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ARTICLE

Ecology of Critical Zones

Can seasonal fire management reduce the risk of carbon loss from wildfires in a protected Guinea savanna?

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Abstract

Fire is fundamental to the functioning of tropical savannas and routinely used as a management tool. Shifting prescribed burning from later to earlier in the growing season has the potential to reduce greenhouse gas emissions. However, large uncertainties surround the impact of seasonal burning on longer term plant and soil carbon sequestration. In this study, we quantify ecosystem carbon storage across burn seasons and histories in a wet-to-mesic Guinea tropical savanna in Mole National Park, Ghana. Aboveground (plant and litter) and belowground (soil plus roots) carbon storage was quantified across four burning seasons and histories: recent (<3 years) early-season burns, recent late-season burns, old (>4 years) late-season burns, and long-unburned (>15 years) sites. We found that recent late-season burns significantly lowered belowground carbon storage to a depth of 17 cm compared with all other burn seasons and histories. Belowground carbon was 1.2 kg C m^{-2}, or 27% lower, for recent late-season burns compared with prescribed early-season burns. However, in older late-season burns sites, belowground carbon "recovered" after 4–13 burn years to comparable storage as long-unburned and early-season burn sites. For most aboveground carbon pools, there was no significant difference in carbon storage across burn seasons and histories, except higher aboveground tree carbon in long-unburned sites. We suggest that observed changes in belowground carbon are likely due to the turnover and production of root carbon. Prescribed early-season burning is promoted to reduce greenhouse gas emissions and our findings affirm that early-season burning has limited impact on plant and soil carbon stocks compared with long-unburned sites. While early-season burning regimes will have some patches that become late-season wildfires, our results suggest on balance early-season burning regimes are a low-risk land management practice in reducing plant and soil carbon storage losses and sustaining a patch-mosaicked landscape with multiple other ecosystem service benefits for savannas.

Joana Awuah and Stuart W. Smith contributed equally to the work reported here.

KEYWORDS
carbon financial markets, dry season fires, fire management, MODIS burn area product, pyrobiome, soil carbon, soil organic matter, West Africa, wildlife protected areas, woody cover

INTRODUCTION

Fires shape the structure and function of tropical savannas and grasslands. Fires trigger plant reproduction, for example, reseeding and seed germination (Buisson et al., 2019; Gashaw & Michelsen, 2002). Fires prevent the dominance of trees allowing coexistence with C4 grasses (Bond & Keeley, 2005; Higgins et al., 2000). Spatial and temporal variation in fires (pyrodiversity) generates structural diversity that promotes bird and mammal diversity (Beale et al., 2018; Martin & Sapsis, 1992). Fire management represents a cultural heritage for indigenous communities (Shaffer, 2010; Whitehead et al., 2008). Despite prescribed burning being a widely used land management practice in savannas, fires influence the balance between greenhouse gas emissions and carbon stored in terrestrial plant and soil pools.

Fire management through the timing of prescribed fires offers a potential tool to control greenhouse gas emissions. Shifting prescribed burns from late to earlier growing season has been proposed to reduce greenhouse gas emissions (Lipsett-Moore et al., 2018; Russell-Smith et al., 2003). Lower carbon emissions following early-growing-season burns is linked to less plant biomass and litter burned compared with later in the growing season (Russell-Smith et al., 2003; Russell-Smith et al., 2021); however, other factors such as the higher water content of fuel can also influence greenhouse gas emissions, for example, methane (Laris, 2021). A pan-savanna study across 50 countries calculated that shifting from late- to early-growing-season fires reduced carbon-equivalent nitrous oxide and methane emissions by 89.4 Mt CO_2-e $year^{-1}$ (Lipsett-Moore et al., 2018). Reducing greenhouse gas emissions through fire management can be sold as part of voluntary carbon market schemes (Russell-Smith et al., 2015). Wildlife protected areas regularly manage vegetation by prescribed burning, shifting the timing of burning has been proposed as a potential source of financial revenue for wildlife conservation (Lipsett-Moore et al., 2018; Russell-Smith et al., 2021; Tear et al., 2021).

While early-growing-season fires may provide reductions in carbon-equivalent emission, large uncertainties remain surrounding the impact of fires on longer term plant and soil carbon sequestration. Soil carbon is the largest terrestrial carbon pool and the timing and frequency of fires (or fire return interval) can influence soil carbon storage (Richards et al., 2011). Fires are often considered to lead to carbon losses, because fires combust plant biomass and organic soil layers, promote erosion and leaching, and subsequently reduce plant input, especially woody carbon inputs, to the soil that can persist for several years (Bird et al., 2000; Grace et al., 2006; Pellegrini et al., 2015; Pellegrini, Hobbie, et al., 2020). A review of global fire manipulation experiments found that frequent fires (annual burning) reduced soil carbon storage in savannas with a larger decline in longer term experiments (Pellegrini et al., 2018). Nevertheless, several studies either show no significant difference or a positive effect of fires on soil carbon storage (Aynekulu et al., 2021; Coetsee et al., 2010; Nghalipo et al., 2019; Savadogo et al., 2007). Given the remarkably high productivity of tropical savannas, aboveground and belowground plant primary productivity can recover within months following a fire (Beringer et al., 2007; Van de Vijver et al., 1999). Elevated plant inputs could potentially facilitate the rapid recovery of soil carbon storage following depletion by fires. Fires may also stabilize soil carbon through the formation of recalcitrant pyrogenic carbon as well as formation of soil aggregate formation and organic-mineral complexes, promoting fungal abundance and/diversity and lowering plant litter decomposition rates (mechanisms reviewed in Pellegrini et al., 2022). Thus, the potential for carbon loss and the timescale of recovery following fires in savannas presents a large unknown.

