising from changes in grass
114 community flammability in time or space [32-33]. For example, the invasion of grasses with
115 contrasting flammabilities to native species has drastically altered fire frequency and severity
116 in northern Australian savannas [34], US tallgrass prairie [35] and the Brazilian Cerrado [36].
117 However, more subtle turnover in grass community composition may also substantially alter
118 fire activity over small spatial scales, such as grass-mediated changes in fire intensity at the
119 savanna-forest interface [37]. Alternatively, having a similarly flammable grass layer can result
120 in convergent fire regimes in savannas that experience very different climatic conditions (e.g.
121 Longleaf pine savanna in the USA vs. Eucalyptus savanna in Australia [38]). Based on this
122 emerging evidence base, we therefore argue that functional variation in the grass communities
123 of savannas has important implications for fire regimes, with those dominated by different
124 species having contrasting fire regimes arising from the traits of species present. Therefore, the
125 assumption that grasses are a homogenous fuel to fire is incorrect, and there is potential to
126 significantly improve global-scale fire predictions through more nuanced specification of the
127 grassy fuels. Limited classifications of grassy vegetation in global fire behaviour models mask
128 considerable, important, community variation in flammability.

129

130 Continental differences in savanna fire regimes

131 Divergent evolutionary histories over millions of years have created contrasting savanna grass
132 communities across continents, with differing species present and dominant (Figure 2) [39].
133 Alongside this phylogenetic diversity is substantial variation in the traits of the species present.
134 In comparison to dominant Australian and South American grasses, data from Jardine et al [40]
135 shows African grasses are on average taller in stature (+42 and +64% respectively), have a
136 higher **specific leaf area** (a proxy for growth rate; +52 and +28% respectively) and lower
137 carbon to nitrogen ratio (a proxy for decomposability; -45 and -21% respectively). There are
138 several lines of evidence that suggest these trait differences may be responsible for the variation
139 in savanna fire regime across continents.

140

141 Firstly, the most striking examples of altered savanna fire regimes caused by species invasions
142 are when the invasive species originates from another continent. African grasses in particular
143 are responsible for substantial changes in fire activity where they have invaded, such as Gamba
144 grass (*Andropogon gayanus*) in Australian savannas [34] and *Urochloa* species in the Brazilian
145 Cerrado [36]. Invasion by such species can greatly increase fuel loads and connectivity,
146 resulting in larger, hotter and more frequent fires. Therefore, the greater flammability of
147 African grasses, relative to those of Australia and South America, may contribute to the
148 explanation of why fire is more frequent in African savannas.

149

150 Secondly, continental differences in fire behaviour cannot be sufficiently explained by climate
151 and land management, implicating a role for grass community composition [41]. Savanna fires
152 are limited either by the amount of biomass available (insufficient fuel) or by its moisture
153 content (too wet), and which of these traits is more limiting to fire varies spatially [19]. Climatic
154 differences exist between African, Australian and South American savannas in the transition
155 from fuel build-up to fuel-moisture limitation. Savanna fires in South America are principally

156 limited by fuel moisture, and only by fuel build-up below ~500mm mean annual rainfall
157 (MAR). In contrast, fuel moisture only starts to limit fire above 800-1000mm MAR in Africa
158 and Australia [19]. Therefore, at the same rainfall, fire is restricted by one of the two key grass
159 flammability traits, which differs by continent. This suggests fundamental differences in the
160 traits of grass communities between continents that cause contrasting fire behaviour
161 independently of climate.

162

163 Together, these lines of evidence implicate grass traits as a key driver of trans-continental
164 savanna fire activity, and stress the need to better understand grass-fire relationships at larger
165 spatial scales. Indeed, contrasting histories of megafaunal extinctions across continents suggest
166 that changes in herbivore consumption may actually mask much larger inherent differences in
167 fire regime. In South America, Late Quaternary grazer extinctions were much more severe than
168 on other continents, resulting in increased fire activity [42] Therefore, African savannas are
169 much more fire-prone than those in South America (Figure 1), despite the grazer community
170 being much more intact in the former, which means that more African grass biomass is
171 consumed by herbivores and therefore not available to burn in fires.

