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RESEARCH PAPER

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Flammability of tropical grasses: Towards a functional ecology of fire in savannas

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ABSTRACT

Fire is a key ecological process in tropical savannas, yet species-specific contributions to fuel flammability remain poorly understood in West Africa. Here, we present the first experimental assessment of flammability traits in the Lamto humid savanna (Côte d'Ivoire), focusing on five dominant perennial grasses, litter, and realistic mixtures. We quantified four plant flammability traits (ignitibility, combustibility, sustainability, consumability) and six fire behavior parameters (flame height, fuel consumption, and maximum temperatures at three heights). Our results show that ignitibility varied strongly among species, with *Hyparrhenia diplandra* and *Loudetia simplex* igniting more rapidly than others. In contrast, combustibility, sustainability, and consumability were relatively consistent across fuel types. Fire behaviour also varied: complete combustion occurred in some mixtures, whereas *Andropogon schirensis* and litter-containing mixtures left significant unburned material, likely due to lower fuel porosity. Importantly, mixture flammability was non-additive: mixtures did not reflect the sum of their components but instead approximated the average flammability of constituent species. Principal Component Analysis and hierarchical clustering identified three functional flammability groups: (i) highly flammable fuels (*Imperata cylindrica*, *L. simplex*, litter), (ii) moderately flammable fuels (*A. schirensis*, *H. diplandra*, mixture 3), and (iii) poorly flammable fuels (*A. canaliculatus* and mixtures 1, 2, 4). These findings highlight the non-additive and species-specific nature of savanna fuel flammability, with direct implications for fire intensity, severity, and management. This trait-based approach provides a foundation for predicting fire behavior in West African savannas and for integrating species-level flammability into conservation-oriented fire management.

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INTRODUCTION

Fire is one of the most influential ecological disturbances shaping tropical savannas, governing not only vegetation structure and species composition but also the evolutionary trajectories of many plant species (Bond and Keeley, 2005; Pausas *et al.*, 2017). In these fire-prone systems, recurrent burning maintains open habitats and suppresses woody encroachment, allowing grasses and other herbaceous species to dominate (Beckage *et al.*, 2009; Case and Staver, 2017). Understanding the mechanisms that govern fire behavior is fundamental to both ecological theory and effective conservation. Among these mechanisms, the flammability of plant material plays a critical role. Plant flammability (the ability of plant material to ignite and sustain combustion) is now recognised as a functional trait that can influence, and be influenced by, fire regimes (Anderson, 1970; Pausas *et al.*, 2017). It encompasses four interrelated components: ignitibility (how easily a plant catches fire), sustainability (how long it burns), combustibility (how fast it burns), and consumability (how completely it burns) (Gill and Zylstra, 2005; White and Zipperer, 2010). These flammability traits can vary across species due to differences in tissue chemistry (e.g., terpenes, essential oils), morphology (e.g., bulk density, surface area), and moisture content (Alessio *et al.*, 2008; Cornwell *et al.*, 2015; Alam *et al.*, 2020). Increasingly, flammability is viewed as a functional trait (analogous to leaf area or seed size) shaped by evolutionary pressures in fire-prone environments (Bowman *et al.*, 2014; Pausas *et al.*, 2017). This perspective has fostered a new discipline: the functional ecology of fire, which explores how species-level traits influence, and are influenced by, fire regimes (Midgley, 2013; Cornwell *et al.*, 2015).

However, empirical data on flammability traits in tropical ecosystems remain heavily biased toward regions such as Australia, North America, and South Africa (Clarke *et al.*, 2014; Calitz *et al.*, 2015; Simpson *et al.*, 2016). West Africa, despite hosting some of the most frequently burned savannas globally (Osborne *et al.*, 2014), has been largely overlooked. A rare exception is the study by Cardoso *et al.* (2018) in Gabon, which highlighted the importance of species-specific flammability over biomass quantity in determining fire behavior. The lack of data from other parts of West Africa constitutes a major gap in our understanding of how fire operates in these ecosystems.