Across Africa, burning during the early or mid-growing season is widely practiced in many regions, notably the wet-to-mesic savanna belt in West Africa, including Burkina Faso, Senegal, Benin, Togo, and Ghana (Laris, 2021; Laris et al., 2016; Le Page et al., 2010). Early-growing-season burning regimes create a patchy mosaic of burns, targeting grass–woody patches just dry enough to burn, although some wetter areas remain unburned. Unburned areas can become unintentional and high-intensity late-growing-season wildfires (Sackey et al., 2012; Sackey & Hale, 2008). In this study, we used Mole National Park, Ghana, to investigate the impact of the timing and recovery of seasonal prescribed burning on Guinea savanna carbon storage. Our main aim was to determine the longer term impact of late-growing-season wildfires on plant and soil carbon storage compared with early-growing-season prescribed burning practices in the park. Using remote sensing, we identified four burn season and history types, specifically recent (<3 years) early-growing-season burns, recent late-growing-season burns, old (4–10 years old) late-growing-season burns, and long-unburned (>15 years) patches. By measuring carbon storage across these burn seasons and histories, our specific questions were as follows: (1) Do late-growing-season wildfires cause a major reduction in aboveground and belowground carbon storage compared with other burn seasons and histories, and, if reduced, (2) does the aboveground and belowground carbon storage recover, and over what timescale, for example, years to decades, when compared with other burn seasons and histories?

METHODS

Study area

The study was conducted in Mole National Park, approximately 4800 km^2, in northern Ghana (N 9°12′–10°06′, W 1°25′–2°17′). The park was established in 1958 and has been managed by the wildlife division of the Ghana Forestry Commission as a Category II National Park, under the International Union for Conservation of Nature classification of protected areas (Cole Burton et al., 2011). The park is located 120–490 m above sea level with a tropical wet climate. Annual air temperature averages 29°C, annual rainfall ranges between 950 and 1100 mm and occurs mainly during a single wet season from May to October (Cole Burton et al., 2011; Mikkelsen & Langohr, 2004). The dominant soil types across the park include ferrosols that are high in available iron but well structured, nitisols that are well drained and typically composed of 30% clay, and vertisols with high expansive clay contents, yet organic rich (Bowell & Ansah, 1994). The main habitat in the park is open savanna-woodland (Guinea savanna) with a grass layer that can be 3 m tall (e.g., *Andropogon gayanus* Kunth) during the wet season (Sackey & Hale, 2008). Common tree species include *Terminalia avicennioides* (Guill. & Perr), *Combretum molle* (R. Br. Ex G. Don), *Vitellaria paradoxa* (C.F. Gaertn), *Combretum adenogonium* (Steud. Ex A. Rich), and *Anogeissus leiocarpa* (DC. Guill. & Perr.) (Appendix S1: Table S1). Wild herbivore densities within the park are typically low, but the park encompasses a diverse herbivore guild (Afriyie et al., 2021).

Park managers burn vegetation annually aiming to maximize areas burned earlier in the growing season (November and December) to prevent higher intensity wildfires later in the growing season (December–April) (Sackey et al., 2012; Sackey & Hale, 2008). However, early in the growing season, some vegetated areas are too wet to burn. These can undergo late-growing-season wildfires or remain unburned into the next growing season. Unburned vegetated areas are at risk of late fires creeping into the park from neighboring communities and poaching activity (Umaru Faruk Duberu, Mole National Park Manager, personal communication). For simplicity, we often refer to "burns" in the paper, though we recognize late-growing-season burns are viewed as unintentional wildfires from the perspective of park managers.

Site selection and study design

We adopted a space-for-time substitution design where the impact of burn season and history was assessed for a series of sites with different times since burning (Nghalipo et al., 2019; Pickett, 1989). To determine the season and history of burning across Mole National Park, we obtained satellite imagery from NASA's Moderate Resolution Imaging Spectroradiometer (MODIS) Collection 6 Active Fire data downloaded from NASA (Near Real-Time and MCD14DL MODIS Active Fire Detections on 13 March 2016 [https://earthdata.nasa.gov/active-fire-data]). This dataset has a resolution of 1 km at nadir and dates from November 2000. To avoid potential false-positive fire identification, only fire events with greater than 90% confidence level were used. Fires were classified into four categories: (1) recent early-season burns that occur early in the growing season between November and December within the three years (2012–2015) prior to field sampling with a mean time since last fire of 271 days (SD = 149); (2) recent late-season burns occurring between January and April within the four years (2013–2015) prior to field sampling with a mean time since last fire of 650 days (SD = 348); (3) old late-season burns were sites burned late in the growing season over four years (2003–2012) prior to field sampling with a mean time since last fire of 2789 days (SD = 1430); (4) long-unburned sites with no detection of fires between 2000 and 2015. These four fire histories were based on findings by Sackey et al. (2012) who suggested a rotational system of three-year fire-free interval was needed for the survival of most of the woody plant species in Mole National Park. Since the burn season straddles two calendar years, we refer to time since the last fire as burn years.