172

173 Global change impacts on grass diversity

174 Savanna grass communities are not static, but instead are being altered by human activities,
175 either directly (via the introduction of species or changes in land management), or indirectly,
176 through anthropogenic climatic changes (e.g. increasing temperatures and atmospheric CO₂
177 concentrations). Such changes will alter fire regimes if the flammability of the grass
178 community is impacted. The effects of some community changes on fire regime are well-
179 documented, such as those relating to invasive grass species, but others are less studied and
180 may depend upon which fuel factor is limiting fire regimes (Box 2).

181

182 The study of grass-driven alterations to fire regime is complicated by a background of
183 anthropogenic changes to savanna fire activity. Conversion of savanna to cropland and heavy
184 grazing by livestock have reduced grass biomass and fragmented grass-covered areas, resulting
185 in a significant reduction in the global area of savanna burned each year [15,17]. A change to
186 fire regime itself can also feedback to influence the composition of a community, because
187 species are adapted to a particular fire regime rather than fire *per se* [43]. Deviations from
188 particular fire regimes may cause the local loss of species. For example, fires can become too
189 frequent, such that stored resources cannot support repeated **resprouting** [8] or not frequent
190 enough, causing grasses to become fatally **moribund** [44]. Even when community composition
191 remains the same, altered fire regimes can still change plastic grass traits relating to
192 regeneration and flammability [45].

193

194 Reductions in savanna fire activity have an additional indirect effect on grass communities by
195 increasing the competitive ability of savanna trees [46]. Trees are increasing in density across
196 the world's savannas (i.e. '**woody plant encroachment**') [47], in part due to declining fire
197 occurrence [48-49]. Since trees shade grasses and compete with them for limited water and soil
198 nutrients, woody plant encroachment alters grass community trait and species composition [50-
199 51]. Recent work shows shading decreases grass flammability by reducing grass biomass,
200 increasing grass moisture content and favouring less-flammable shade-tolerant species [30, 52-
201 53]. Therefore, fire-driven changes to grass communities may cause a positive feedback on fire
202 regimes, further reinforcing reduced fire activity via changes in grass traits. In direct contrast,
203 invasive grass species suppress tree recruitment in certain savanna ecosystems by fuelling
204 hotter fires (e.g. Longleaf Pine savannas invaded by Cogon grass, *Imperata cylindrica* [54]).

205

206 Improving grass representation in fire models

207 Fire behaviour and Land Surface Models are vital tools for understanding, projecting, and
208 predicting fire-vegetation dynamics and their roles within the Earth system under global
209 change. By necessity, models reduce plant functional diversity into groupings of ecologically-
210 similar species. For grasses, species are represented in fire models as a small number of
211 categories based on structure ('short' vs 'tall' grass fuel [31]; expanded by [55]) or in Land
212 Surface Models via physiology (temperate C₃ grasses vs subtropical or tropical C₄ grasses; e.g.
213 [56]). Given the compositional and functional diversity in savanna grass communities, these
214 limited classifications omit important variation.

215

216 One strategy for improving grass trait diversity in models is to collect data on relevant traits,
217 such as fuel load and fuel moisture content, across large spatial scales and include this in
218 savanna fire models. Whilst there is an expanding evidence-base of grass trait influences on
219 savanna fire behaviour within landscapes, data on how these relationships scale-up to regional
220 or trans-continental scales is lacking. The only practical way of collecting data and establishing
221 these large-scale relationships would be to quantify grass traits directly using **remote sensing**
222 (Box 3). Parameterising models with this data would greatly improve our ability to explain
223 savanna fire regime variation.