The Lamto Reserve in Côte d'Ivoire represents a model site for studying fire-vegetation interactions. Situated at the ecotone between semi-deciduous forest and humid savanna, it has been managed through prescribed burning since the 1960s (Abbadie *et al.*, 2006). Yet, the selection of fire regimes in Lamto has been historically guided by empirical observation rather than by a mechanistic understanding of fuel flammability. Perennial grasses, which dominate the herbaceous layer and serve as the primary fuel, vary in morphology and abundance, but their flammability traits remain undocumented. Such knowledge is crucial for at least three reasons. First, it can inform fire management decisions aimed at biodiversity conservation, carbon storage, and the prevention of woody encroachment (Archer *et al.*, 2017; N'Dri *et al.*, 2021). Second, it can shed light on the role of fire as an evolutionary filter, selecting for traits that either promote or resist combustion (Pausas *et al.*, 2012; Cui *et al.*, 2020). Third, understanding how different species contribute to community-level flammability can help predict fire behavior under shifting climatic conditions (Dayamba *et al.*, 2010; Guerrero *et al.*, 2021).

In this study, we provide the first quantitative analysis of plant flammability in the Lamto savanna. We assess four flammability traits and six fire behavior parameters across five dominant perennial grass species, litter, and their realistic mixtures. We specifically asked whether flammability traits differ among dominant fuels, whether mixture flammability is predictable from species identity, how fuels can be functionally classified, and what this means for fire intensity and management. By addressing these questions, we aim to contribute not only to the fire ecology of West African savannas but also to broader theories of functional ecology and evolutionary adaptation to disturbance. In doing so, we offer a framework for integrating species traits into fire management practices and for understanding the eco-evolutionary dynamics of flammability in tropical systems.

MATERIALS AND METHODS

Study site description

This study was conducted in the Lamto Reserve, located at the southern edge of the Guinean savanna zone in Côte d'Ivoire (6° 9′-6° 18′ N; 5° 15′-4° 57′ W). This area represents a transitional zone between semi-deciduous forest in the south and humid savanna in the north. The average annual rainfall is approximately 1200 mm and the mean temperature is around 27°C (Tiemoko *et al.*, 2020). The vegetation forms a mosaic of forest and savanna patches with varying tree and shrub densities. The herbaceous layer is dominated by perennial grasses (Menaut and Abbadie, 2006), with approximately ten coexisting species, most of which belong to the tribe Andropogoneae Dumort (Poaceae) (Abbadie *et al.*, 2006).

This study focused on litter and the five dominant perennial grass species in the savanna: four C4 tussock species (*Andropogon canaliculatus* Schumach., *Andropogon schirensis* Hochst. ex A. Rich., *Hyparrhenia diplandra* (Hack.) Stapf, and *Loudetia simplex* (Nees) C.E. (Hubbard) and one rhizomatous species, *Imperata cylindrica* (L.) P. Beauv. The tussock species constitute the bulk of fire fuel, whereas *I. cylindrica*, considered one of the world's 100 most harmful invasive species (Lowe *et al.*, 2007), has become dominant in certain areas of the Lamto savanna that have experienced repeated late dry-season fires over the past decade (Koffi *et al.*, 2019, 2022; N'Dri *et al.*, 2021).

Fuel sampling and preparation

Sampling was conducted at three shrub savanna sites where all target species were abundant in the herbaceous layer and litter was sufficiently present. This resulted in three litter samples and three samples per species. For each tussock species, ten individuals were randomly selected per site in October 2020, at the end of their annual growth cycle, to ensure sufficient biomass. Their aerial parts, including live and dead tillers, leaves, and inflorescences, were collected. For the rhizomatous species *I. cylindrica*, leaves were sampled from ten 1 m × 1 m quadrats per site. Litter was also collected from the same quadrats.

All samples were oven-dried at 60°C to constant weight to ensure full moisture removal. To evaluate the contribution of each species and litter to overall fuel flammability, each species was tested individually, and four mixtures were created to simulate realistic field conditions based on the dominant species. In areas dominated by *I. cylindrica*, the three main species are *I. cylindrica*, *A. canaliculatus*, and *H. diplandra*. Where *I. cylindrica* is absent, *A. canaliculatus* is the most abundant, followed by *H. diplandra* and *L. simplex* (Koffi, 2019).