Within each burn season and history classification, seven sites were randomly selected from each fire category making 28 sites in total (Figure 1d,e). The number of required sites was based on power analyses to detect weak statistical difference between burn seasons and histories (Appendix S1: Figure S1). Sites were selected primarily to differ in fire interval classification while

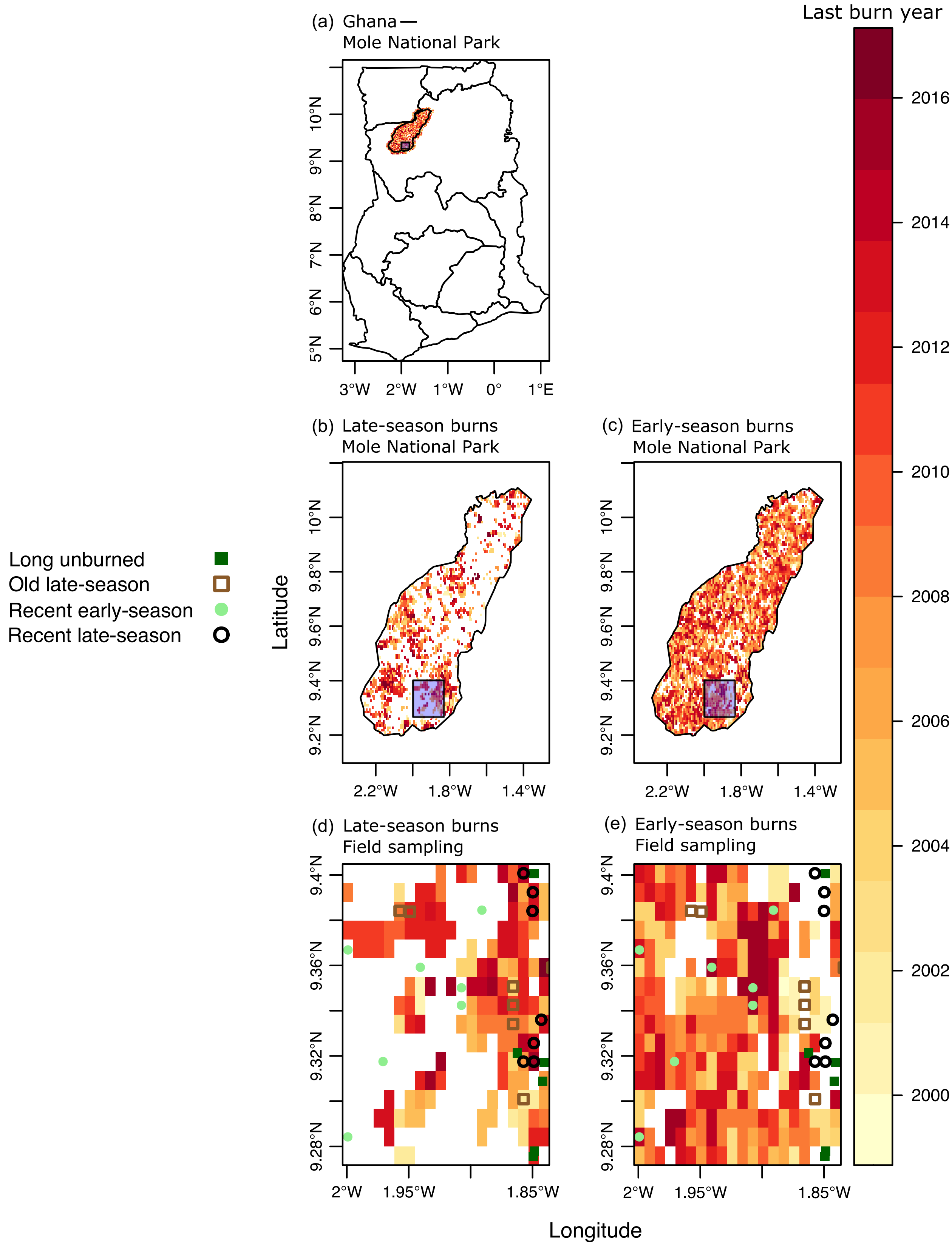

FIGURE 1 Burn season and history (2000–2016) in Mole National Park, Ghana. Maps show (a) the location of Mole National Park in Ghana, (b) late-dry-season burns and (c) early-dry-season burns in Mole National Park, and the distribution of study sites in relation to (d) late-season and (e) early-season burns. In total we identified 28 sites across recent late-season and early-season burns, old late-season burns (older than 4 burn years), and long-unburned (>15 burn years) sites.

maintaining other characteristics such as dominant vegetation type, soil type, aspect, and elevation. For recent burns, potential selected sites were ground-truthed by searching for evidence of fires (i.e., charring, scars, and burned fallen trees) (Appendix S1: Figure S2) and through discussion with park officials. Site where the visual evidence of fires was not consistent with the satellite-imagery-based classification were discarded, totaling 13 potential sites visited in the field. Our stratified random field sampling campaign was concentrated in the southeastern/Samole range of the park because this is an area surrounded by many local communities with higher incidence of late-season burning, creating a rich mosaic of burning seasons and histories (Figure 1). Where possible, each site was located a minimum of 1 km away from neighboring sites. This was to reduce spatial autocorrelation in aboveground and belowground carbon sampling.

Data collection

Field sampling of aboveground and belowground carbon was conducted between June and July 2016 during the peak wet season. At each site, a 25-m^2 quadrat was marked out for sample collection. All woody plants were sampled non-destructively inside the quadrat and classified into either shrub (from 0.5 to 2 m tall) or trees (>2 m) based on height. For shrubs, height and diameter at stem base were recorded, while for trees, dbh (1.3 m) was recorded. All woody individuals were identified at the species level. All deadwood debris (i.e., fallen dead trees and branches) were sampled by measuring the total length and diameter of fragments >4 cm diameter.