224

225 For models that incorporate plant trait variation as a categorical variable (i.e. plant functional
226 types), a way to more explicitly represent grass diversity is to organise grassy vegetation types
227 in a way that is consistent with evolutionary history [57]. Using phylogeny to generate
228 classifications would be effective for grasses, which show strong conservatism in traits and
229 niches that are relevant for- [58-59] or directly related to- fire [39,60]. For example, there are
230 strong phylogenetic signals in the fire regime experienced by grass species and in their traits

231 responsible for flammability and recovery after fire [8,26,39,60], meaning that closely related
232 species share similar traits. Consequently, the grouping of grass species into functional types
233 for Land Surface Models based on three globally dominant grass lineages (Andropogoneae
234 (C₄), Chloridoideae (C₄) and Pooideae (C₃)) has been proposed [57]. This ‘lineage-based
235 functional type’ approach, although it has the disadvantage of being one step removed from
236 the functional traits themselves, might usefully be expanded to other key lineages that are
237 prominent in savanna grass communities (e.g. MPC (Melinidinae, Panicinae and Cenchrinae),
238 Aristida, Axonopus; Figure 2) across continents.

239

240 **Concluding remarks**

241 Savanna grass communities vary in their species and trait compositions. These compositional
242 and functional differences give rise to significant spatial variation in savanna fire regimes
243 across the world that cannot be otherwise explained. The strong control grasses have on local
244 fire behaviour, through their traits, is now well evidenced. However, current representation of
245 grassy fuels in global fire models misses important variation and therefore limits predictive
246 power. We suggest that incorporating grass trait data sampled over large spatial-scales
247 (collected using remote sensing), and/or expanding grass trait diversity representation to
248 encapsulate more functional variation will greatly improve our ability to understand and project
249 savanna fires and their roles in the Earth system. The important next steps are in scaling up
250 grass-fire relationships to explain landscape, regional and trans-continental patterns in fire
251 regimes, and to determine how grass traits will change under future climatic conditions (see

252 **Outstanding Questions**).

253

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260

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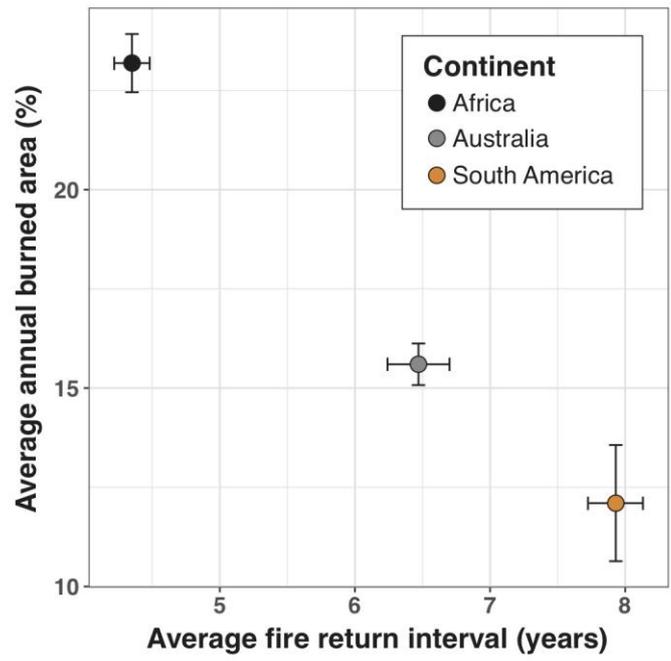
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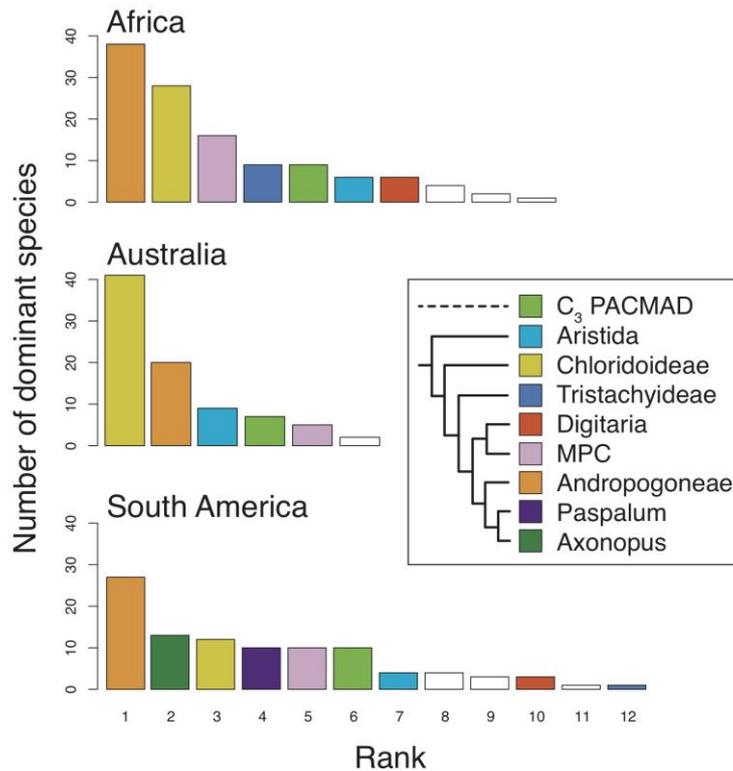
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428