Mixtures were composed as follows: Mixture 1: *A. canaliculatus* + *H. diplandra* + *L. simplex*; Mixture 2: Mixture 1 + litter; Mixture 3: *A. canaliculatus* + *H. diplandra* + *I. cylindrica*; Mixture 4: Mixture 3 + litter. Mixtures 1 and 2 correspond to the general composition of the savanna, while Mixtures 3 and 4 reflect areas where *I. cylindrica* is dominant. All samples were cut into small pieces for easier handling and uniformity. For each mixture and fuel type, 100 g of biomass from each component was homogenised in a tank, and five 100 g subsamples were prepared for experiments.

Flammability experiment

Flammability testing followed protocols adapted from Plucinski and Anderson (2008) and Prior (2017). Each 100 g sample (cut into twig-sized pieces) was placed in a circular pan with a fiber cement base and wire mesh sides and ignited under ambient conditions. The pan was enclosed in a three-sided box to minimize airflow.

A lit matchstick was placed at the center of the fuel to initiate combustion. Three stopwatches were used: one to record ignition time (ignitability), one to measure the time until the flame reached the pan's edge (used to calculate combustibility), and one to record total burning time (sustainability). Combustibility was calculated by dividing the radius of the pan by the time to reach the edge. Consumability was calculated as the ratio of the amount of fuel burned to the combustion duration.

Fire behavior parameter measurement

To measure flame height, a plywood panel marked in centimeters was fixed vertically behind the pan inside the three-sided box. Flame height was assessed using video recordings of the combustion process, with still images extracted at three-second intervals.

Three thermocouples were positioned at 5 cm, 15 cm, and 30 cm above the sample to record flame temperatures at one-second intervals. At the end of combustion, the remaining unburned material was weighed after sieving out the ash using a precision electronic scale, allowing estimation of the quantity of fuel consumed.

Data analyses

Flammability traits (ignitability, combustibility, sustainability, and consumability) and fire behavior parameters were compared among fuel types (species, litter, and mixtures) using one-way ANOVA. To assess the contribution of each fuel type to the overall flammability of mixtures, we compared, for each parameter, the mixture values to the sum and the average of the individual components using one-way ANOVA. Tukey's HSD test was used for post hoc comparisons.

We also used Principal Component Analysis (PCA) to explore covariation patterns and characterise fuel types. A hierarchical ascending classification (cluster analysis) based on the PCA components was conducted to categorise fuel types into low, medium, and high flammability classes. All statistical analyses were performed using R software (R Core Team, 2021) with a significance threshold of $\alpha = 0.05$.

RESULTS

Flammability of the different fuel types

Ignitability differed significantly among fuel types ($F = 4.13$; df = 9; $p < 0.001$). The highest ignitability values were observed in litter (1.83 s) and mixture 4 (1.85 s), whereas the lowest values were recorded for *H. diplandra* (0.26 s) and *L. simplex* (0.45 s). Among the fire behavior parameters, only the amount of burned biomass varied significantly between fuel types ($F = 3.43$; df = 9; $p < 0.01$). The maximum burned biomass was found in mixture 1 (100 g), while the lowest values were recorded for *A. schirensis* (97.4 g) and mixture 4 (97.4 g). Other fire behavior parameters showed no significant variation among fuel types (Table 1).

Table 1. Comparison of the different fuel types based on their flammability traits and fire behavior parameters