Five quadrats, each 0.16 m^2, were marked out in the four corners of the larger quadrat and one in the center, avoiding areas of rocks, dense woody debris, animal dung, and termite mounds. Herbaceous biomass was sampled in these quadrats by clipping herbaceous biomass to the ground surface, woody biomass was excluded as this was quantified in the larger quadrat sampling. Within the smaller quadrat, plant litter (woody and herbaceous) found on the ground was collected. Harvested plant material and litter were oven-dried at 70°C for 72 h and weighed using analytical laboratory balance (±0.001 g).

Within the smaller quadrats, four soil samples were extracted to a depth of 12 cm and one to a depth of 17 cm. For many quadrats, we were unable to reach the deeper soil and therefore limited deeper soil sampling to one small quadrat. Soil samples were extracted using a gouge auger with an internal diameter of 1.9 cm. The soil from each core was subdivided into layers: 0–2, 2–7, 7–12, and 12–17 cm deep. In total 448 soil samples (336–12 and 112–17 cm deep) were collected and stored in a refrigerator at 6°C to reduce microbial activity for 1.5 months before processing. Dry mass was estimated after drying soil samples in an oven at 105°C for 48 h. Soils were sieved to 2 mm to remove stones and homogenized using a pestle and mortar. For each sample, a standard 2.75 ± 0.03 g subsample was weighed into a crucible and ignited at 550°C for 5 h to determine organic matter content through mass-based loss on ignition (LOI). Due to concerns over the accuracy of LOI for low carbon content soils (McCarty et al., 2010), a subset of 75 soil samples spanning the entire range of LOI were analyzed using an elemental analyzer. Soil samples between 4 and 22 mg were analyzed for total carbon and nitrogen using an automated dry combustion elemental analyzer (Vario Micro Cube, Elementar, Germany). LOI and elemental analyzer carbon percentages showed a significant positive correlation, and this relationship was used to predict elemental analyzer equivalent soil carbon percentages (linear model: $0.343 + 0.116x$, $r^2 = 0.69$) (Appendix S1: Figure S3).

Carbon storage calculations

Aboveground carbon was estimated for the tree, shrub, litter, deadwood, and herbaceous pools. Tree and shrub biomass was estimated using allometric equations based on Guinea savanna vegetation or African savanna types with similar climatic conditions.

Tree biomass was estimated using the dbh following Brown (1997).

$$\text{Tree biomass (kg)} = \text{Exp}(-1.996 + 2.32 \times \ln(\text{dbh (cm)})).$$

Shrub biomass was estimated using the diameter at the stem base and total shrub height derived from Guy (1981).

$$\text{Shrub biomass (kg)} = \left(\text{basal diameter (cm)}^2 \times \text{height (m)}\right)^{0.7839} \times 0.0890.$$

The volume of deadwood was obtained using the formula of a cylinder, then its biomass was calculated as the product of volume and decay class-specific density (Harmon et al., 1995). Following Pfeifer et al. (2015), all sampled wood debris was defined in decay class number (3). Carbon storage across aboveground plant pools (trees, shrubs, deadwood, herbaceous layer, and litter) was calculated by assuming biomass comprised 50% carbon, although tropical tree and deadwood carbon contents may be fractionally lower (Martin et al., 2021; Martin & Thomas, 2011).

Belowground carbon storage was calculated for each layer by multiplying bulk density (dry mass per unit volume adjusting for stone content mass and volume; Appendix S1: Table S2) by elemental-analyzer-corrected carbon percentage and the depth of the layer. Finally, ecosystem carbon was calculated as the sum of aboveground and belowground carbon storage. Aboveground, belowground, and ecosystem carbon are expressed as kilograms of carbon per square meter.

Statistical analysis

Linear mixed-effect models were used to assess the impact of burn season and history on aboveground and belowground carbon storage in separate models by assuming a Gaussian distribution. For aboveground carbon storage, burn season and history, plant pool (trees, shrubs, herbaceous layer, litter, and deadwood), and burn season and history nested within plant pool were fixed factors in the model. The random component was generated through spatial cluster analysis of site locations, grouping sites within 10 km of one another, which resulted in five clusters. To compile with homoscedasticity of residuals, all aboveground carbon pool data were transformed by the power of 0.2. For the belowground carbon model, we adopted the same model design with the difference of using soil layer (0–2, 2–7, 7–12, and 12–17 cm) as fixed term rather than aboveground carbon pool. No data transformation was required when analyzing belowground carbon. The overall significance of factors in our models, namely, burn season and history, plant pool, soil layer, and nested terms, were obtained by comparing Akaike information criterion values via the likelihood ratio test and contrasting models with and without these fixed factors to generate p values (Bolker et al., 2009; Zuur et al., 2009). Significant differences ($p < 0.05$) in burn season and history, plant pools, and soil layers within terms and interactions were obtained through multiple contrasts as a function of least-square means (Lenth, 2016). Ecosystem C storage (aboveground plus belowground) was analyzed using a linear model with differences in burn season and history determined via post hoc Tukey's honestly significant difference test using a significance threshold $p < 0.05$. All analyses were carried out in R statistical software v4.0.2 (R Core Team, 2020) using the linear mixed-effect and generalized mixed-effect functions "glmm" in the "glmmTMB" package (Brooks et al., 2017) and "lmer" in the "lme4" package (Bates et al., 2015). All results are presented as mean $\pm$ 1 SD unless otherwise stated.

RESULTS

Status of burn season and history across Mole National Park

Early-season burns were the most common fire management strategy applied throughout Mole National Park. Approximately 79% of the park area had experienced an early-season burn between 2000 and 2015 (Figure 1c). Late-season burns were less common, occurring in 31% of the total park area (Figure 1b). In the last three burn years, 31% of the park area experienced an early-season burn, whereas only 3% of the park had experienced a late-season burn in the last four burn years. Approximately 13% of the park had not burned for more than 15 burn years according to the MODIS data.