429 **Figure 1. Continental differences in savanna fire regimes.** Data is from [5] for the period
430 1900-2000.

431



432

433 **Figure 2. Continental differences in grass communities.** The distribution of dominant grass
 434 species on the phylogeny differs between continents (data specific to C₄ grass-dominated
 435 ecosystems; from [39]). The nine grass lineages containing most dominant species are
 436 indicated in the figure legend (and as coloured bars in the plots). The phylogeny is based on
 437 [61] and for simplicity excludes C₃ sisters to the C₄ groups, and less common C₄ lineages
 438 (indicated in the plots as uncoloured bars).

439

440 **Text boxes**

441

442 **Box 1. Key grass traits that influence fire behaviour and the underlying physiological**
443 **processes creating variation in them.**

444 Grass biomass quantity and moisture content are two key traits that determine grass
445 flammability and therefore fire behaviour (Figure I). Variation in these traits, which exist both
446 between and within grass species [37,45,60], result from differences in fundamental
447 physiological processes.

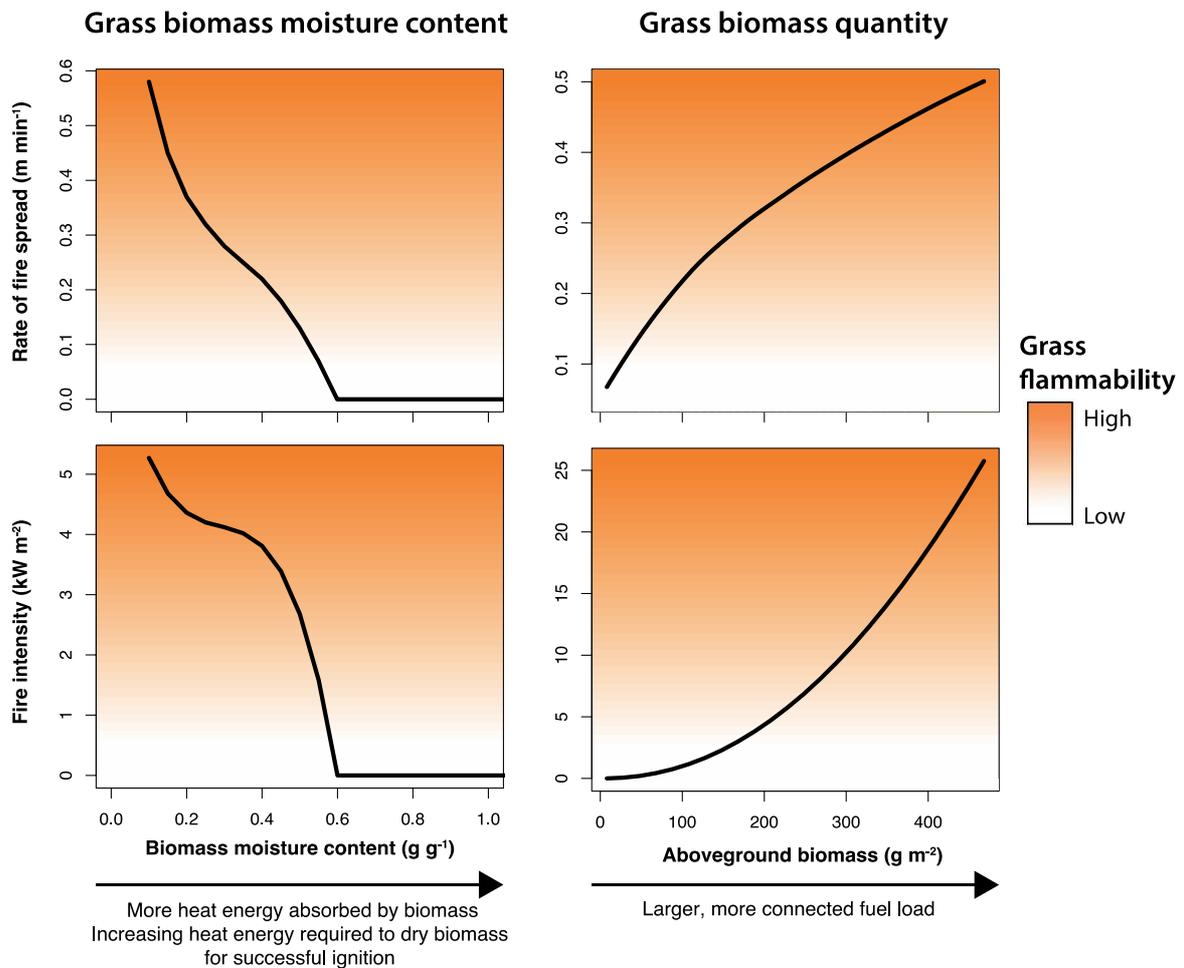
448

449 Aboveground grass biomass quantity determines the amount of fuel available to burn. It is
450 influenced by plant growth rate, where rapid growth produces more biomass per unit time,
451 allowing sufficient fuel for a spreading fire to be produced more rapidly when grasses grow
452 quickly. This, combined with the decomposability of biomass determines the amount of dead
453 standing biomass (fuel load). The rate of grass biomass breakdown by decomposers is