Parameters	Litter	Ac	As	Hd	Ic	Ls	Mixture				F-stastistic	*p*-value, df
							1	2	3	4		
Ignitability (s)	1.8^{a}	1.5^{ab}	0.8^{ab}	0.3^{b}	1.0^{ab}	0.5^{b}	1.5^{ab}	1.3^{ab}	1.3^{ab}	1.9^{a}	4.1	< 0.001, 9
Combustibility (cm.s^{-1})	0.5	0.4	0.6	0.5	0.6	0.6	0.5	0.5	0.6	0.5	1.7	0.118, 9
Sustainability (s)	72.4	113.4	83.7	81.3	68.3	72.7	99.2	93.5	90.5	94.7	1.7	0.131, 9
Consumability (g.s^{-1})	1.4	1.0	1.2	1.24	1.5	1.5	1.1	1.1	1.2	1.1	1.7	0.122, 9
Burned biomass (g)	99.6^{ab}	99.8^{ab}	97.4^{b}	98.6^{ab}	99^{ab}	98.6^{ab}	100^{a}	99.8^{ab}	99.8^{ab}	97.4^{b}	3.4	< 0.01, 9
AFH (cm)	63.8	52.3	49.2	54.7	66.6	65.4	53.4	51.7	59.0	56.2	1.2	0.303, 9
MFH (cm)	122.4	98	97.8	92.4	107.4	122.4	91.4	102.6	101.8	103.4	1.5	0.192, 9
Max. T° 5cm (°C)	524.8	528.7	458.6	489.5	529.8	522.7	526.8	504.2	500.9	501.6	0.6	0.802, 9
Max. T° 15cm (°C)	468.6	415.0	384.2	496.3	467.1	344.4	412.6	535.0	462.7	420.7	1.6	0.146, 9
Max. T° 30cm (°C)	274.4	250.0	204.3	229.4	257.3	269.8	289.3	273.7	260.7	145.3	0.9	0.529, 9

Values sharing the same superscripts are not significantly different under the Tukey's HSD test. Species are: Ac: *Andropogon canaliculatus*, As: *Andropogon schirensis*, Hd: *Hyparrhenia diplandra*, Ic: *Imperata cylindrica*, Ls: *Loudetia simplex*. Mixtures are: Mixture 1= *A. canaliculatus* + *H. diplandra* + *L. simplex*, Mixture 2= Mixture 1 + litter, Mixture 3= *A. canaliculatus* + *H. diplandra* + *I. cylindrica*, Mixture 4= Mixture 3 + litter. The fire behavior parameters are: AFH: average flame height; MFH: maximum flame height; Max. T°: Maximum temperature at 5, 15 and 30 cm height.

Contribution of each species to the flammability of the mixtures

The values of flammability traits and fire behavior parameters observed for the mixtures were significantly lower than the sum of their component values (ANOVA, df = 2; p < 0.001). However, they were not significantly different from the averages of the individual components (Table 2), suggesting that mixture flammability cannot be predicted by a simple additive model.

Table 2. Comparison of the sum and the mean of the mixture components, to the corresponding mixtures, based on the flammability traits and the fire behavior parameters

Mixtures	Statistic parameters	Ignit. (s)	Comb. (cm.s^{-1})	Sust. (s)	Cons. (g.s^{-1})	AFH (cm)	MFH (cm)	Max. T° 5cm (°C)	Max. T° 15cm (°C)	Max. T° 30cm (°C)
Mixture 1	Sum	2.2^{a}	1.5^{a}	267.3^{a}	3.7^{a}	172.4^{a}	312.8^{a}	1540.9^{a}	1255.7^{a}	749.1^{a}
	Mean	0.7^{a}	0.5^{b}	89.1^{b}	1.2^{b}	57.5^{b}	104.3^{b}	513.6^{b}	418.6^{b}	249.7^{b}
	Mixture	1.5^{a}	0.5^{b}	99.2^{b}	1.1^{b}	53.4^{b}	91.4^{b}	526.8^{b}	412.6^{b}	289.3^{b}
F-value;df		3.4; 2	43.3; 2	26.7; 2	34.6; 2	161.9; 2	273.9; 2	153.6; 2	47.5; 2	14.9; 2
p-value		0.069	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
Mixture 2	Sum	4.0^{a}	2.0^{a}	339.8^{a}	5.1^{a}	236.3^{a}	435.2^{a}	2065.7^{a}	1724.3^{a}	1023.4^{a}
	Mean	1.0^{b}	0.5^{b}	84.9^{b}	1.3^{b}	59.1^{b}	108.8^{b}	516.4^{b}	431.1^{b}	255.9^{b}
	Mixture	1.3^{b}	0.5^{b}	93.5^{b}	1.1^{b}	51.7^{b}	102.6^{b}	504.2^{b}	535.0^{b}	273.7^{b}
F-value; df		14.6; 2	363.7; 2	69.5; 2	102.5; 2	467.5; 2	692.4; 2	347.1; 2	123.8; 2	64.1; 2
p-value		<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
Mixture 3	Sum	2.8^{a}	1.6^{a}	263.0^{a}	3.7^{a}	173.6^{a}	297.8^{a}	1548.0^{a}	1378.4^{a}	736.6^{a}
	Mean	0.9^{b}	0.5^{b}	87.7^{b}	1.2^{b}	57.9^{b}	99.3^{b}	516.0^{b}	459.5^{b}	245.5^{b}
	Mixture	1.3^{b}	0.6^{b}	90.5^{b}	1.2^{b}	59.0^{b}	101.8^{b}	500.9^{b}	462.7^{b}	260.7^{b}
F-value; df		13.4; 2	106.9; 2	47.8; 2	105.1; 2	243.4; 2	158.6; 2	287.2; 2	112.5; 2	76.7; 2
p-value		<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
Mixture 4	Sum	4.6^{a}	2.1^{a}	335.4^{a}	5.1^{a}	237.4^{a}	420.2^{a}	2072.8^{a}	1847.0^{a}	1011.0^{a}
	Mean	1.1^{b}	0.5^{b}	83.8^{b}	1.3^{b}	59.4^{b}	105.1^{b}	518.2^{b}	461.7^{b}	252.8^{b}
	Mixture	1.9^{b}	0.5^{b}	94.7^{b}	1.1^{b}	56.3^{b}	103.4^{b}	501.6^{b}	420.7^{b}	145.3^{b}
F-value; df		16.5; 2	1110; 2	106.8; 2	261.2; 2	374.3; 2	655.8; 2	481.7; 2	372.6; 2	348.2; 2
p-value		<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001