Impacts of burn season and history on aboveground carbon storage

Long-unburned savanna sites had numerically higher aboveground carbon storage 4.0 $\pm$ 2.8 kg C m^{-2}, followed by recent early-season burns 2.8 $\pm$ 0.9 kg C m^{-2}, old late-season burns 2.4 $\pm$ 1.8 kg C m^{-2}, and then recent late-season burns 2.2 $\pm$ 0.4 kg C m^{-2} (Figure 2). However, there was no significant difference in aboveground carbon storage across burn seasons and histories (Table 1). The only aboveground plant pool to significantly differ across burn seasons and histories was tree carbon, which was significantly higher in long-unburned sites compared with recent late-season burn sites (Figure 3; Table 1). This difference was largely driven by two long-unburned sites that had above 200 trees ha^{-1} compared with the site average of 76 trees ha^{-1} across burn seasons and histories. Except for long-unburned sites, carbon stored in shrubs was the largest aboveground carbon, comprising between 36% and 80% of total aboveground carbon across burn histories, followed by trees at 15%–59% and all other pools accounted for <3% aboveground carbon (Figure 2).

Impacts of burn season and history on soil carbon storage

Recent late-season burns had significantly lower belowground carbon storage compared with other burn seasons and histories (Table 2). Belowground carbon was 1.2 kg C m^{-2} or 27% lower in recent late-season burns compared with early-season burn sites. In recent late-season burn sites, belowground carbon storage averaged 2.8 $\pm$ 0.9 kg C m^{-2}, compared with

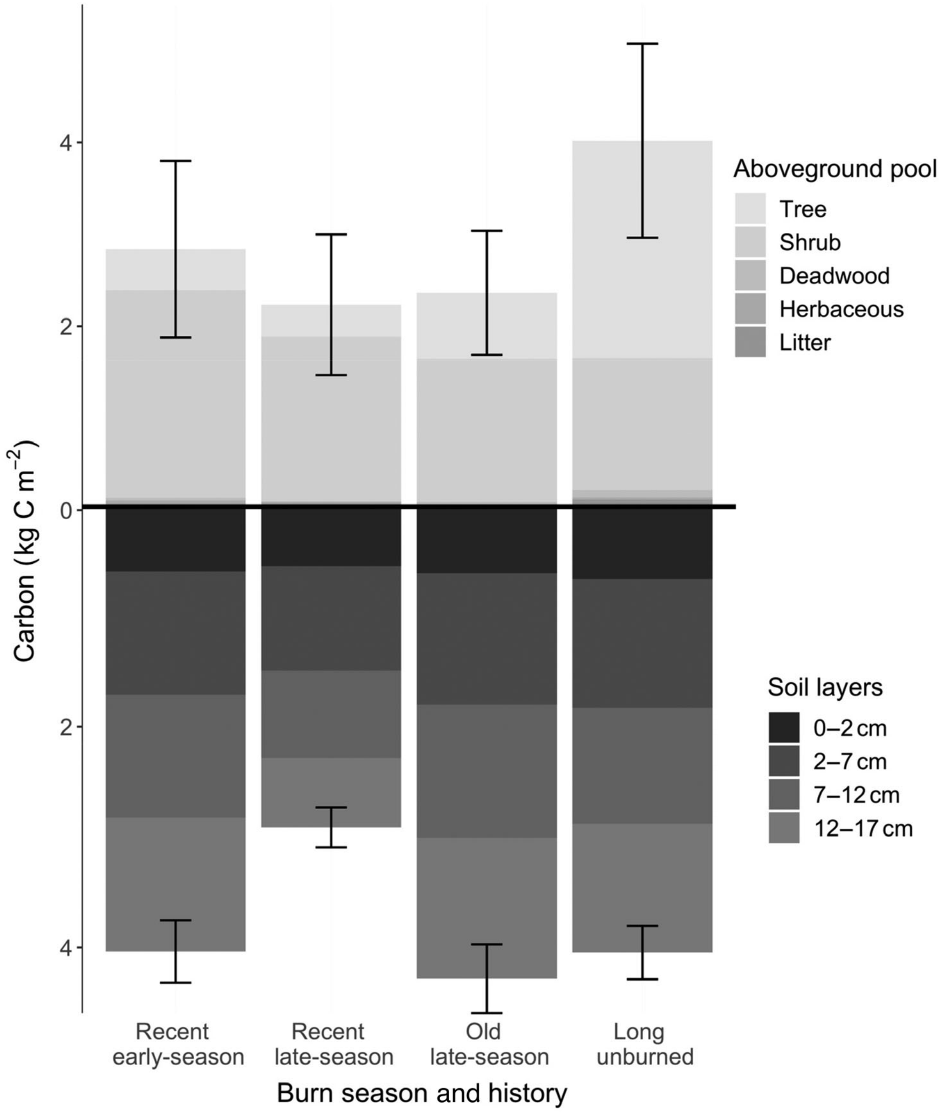

FIGURE 2 Ecosystem carbon storage (in kilograms of carbon per square meter) for four savanna burn seasons and history types in a Guinea savanna across Mole National Park, Ghana. The zero line on the *y*-axis separates aboveground and belowground carbon pools. Aboveground deadwood, herbaceous, and litter carbon pools are present, but small, and can be seen in more detail in Figure 3. Error bars are for total aboveground and belowground carbon storage ($\pm$1 SD).

3.9 ± 0.8 kg C m^{-2} in recent early-season burns and then 4.0 ± 1.0 kg C m^{-2} in long-unburned sites and 4.1 ± 0.9 kg C m^{-2} in old late-season sites (Figure 2).