454 influenced by chemical properties of biomass such as its carbon to nitrogen ratio and dry matter
455 content [62]. Most tropical grasses do not show leaf abscission and dead leaves remain held in
456 the grass canopies, which slows decomposition rates [63]. How tightly linked decomposability
457 and flammability are has been explored in other vegetation fuel types [64-65], but not yet in
458 grasses. The way that grasses persist after fire (either recruiting from the seedbank or by
459 resprouting from protected meristems) also contributes to the speed of biomass production after
460 a fire, since biomass recovery is faster from established resprouting plants than those recruiting
461 from seed.

462

463 The moisture content of grass biomass determines how much heat energy must be absorbed for
464 successful ignition, with “wetter” plants associated with a lower likelihood of ignition and

465 cooler flaming temperatures. As the fire season coincides with low rainfall in savannas, the
 466 survival strategies used by plants under water limitation influence their biomass moisture
 467 content at the time of fire occurrence. Grass species fall on a continuum between two opposing
 468 hydraulic strategies: drought-avoiders (which follow an **isohydric** strategy) or drought-
 469 tolerators (which follow an **anisohydric** strategy) [66]. Drought-avoiders stay green in drought
 470 by closing their stomata to avoid water loss. They therefore maintain the moisture content of
 471 their biomass despite declining water availability. In contrast, drought-tolerators leave their
 472 stomata open (and so can continue to photosynthesize), and allow their biomass moisture
 473 contents to decline as soils dry.