The flammability traits: Ignit.: ignitability, Comb.: combustibility, Sust.: sustainability, Cons.: consumability. The fire behavior parameters: AFH: average flame height, MFH: maximum flame height and Max. T°: maximum temperatures at 5cm, 15cm and 30cm height. The composition of the mixtures: Mixture 1 = *A. canaliculatus* + *H. diplandra* + *L. simplex*, Mixture 2 = Mixture 1 + litter, Mixture 3 = *A. canaliculatus* + *H. diplandra* + *I. cylindrica*, Mixture 4 = Mixture 3 + litter. The values with the same superscripts are not significantly different.

Characteristics of the fuels

Principal Component Analysis (PCA) was used to investigate patterns of covariance among flammability traits and fire behavior parameters. The first two principal components explained 67.7% of the total variance (Axis 1 = 39.4%; Axis 2 = 28.3%). These axes exceeded the 95th percentile of the null distribution (60.88%), indicating that they contained meaningful ecological information. Axis 1 was strongly associated with combustibility (cor = 0.71; p < 0.001), sustainability (cor = –0.94; p < 0.001), consumability (cor = 0.98; p < 0.001), average flame height (cor = 0.84; p < 0.001), and maximum flame height (cor = 0.74; p < 0.001). This axis effectively separated fast-burning fuels (*I. cylindrica*, *L. simplex*, and litter), characterized by high combustibility and low sustainability, from slow-burning fuels (*A. canaliculatus*, mixtures 1, 2, and 4), which exhibited greater sustainability. Axis 2 was primarily correlated with consumability (cor = 0.88; p < 0.001), maximum temperature at 5 cm (cor = 0.88; p < 0.001), and maximum temperature at 30 cm (cor = 0.74; p = 0.012). This axis differentiated fuels with higher near-surface flame temperatures (*A. canaliculatus*, *I. cylindrica*, litter, mixtures 1 and 2) from fuels with lower temperatures (*A. schirensis*, *H. diplandra*, and mixture 4). Variables such as ignitability and flame temperature at 15 cm did not load strongly on either axis and were therefore excluded from interpretation (Fig. 1).