The greatest difference in belowground carbon between burn seasons and histories was in the deepest 12–17-cm soil layer, which had significantly lower carbon in recent late-season burns than the same soil layer in all other burn seasons and histories (Figure 4). For the other soil layers, there was no statistical difference between burn seasons and histories (Table 2; Figure 4). Except for the 0–2-cm soil layer due to a smaller volume for this layer, all soil layers did not significantly differ from one another (Table 2). Old late-season burns varied from 4 to 13 burn years (fires in the years 2012, 2010, 2004, and 2003; ranging from 1639 to 4903 days since last fire) since the sites with the last fire; of these older burn histories, >12 burn years (4563 days) had on average 6.1% higher soil carbon storage across soil layers than the late-season burn sites from 4 to 6 burn years ago (1639–2703 days).

Ecosystem carbon storage

Recent late-season burns had significantly ($p = 0.015$) lower ecosystem carbon than long-unburned sites, whereas the other burn seasons and histories did not differ (linear model: $F_{3,24} = 2.3$, $p = 0.103$) (Figure 2).

TABLE 1 Statistical output for modeling burn season and history, plant pool, and burn season and history nested within plant pool differences in aboveground carbon storage (mean ± SE).

Term	Factor	Carbon (kg m^{-2})	*p*
Intercept	…	0.45 ± 0.07	…
Burn season and history	Old late	0.02 ± 0.1	0.596
Burn season and history	Recent early	0.08 ± 0.1	0.934
Burn season and history	Recent late	0.03 ± 0.1	0.397
Plant pool	Deadwood	**−0.25 ± 0.1**	**<0.001**
Plant pool	Litter	0.19 ± 0.1	0.498
Plant pool	Shrub	**0.6 ± 0.1**	**<0.001**
Plant pool	Tree	**0.61 ± 0.1**	**<0.001**
Plant pool/burn season and history	Old late—deadwood	0.04 ± 0.14	0.917
Plant pool/burn season and history	Recent early—deadwood	−0.07 ± 0.14	1.000
Plant pool/burn season and history	Recent late—deadwood	−0.13 ± 0.14	0.718
Plant pool/burn season and history	Old late—litter	−0.18 ± 0.14	0.430
Plant pool/burn season and history	Recent early—litter	−0.16 ± 0.14	0.835
Plant pool/burn season and history	Recent late—litter	−0.11 ± 0.14	0.855
Plant pool/burn season and history	Old late—shrub	−0.06 ± 0.14	0.984
Plant pool/burn season and history	Recent early—shrub	0.03 ± 0.14	0.725
Plant pool/burn season and history	Recent late—shrub	0.01 ± 0.14	0.985
Plant pool/burn season and history	Old late—tree	−0.28 ± 0.14	0.062
Plant pool/burn season and history	Recent early—tree	−0.34 ± 0.14	0.053
Plant pool/burn season and history	Recent late—tree	**−0.33 ± 0.14**	**0.018**

Note: Long-unburned sites and herbaceous vegetation pools were used as reference levels in the model. The *p* values were generated from multiple contrasts and significant differences appear in boldface.

DISCUSSION

Our study sits within a protected savanna where national park managers undertake considerable effort to ensure prescribed burns occur at the earliest opportunity in the growing season to reduce the risk of late-growing-season wildfires. Despite these efforts, late-season wildfires still occur within the park and we show that they can substantially reduce belowground carbon storage compared with early-season burning in the short-term. Although a sizeable quantity, this loss of belowground carbon was "recovered" between 4 and 13 burn years when compared with late-season sites that historically experienced wildfires. Tropical West African forested ecosystems are productive, but have a low soil carbon density (Moore et al., 2018). Our findings agree with a long-term pan-West African analyses showing soil carbon can recover in less than a decade following human disturbance such as forest clearance (Poorter et al., 2021). Specifically, for fire disturbances, our study raises questions surrounding the mechanisms that might govern loss and subsequent gain of belowground carbon following late-season wildfires.

Fires combust plant biomass and our finding of lower aboveground tree carbon in recent late-season wildfires compared with long-unburned sites is consistent with observations in other savannas (Coetsee et al., 2010; Higgins et al., 2000; Pellegrini, Hobbie, et al., 2020). The response of soil carbon to fire can be highly variable and this has been attributed to differing mechanisms. High-intensity fires can combust soil organic matter, yet sufficient temperatures are only found in the top couple of centimeters of soil (González-Pérez et al., 2004), and we found no difference in soil carbon for the uppermost 0–2-cm layer between late-season and other burn seasons and histories. Instead, we found a significant difference in belowground carbon at a depth of 12–17 cm. At this depth, a more plausible mechanism for reduced belowground carbon could be root turnover. In temperate savannas, root biomass declined by 39% with more frequent burning in the upper 20 cm of soil (Pellegrini, McLauchlan, et al., 2020). The region of 10–20 cm below the soil surface is also usually the densest rooting zone of tropical savannas (McNaughton et al., 1998; Pandey & Singh, 1992).