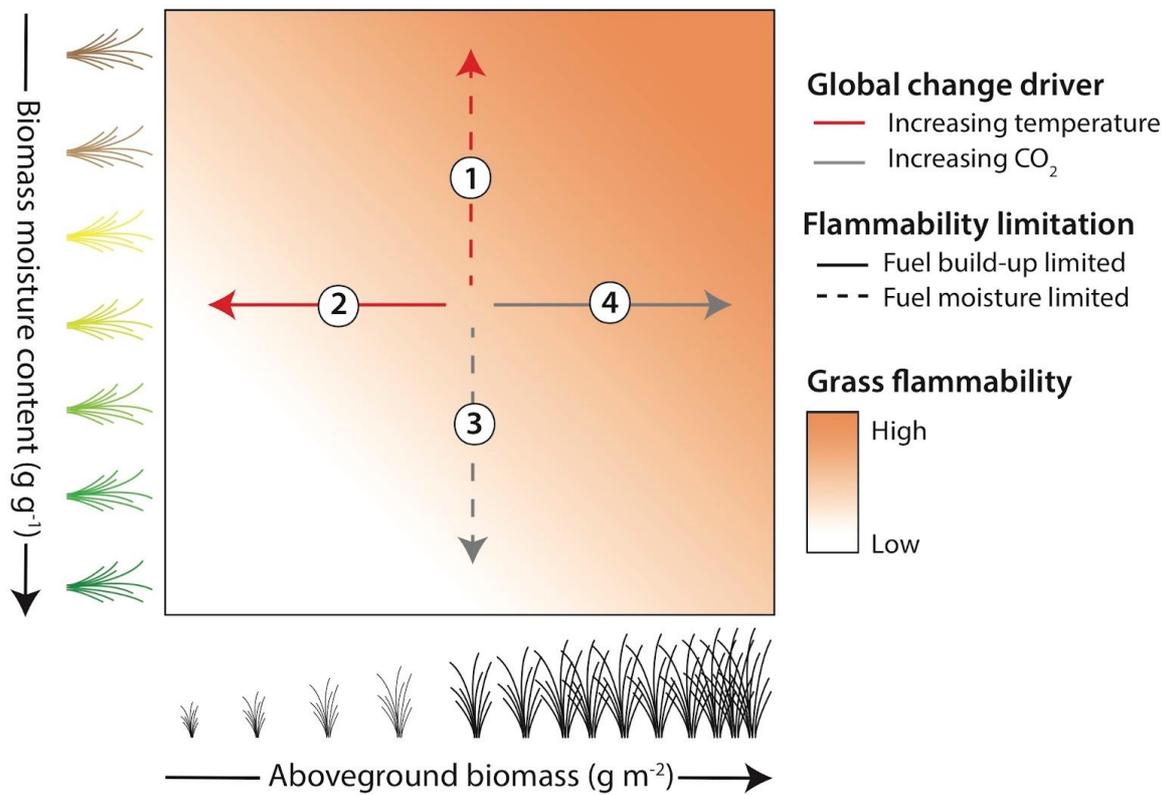
474

475 Figure I. Relationships between fire characteristics (fire spread rate and fire intensity, estimated
 476 using the Rothermel fire spread model [67]) and two grass traits: grass biomass quantity and

477 biomass moisture content. The ranges of grass trait values represent those found in savanna
 478 grasses in the dry season (when fire activity peaks; from [26]). To fit the response, all other
 479 grass traits (except the one of interest) were given a value which represented an average across
 480 25 savanna grass species [26]. All other model inputs followed [26]. In the Rothermel model
 481 [67], a spreading fire cannot be sustained by biomass with a moisture content above 0.6 g g^{-1} .
 482