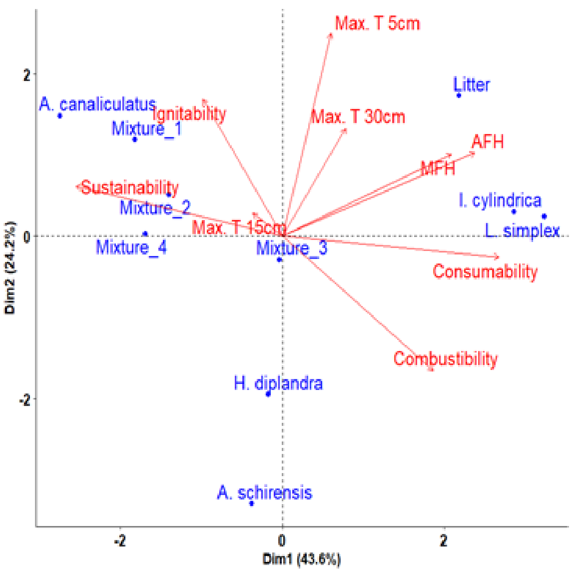

Fig. 1. Principal component analysis showing the characteristics of the fuel types based on the flammability traits and the fire behavior parameters

The fuel types are: the litter, the grass species (*Andropogon canaliculatus*, *Andropogon schirensis*, *Hyparrhenia diplandra*, *Imperata cylindrica*, *Loudetia simplex*) and the following mixtures: Mixture 1 = *A. canaliculatus* + *H. diplandra* + *L. simplex*, Mixture 2 = Mixture 1 + litter, Mixture 3 = *A. canaliculatus* + *H. diplandra* + *I. cylindrica*, Mixture 4 = Mixture 3 + litter. The fire behavior parameters are: AFH: average flame height; MFH: maximum flame height; Max. T 5cm, Max. T 15cm and Max. T 30cm: Maximum temperature at respectively 5, 15 and 30 cm above the fuel.

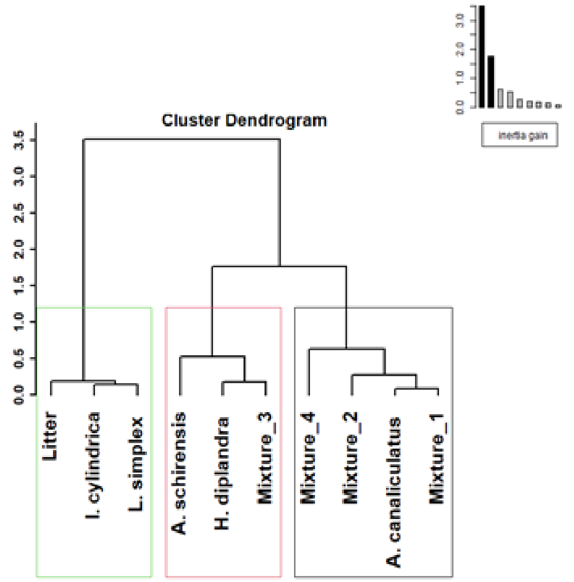

Fig. 2. Dendrogram showing the hierarchical classification of the fuel types based on the flammability traits and the fire behavior parameters

The fuel types are: the litter, the grass species (*Andropogon canaliculatus*, *Andropogon schirensis*, *Hyparrhenia diplandra*, *Imperata cylindrica*, *Loudetia simplex*) and the following mixtures: Mixture 1 = *A. canaliculatus* + *H. diplandra* + *L. simplex*, Mixture 2 = Mixture 1 + litter, Mixture 3 = *A. canaliculatus* + *H. diplandra* + *I. cylindrica*, Mixture 4 = Mixture 3 + litter.

Classification of the fuels

Hierarchical cluster analysis based on flammability traits and fire behavior parameters identified three distinct fuel groups. The first group, composed of *A. canaliculatus*, mixtures 1, 2, and 4, showed low flammability, burning slowly and incompletely due to low consumability and high sustainability. The second group, consisting of *A. schirensis*, *H. diplandra*, and mixture 3, exhibited moderate flammability, characterized by complete but slower combustion. The third group included *I. cylindrica*, *L. simplex*, and litter, which were highly flammable and burned rapidly and completely (Fig. 2).