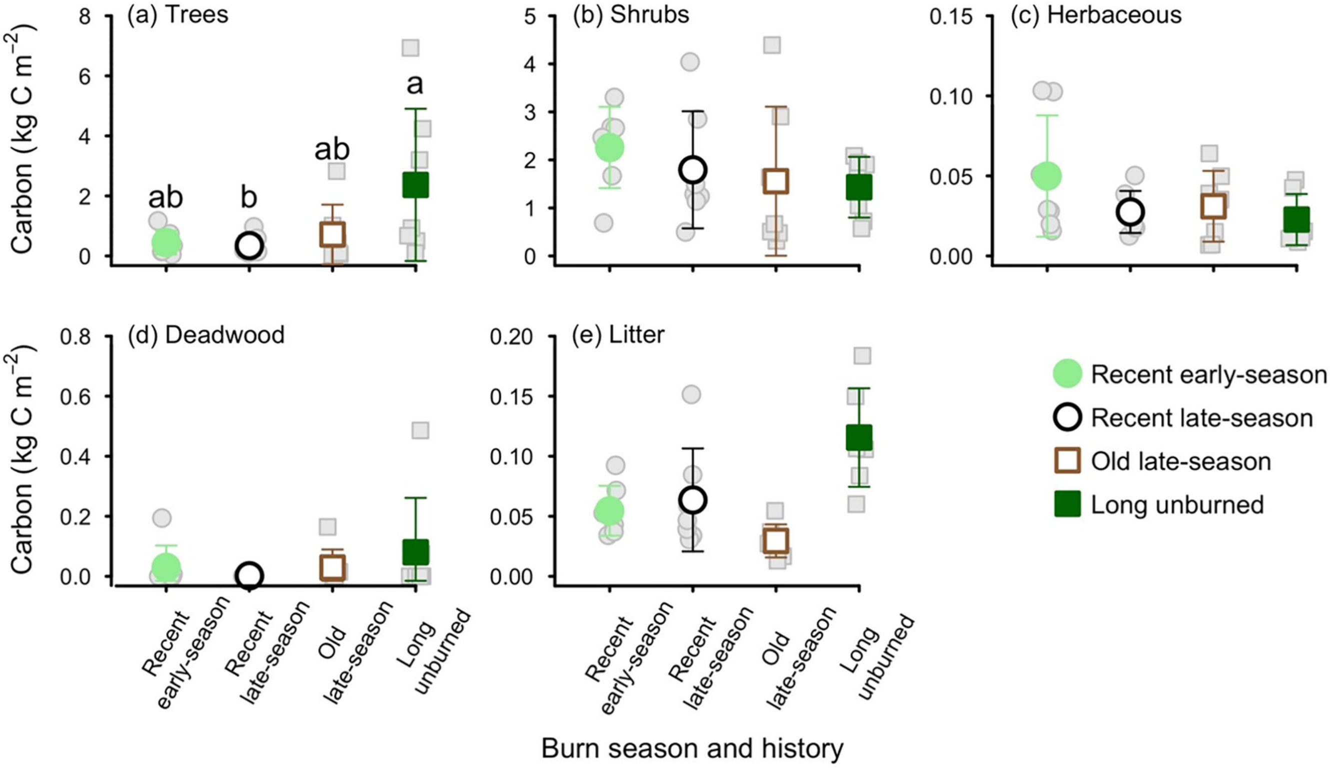

FIGURE 3 Savanna aboveground plant carbon storage (in kilograms of carbon per square meter) for (a) trees, (b) shrubs, (c) herbaceous layer, (d) deadwood, and (e) litter across four fire histories. Differences in lettering above the fire history denote significant differences following least squares means ($p < 0.05$) and all error bars ±1 SD.

TABLE 2 Statistical output for modeling burn season and history, soil layer, and burn season and history nested within soil layer differences in belowground carbon storage (mean ± SE).

Term	Factor	Carbon (kg m^{-2})	p
Intercept	…	0.66 ± 0.11	…
Burn season and history	Old late	−0.06 ± 0.16	0.930
Burn season and history	Recent early	−0.07 ± 0.15	1.000
Burn season and history	Recent late	**−0.12 ± 0.15**	**0.033**
Layer	2–7 cm	**0.51 ± 0.15**	**<0.0001**
Layer	7–12 cm	**0.39 ± 0.15**	**<0.0001**
Layer	12–17 cm	**0.51 ± 0.15**	**<0.0001**
Layer/burn season and history	Old late—layer 2–7 cm	0.1 ± 0.23	0.996
Layer/burn season and history	Recent early—layer 2–7 cm	0.02 ± 0.22	0.989
Layer/burn season and history	Recent late—layer 2–7 cm	−0.11 ± 0.22	0.515
Layer/burn season and history	Old late—layer 7–12 cm	0.22 ± 0.23	0.803
Layer/burn season and history	Recent early—layer 7–12 cm	0.13 ± 0.22	0.981
Layer/burn season and history	Recent late—layer 7–12 cm	**−0.13 ± 0.22**	0.419
Layer/burn season and history	Old late—layer 12–17 cm	0.17 ± 0.23	0.920
Layer/burn season and history	Recent early—layer 12–17 cm	0.11 ± 0.22	0.993
Layer/burn season and history	Recent late—layer 12–17 cm	**−0.42 ± 0.22**	**0.010**

Note: Long-unburned sites and surface 0–2-cm layers were used as reference levels in the model. The p values were generated from multiple contrasts and significant differences appear in boldface.