483 **Box 2. Climate change drivers of savanna grass flammability**

484



485

486 Figure I. Changes in savanna grass flammability under future climatic conditions depend on
 487 whether fire regimes are limited by fuel build-up or fuel moisture. The mechanisms underlying
 488 the changes (arrows) to grass traits are described in the text below (numbered 1-4).
 489

489

490 In savannas where fire is primarily limited by biomass moisture content (as in much of South
491 America [19]), increasing temperatures will likely dry fuels and enhance grass flammability
492 (Figure I, arrow 1). However, the same effects are not expected in the fuel-limited savanna
493 fires predominating on other continents, where these conditions may impair grass growth and
494 reduce fuel loads (Figure I, arrow 2) [15].

495

496 Increasing atmospheric CO₂ concentrations are also predicted to alter savanna grass
497 flammability. Elevated CO₂ improves plant water relations (since less water is lost through
498 **stomata**), which may increase grass productivity as well as biomass moisture content [68].
499 Increased CO₂ may also directly enhance grass biomass production via improvements to
500 photosynthetic rates (**CO₂-fertilisation**), although this will likely vary across grass species,
501 especially in species with the CO₂-concentrating mechanism of C₄ photosynthesis [69-70]. In
502 fuel-moisture-limited fire regimes, CO₂-induced increases in grass moisture contents will
503 reduce flammability (Figure I, arrow 3), whereas in fuel-build-up-limited systems, greater grass
504 productivity will increase flammability (Figure I, arrow 4).

505

506 **Box 3. Monitoring grass flammability using remote sensing tools**

507 The assessment of grass flammability traits over large spatial scales and through seasons is
508 only possible using remote-sensing tools. Although the remote monitoring of vegetation
509 structure has focused on closed-canopy forests, there is great potential for these tools to be used
510 in grass-dominated systems to measure flammability traits [71-74]. Spectral indices derived
511 from remote sensing can be used to effectively track changes in grass biomass quantity (e.g.
512 **Enhanced Vegetation Index** or EVI), and water content (e.g. **Normalised Difference Water**
513 **Index** or NDWI). With the growing availability of frequently sampled and spatially resolved
514 satellite imagery (MODIS NDWI and Landsat EVI data), it is possible to monitor temporal and

515 spatial changes in these traits. This quantitative data could directly be used to incorporate grass
516 trait variation in models and greatly improve their ability to explain and project savanna fire
517 behaviour. Another remote sensing approach (albeit with less explanatory power) is the
518 development of maps of grass community functional groupings. Spectral data could be used to
519 distinguish communities dominated by diverse grass lineages since optical differences exist
520 between grass lineages (e.g. species of the Chloridoideae lineage have higher near infra-red
521 reflectance than other lineages [57]). These maps and associated lineage-level trait data could
522 then be used in fire models with categorical fuel classes to improve grass trait representation.

523

524 **Glossary Box**

525 Anisohydric - Anisohydric plants keep their stomata open and photosynthetic rates high for
526 longer into periods of water limitation. They allow their water status to decline (decreasing leaf
527 water potential) as the soil dries.

528

529 C₄ – a derived form of photosynthesis that is successful in hot conditions. C₄ photosynthesis
530 differs from the ancestral C₃ pathway in having a carbon-concentrating mechanism that makes
531 photosynthetic carbon fixation more efficient at high temperatures. C₄ photosynthesis evolved
532 multiple times, and has at least 22 independent origins in the grasses.

533

534 CO₂-fertilisation - an increase in photosynthetic carbon fixation under higher atmospheric CO₂
535 levels.

536

537 Enhanced Vegetation Index (EVI) - a remote sensing-derived index used to quantify vegetation
538 structure and greenness. EVI is ‘enhanced’ because it corrects for some atmospheric conditions
539 and canopy background noise and is more sensitive in areas with dense vegetation.