DISCUSSION

Variation in fuel flammability

The results showed that only one of the four flammability traits (i.e. ignitability) varied between fuels, with faster ignition observed for *H. diplandra* and *L. simplex*. Among the factors that influence plant fuel flammability, anatomical structure, plant material size, and the presence of flammable chemical compounds in plant tissues are typically those that explain differences in ignitability (Schwilk and Ackerly, 2001; Alessio *et al.*, 2008; Bowman *et al.*, 2014). Since the anatomical structure and size of plant materials were similar across all species, all species and mixtures without litter were expected to exhibit high ignitability. This is because they consist of fine fuels, which are known to increase ignitability (Davies and Legg, 2011; Santana and Marrs, 2014; Burger and Bond, 2015). However, this was not the case, suggesting that the only factor likely to explain the observed differences in ignitability among species is the presence of flammable chemical compounds, which are species-specific (Alessio *et al.*, 2008; Guerrero *et al.*, 2021, 2022). This suggests that species such as *H. diplandra* and *L. simplex*, which exhibited higher ignitability, likely contain a greater quantity or higher quality of flammable chemical compounds. In addition to this probable chemical difference, the variation in flammability observed in fuel mixtures containing litter may also be due to the physical structure of the litter. Since the litter was not sorted, it included a variety of plant parts such as leaves and woody twigs, which are generally more difficult to ignite (Burger and Bond, 2015; Alam *et al.*, 2020; Kraaij *et al.*, 2022, 2024).

The other flammability traits (combustibility, sustainability, and consumability) did not vary significantly between fuel types. This suggests that overall flammability is relatively consistent among the perennial grass species of the Lamto savanna and between these species and the litter. However, savannas dominated by *H. diplandra* and *L. simplex* are likely to ignite more rapidly than others.

Differences between fuel types were also observed in fire behavior parameters. Only the amount of burned material differed significantly, with complete combustion observed in mixture 1, and the lowest combustion levels found in *A. schirensis* and mixture 4. Fuel porosity (also known as void volume fraction) likely explains this variation, as it directly affects the availability of oxygen for combustion (Saura-Mas *et al.*, 2010; Santoni *et al.*, 2014; Burger and Bond, 2015). Mixture 4 contained less porous litter. Similarly, *A. schirensis* has a dense, silky indumentum, which results in lower fuel porosity. As a result, these two fuels burned less completely than mixture 1, which consisted of species that are generally less hairy and more porous. This was evident during the experiment, as large amounts of smoke and unburned material were observed for mixture 4 and *A. schirensis*.

Contribution of fuel components to overall fuel flammability

Results show that flammability is not an additive function, but rather reflects the average flammability of the species making up the fuel. This is shown by the fact that, for all parameters, there was no significant difference between the mean values of the mixture's components and the mixture itself. In contrast, in nearly all cases, the mixtures differed from the sums of the components. The three highly flammable fuels (*I. cylindrica*, *L. simplex*, and litter) were included in the mixtures tested. Yet, none of the mixtures were classified as highly flammable. This confirms that the flammability characteristics of the components are non-additive. Therefore, the coexistence of perennial grass species in the Lamto savanna does not imply an increase in the overall flammability of the savanna. In other words, there is no synergistic effect between these species. Synergy would imply that the overall flammability is greater than, or at least equal to, the sum of the individual species (Zhang and Liu, 2015).

More precisely, the interaction among these species can be seen as a redundant functional relationship (Biggs *et al.*, 2020; Fischer and De Bello, 2023), where the contributions of each species, although highly flammable, do not combine to enhance overall flammability. One might also consider the idea of collaborative neutrality (Allaerts, 2023), where species have neither a positive nor negative effect on the flammability of the mixture. All this may reflect a lack of complementarity in flammability traits or suboptimal coordination (Gross *et al.*, 2007), which limits the flammability of the mixtures.

Flammability characteristics of fuels

No fuel type perfectly met our criteria of highly flammable fuel (low ignitability, low sustainability, high combustibility and high consumability), but some fuel types satisfied the conditions for three of the four flammability traits. These fuels had low sustainability and high combustibility and consumability. This was the case for *I. cylindrica*, *L. simplex*, and the litter, which were classified as highly flammable fuels by hierarchical cluster analysis. On the contrary, *A. canaliculatus*, Mixture 1, Mixture 2, and Mixture 4 were classified as poorly flammable fuels, with high sustainability and low flame height, making them potentially easier to manage. The moderately flammable fuel group includes *A. shirensis*, *H. diplandra*, and Mixture 3, characterised by the highest maximum temperatures at 5 cm height. These results provide a trait-based approach to prescribe fire regimes in West African savannas. Identifying less flammable species could inform buffer zones around human installations.