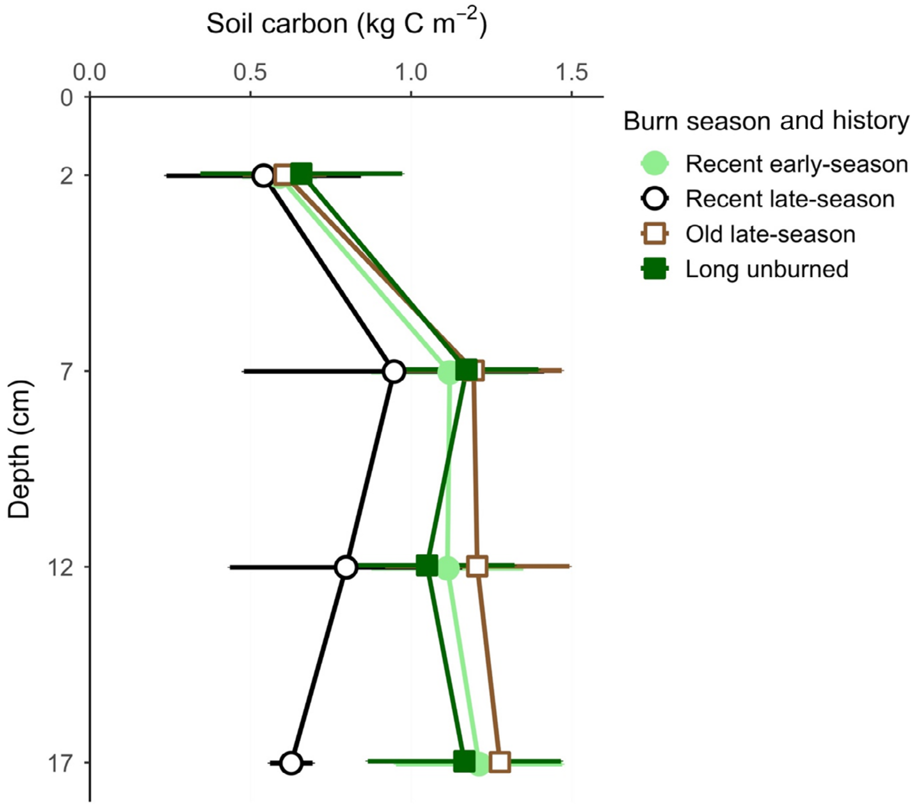

FIGURE 4 Soil carbon storage (in kilograms of carbon per square meter) underneath four fire histories is subdivided into four layers. Soil from the topmost layer 0–2 cm was less thick than others. All error bars ±1 SD.

The "recovery" of belowground carbon in old late-season burns in our study could equally be attributed to root production and turnover. In a Guinean wooded savanna, annual root production has been estimated to be 0.36 kg C m^{-2} $year^{-1}$ in the upper 30 cm of the soil profile (Moore et al., 2018). Such quantities would be comparable to our findings when summed up over 4–13 burn-year timeframe with the expectation that half of the root carbon is lost due to microbial and soil faunal decomposition (Smith et al., 2019). Root production can also increase postfire with studies finding that fine-root growth increased by 25% compared with unburned controls after four burn years (Johnson & Matchett, 2001). While this belowground input-based interpretation of our findings may serve as a plausible explanation, fires influence plant–soil processes that stabilize soil carbon (Pellegrini et al., 2022). For example, we did not account for soil properties, such as soil texture and the formation of mineral-organic complexes that could account for some of the variations in soil carbon between burn seasons and histories (Bird et al., 2000). Nevertheless, our findings point toward belowground plant input or process mechanism, rather than changes in aboveground carbon, in determining losses and gains of belowground carbon storage following late-season wildfires.

Across the West African wet-to-mesic savannas there is a trend of early-season burns (Laris et al., 2016; Le Page et al., 2010), to which management of Mole National Park adheres (Sackey et al., 2012; Sackey & Hale, 2008). Generally, early-season burning is being prompted to reduce greenhouse gas emissions in savannas compared with burning later in the growing season (Lipsett-Moore et al., 2018; Russell-Smith et al., 2003). Despite the shorter recovery time (in days) of recent early-season burns compared with recent late-season wildfires in our study, we show recent early-season burns have limited impact on carbon stocks compared with long-unburned patches. Nevertheless, it is worth noting the high heterogeneity in aboveground carbon, particularly for long-unburned patches that may include unproductive sites where fires are less common due to insufficient aboveground biomass. At a landscape-scale, prescribed early-season burns will result in unburned patches that either later become late-season wildfires or remain unburned for longer. However, our results show that even if these unburned patches become late-growing season wildfires, they will not represent a long-term loss of carbon storage due to the high rate of recovery of carbon stocks.

CONCLUSION

Fire management in protected areas serves several purposes, including managing woody cover, controlling disease vectors, improving forage quality, enhancing species diversity, and mitigating the spread of invasive aliens or problematic native species (Anderson et al., 2018; Bukombe et al., 2018; Nieman et al., 2021). The impact of carbon storage studied here, and related greenhouse gas emissions, is one facet of prescribed burning practices that should be balanced against the other impacts of fires. Our study affirms that early-season burning offers an approach to control fire outbreaks without creating significant physical carbon losses (Russell-Smith et al., 2021). Early-season burning generates a patch-mosaicked landscape where unburned patches are potentially vulnerable to significant carbon losses as late-season wildfires. Fortunately, carbon stocks depleted by late-season wildfires return within 4–13 years, likely due to root production and turnover. Habitat heterogeneity generated by patch-mosaic burns, or pyrodiversity, benefits plant, mammal, and bird species diversity (Beale et al., 2018; Martin & Sapsis, 1992). Given the carbon recovery of late-season wildfire, on balance our study suggests that early-season burning represents a low risk to physical carbon loss, while at the same time maintaining a heterogeneous patch-mosaicked landscape that provides multiple other ecosystem functions and service benefits for savannas.

AUTHOR CONTRIBUTIONS

Joana Awuah, James D. M. Speed, and Bente J. Graae conceived and designed the study. Joana Awuah collected the data. Stuart W. Smith analyzed the data and wrote the first draft of the manuscript and all authors contributed critically to drafts and gave final approval for publication.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data (Awuah et al., 2022) are available from Zenodo: https://doi.org/10.5281/zenodo.6855425.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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