540

541 Fire regime - the pattern, frequency, and intensity of wildfires that prevail in an area over long
542 periods of time.

543

544 Fire return time - the average period of time between fires at one location.

545

546 Flammability – the propensity of biomass to burn. Flammability is a compound property that
547 relates to the ability of biomass to ignite, combust and sustain burning, and is an emergent
548 property of plant chemical and physical traits.

549

550 Fuel load – the total quantity of combustible biomass per unit ground area.

551

552 Functional traits - morphological, physiological or phenological features of a plant measurable
553 at the individual level.

554

555 Isohydric - Isohydric plants maintain their water status (constant midday leaf water potential)
556 when water is limiting, by reducing stomatal conductance to limit water loss via transpiration.

557

558 Moribund – a state of reduced vigour caused by shading. Many grasses are vulnerable to
559 becoming moribund due to their basal growth habit, and require frequent defoliation (from fire
560 or herbivory) to prevent self-shading.

561

562 Normalised Difference Water Index – a remote sensing-derived index that uses the ratio of
563 Near-Infrared and Short Wave Infrared reflectance. It is strongly related to plant water content,
564 and can be effectively used to monitor plant water deficits.

565

566 Woody plant encroachment – a phenomenon characterised by increasing densities of woody
567 plants (trees and shrubs) in open ecosystems at the expense of the herbaceous layer. It
568 predominantly occurs in grasslands and savannas and can cause biome shifts from open- to
569 closed-canopy systems.

570

571 Resprouting – the ability to produce new above-ground biomass from vegetative buds after
572 disturbance (e.g. fire). Resprouting is one of the two main strategies for populations of plants
573 to persist through disturbance, the other being recruitment of seedlings from the seedbank.

574

575 Remote sensing – the process of monitoring characteristics of objects at or near the surface of
576 the Earth by measuring the radiation reflected and emitted from those objects. Information is
577 acquired at a distance, typically from satellites or aircraft.

578

579 Specific leaf area – the ratio of leaf area to leaf dry mass. High values are associated with rapid
580 plant growth rate.

581

582 Stomata - apertures in the leaf epidermis that are involved in the exchange of carbon dioxide
583 and water between plants and the atmosphere.

584

585 **Outstanding Questions**

586

587 How does the flammability of individual grass species affect community-level flammability,
588 and which functional traits are most important for controlling flammability at the community

589 scale? Evidence from other vegetation types suggests that flammability effects are non-additive
590 and are disproportionately influenced by the most flammable members of a community.

591

592 Are remotely-sensed indices relating to grass biomass quantity and moisture content effective
593 estimates of flammability? How do they relate to fire behaviour over regional and trans-
594 continental scales?

595

596 Does enhanced grass representation in Land Surface Models (by incorporating information on
597 grass flammability traits) improve their predictive capacity to model fire behaviour?

598

599 How tightly coupled are flammability and decomposability traits in savanna grasses? Does the
600 rate of decomposition strongly influence flammability, or does the highly frequent fire in
601 savannas mean decomposability contributes little to grass flammability variation? How do key
602 traits that relate to plant life history strategy (e.g. specific leaf area) impact on flammability by
603 influencing both productivity and decomposition of grass fuels?

604

605 The growth response of savanna grasses to future increases in CO₂ concentrations will
606 influence their flammability, but how CO₂ responsiveness varies across species is unclear.
607 Limited evidence suggests responsiveness may depend upon evolutionary history (or C₄
608 subtype more specifically), and may result in CO₂-fertilisation that varies spatially depending
609 on grass community composition.

610

611 What are the general effects of rising CO₂ on grass biomass moisture content and senescence?

612

613 How does drought interact with savanna grass flammability and fire regimes? Severe drought
614 events are increasing in frequency in savannas, and may have contrasting effects on grass
615 flammability (reduced productivity and heightened mortality vs. increased biomass curing).