Influence of fuel types on fire intensity and severity

The litter, *I. cylindrica* and *L. simplex* are expected to contribute most to the intensity and severity of savanna fires. These fuels were the most flammable in our results. They burn relatively quickly, leading to a faster flame spread, an important factor in determining fire intensity (Byram, 1959). As a result, fires involving these fuels are likely to be more intense. In addition, although not significantly different from other fuel types, these three fuels produced the tallest flame heights (e.g. average: 63–67 cm; maximum: 107–123 cm). Such flame heights may cause more damage to fire-sensitive woody species, and potentially affect some arboreal animal species. However, the rapid flame spread might reduce damage to certain plants. The shorter residence time could spare some plant parts, such as bark or grass culms, thereby reducing fire severity. Therefore, these fuel types deserve special attention from savanna managers and farmers, particularly during periods of severe drought.

In areas dominated by *A. canaliculatus*, Mixture 1, Mixture 2, or Mixture 4, fires may be easier to control. Their impact on tall vegetation, such as trees and shrubs, could also be lower. These are the least flammable fuels and tend to burn more slowly, which may reduce fire intensity. One might assume that such fuels are less useful in controlling woody encroachment. However, their slower burning leads to longer residence times, which can increase the mortality of woody species, especially at the seedling or resprouting stage (Kpangba *et al.*, 2022). This can also harm some plant communities, such as perennial grasses. Prolonged burning within a tussock increases the likelihood of tiller death, potentially leading to the death or fragmentation of the tussock. This supports findings by Koffi *et al.* (2019, 2022), who reported *A. canaliculatus* as the most fragmented perennial grass species in the Lamto savanna.

The influence of moderately flammable fuels (*A. shirensis*, *H. diplandra*, and Mixture 3) may be more evident in fire severity. These fuels combine moderate flame spread, residence time, and flame temperature. This balance can have a stronger impact on a wide range of plant species. The average flame temperature recorded in this study was above the lethal threshold for plant cells, which is 60°C (Dayamba *et al.*, 2010; Kelsey and Westlind, 2017). This is sufficient to kill exposed seedlings and saplings if the exposure is sustained. Therefore, these fuels may be highly effective in controlling woody encroachment. They can suppress seed germination and keep saplings and juvenile trees locked in a prolonged regrowth cycle.

Potential for future research

This study highlights several promising areas for future research, especially in understanding the broader ecological and management implications of fire behaviour in savanna ecosystems. One key direction for further investigation is how different fuel types influence ecosystem resilience or degradation following fire. While this study focused on flammability traits, it is also essential to understand the post-fire recovery of different plant species and fuel mixtures. This knowledge is crucial for developing effective fire management strategies.

Future research could also examine the long-term effects of repeated fire exposure on fuel composition and flammability traits. In particular, investigating how successive fires alter the structural and chemical properties of fuels may provide insights into fire-adaptive traits and the evolution of flammability in perennial grasses. Studies might explore possible changes in plant physiology or anatomy in response to frequent fires.

CONCLUSION

This study offers insights into the complex dynamics of flammability and fire behaviour in the West African humid savanna of Lamto. By examining the interactions between different fuel types (including perennial grasses and litter) and their flammability traits (ignitability, combustibility, sustainability, and consumability), we highlight the significant variation in fire behaviour linked to fuel composition. Fuels differ in their flammability, suggesting differences in the quantity and/or quality of chemical compounds within species. We also show that flammability is not an additive function of individual species traits, but rather the result of interactions among fuel components, producing an average outcome. The classification of fuel types into highly flammable, moderately flammable, and poorly flammable categories underscores the variability in fire behaviour among species, an important factor to consider in fire management strategies. This study sets the basis for integrating trait-based flammability into fire management models in tropical Africa.

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