

## RESEARCH ARTICLE

# Effect of fire timing on the regeneration capacity of *Helichrysum* species in Tanzania

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**Abstract**

1. Shrub encroachment poses a significant challenge in many grassland ecosystems, particularly where disturbances such as heavy livestock grazing and uncontrolled fires are prevalent. Fire is frequently employed as a management tool to mitigate shrub encroachment and preserve native vegetation, as it influences both resprouting and seed germination. However, few studies have examined the effects of fire timing on resprouting and seed germination both in the field and *ex situ*.
2. We investigated the resprouting ability of *Helichrysum* shrubs after being completely, partially or not at all burned. In addition, we collected soil seed bank samples from each early burned, late burned and unburned area at depths of 0–2, 2–4 and 4–6 cm to assess plant species recruitment via seedlings. The data were analysed using a generalized linear regression model with a Gaussian link function.
3. We found significant differences in the number of resprouts and seedling abundance across early burned, late burned and unburned sites. Resprouting of both partially burned and completely burned shrubs was more abundant compared to unburned shrubs. The surface soil in unburned sites contained a greater abundance of *Helichrysum* seedlings compared to that of burned sites, suggesting that fire negatively affects seed germination, particularly in the upper soil layers. Overall seedling recruitment was lower in early and late burned areas, whereas resprouting was higher in areas burned later in the season.
4. *Practical implication.* The findings highlight the significance of fire timing in grassland management. We advocate for the implementation of planned early burning to mitigate shrub encroachment, promote biodiversity and save ecologically sensitive grasslands.

**KEYWORDS**

grassland, late burn, prescribed fire, resprouting, seed bank, shrub, soil, wildfire

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## 1 | INTRODUCTION

Secondary successional shrub encroachment is a prevalent issue in most grassland ecosystems where previous disturbances have ceased (Stankeva Terziyska et al., 2020). The primary drivers of shrub encroachment are changes in fire and grazing regimes (Mapiye et al., 2008). The expansion of shrubs into grasslands displaces native herbaceous species due to competition for light, moisture and nutrients (Manish et al., 2016; Ruprecht et al., 2015). This encroachment raises significant ecological conservation concerns (Pornaro et al., 2017), particularly in protected areas and regions with high plant species diversity and endemism (Guido et al., 2017).

In eastern Africa, fire has been used for over decades as a management tool to preserve grassland ecosystems by controlling shrub encroachment (Nyakunga et al., 2018). Prescribed fires (early burning) are typically conducted at the onset of the dry season when some grasses and herbs are still green and the soil retains adequate moisture. These conditions result in relatively cool fires (Bloesch, 1999). In contrast, high-temperature wildfires, often uncontrolled, usually occur in the late dry season when plant moisture levels are low and this phenomenon is referred to as 'late burning' (Bloesch, 1999; Govender et al., 2006; Tangney et al., 2022).

Different plant species vary in their response when exposed to different fire regimes (Drewa et al., 2002). In fire-prone environments, plants survive through either recruitment from soil seed banks or through resprouting (post-fire obligate resprouters) to sustain their populations (Luo et al., 2022). Obligate resprouters depend on resprouting to persist after a fire event has destroyed their seeds (Marais et al., 2014). In contrast, obligate seeders perish following a fire but can regenerate exclusively from seeds stored in the soil (Prior & Bowman, 2020), making seed regeneration their only means of survival (Tangney et al., 2022). Facultative seeders and facultative resprouters can recruit from both seeds and resprout after a fire (Luo et al., 2022). Some post-fire obligate resprouters manage to survive the fire and regenerate from above- or below-ground bud banks (Clarke et al., 2013), making seed regeneration their only means of survival (Tangney et al., 2022). Belowground structures such as lignotubers and roots play a crucial role in storing non-structural carbohydrates, sugars and nutrients, which facilitate resprouting after a fire (Clarke et al., 2013). However, the capacity for resprouting after a fire is also influenced by the frequency and severity of fires (Martínková et al., 2004). When aboveground parts of a plant are damaged or removed, dormant buds or meristematic tissues located in belowground organs are activated to produce new shoots and leaves (Thomsen & Ooi, 2022). Factors contributing to this resprouting response include bud activation and the availability of stored resources. Resprouting species exhibit greater resilience to hot fires compared to reseeded species (Bennett et al., 2016). Fire timing influences the resprouting vigour of plants (Thomsen & Ooi, 2022), with high fire temperatures impairing seed germination while low fire temperatures generally promoting resprouting.

Fire management is used in many National Parks to suppress encroaching shrub or woody species (Brancatelli et al., 2024;

Ling et al., 2023). This shrub encroachment has also been observed in Kitulo National Park (KNP) in Tanzania (URT, 2010), a park renowned for its high floristic diversity and home to over 85 species of grassland-dwelling terrestrial edible orchids (Davenport & Marques, 2018; Davenport & Ndalagasi, 2003; Veldman et al., 2018). This encroachment is a potential threat to these orchids (Ndaki et al., 2021), as most species prefer open grassland habitats and may be adversely affected by the encroachment (Martín-Forés et al., 2022; Slaviero et al., 2016; Vogt-Schilb et al., 2015). Prescribed fires and wildfires have been occurring in KNP for over a decade with the aim to prevent destructive wildfires (Mwinuka & Mushi, pers. comm) but the timing of fires has been rather random or neglected in the management approaches. However, as fire timing often determines fire heat but also affects plants in different phenological stages (Richardson & Wagenius, 2022), timing might have quite severe consequences on which plant species can survive the fire events. In this study, 'late burning' refers to wildfires and 'early burning' denotes prescribed fires. Late burning typically occurs in warmer or drier seasons when organic materials are dry, resulting in high-intensity fires of hot temperatures (Mackenzie et al., 2021). In contrast, early burning occurs at the onset of the dry season when some grasses and herbs are still green and the soil retains adequate moisture.

One of the encroaching species reported in the KNP is *Helichrysum splendidum*, which was most dominant over other *Helichrysum* species (Mgimba et al., 2024). This species can be propagated both through seeds and by cuttings (Giovannini et al., 2008), while other *Helichrysum* species can resprout from roots (Makena et al., 2023). *Helichrysum foetidum* (L.) Moench, *Helichrysum aureonitens* Sch. Bip. and *Helichrysum vestitum* regenerate through resprouting and are fire-ephemeral and sclerophyllous, with seed germination being facilitated by fire (Afolayan et al., 1997; Brown, 1992; Riveiro et al., 2019). Studies have shown that seeds of *Helichrysum cassianum* and *Helichrysum odoratissimum* germinate optimally at air temperatures between 15 and 20°C (Makena et al., 2023; Mott, 1974). On the other hand, a study on the effect of fire on the persistence strategy of *Helichrysum trilineatum* indicated that this species has high resprouting vigour after fire (Kraaij et al., 2017). Up to now, information on resprouting potential has inadequately been explored on *Helichrysum splendidum*, which is dominant in the study area. Further, although several studies have investigated the effect of fire temperature on the seed germination of various *Helichrysum* species (Afolayan et al., 1997; Giovannini et al., 2008; Makena et al., 2023; Mott, 1972; Riveiro et al., 2019), few have explored the effect of fire occurrence on the *Helichrysum* seed bank in the soil (Wube et al., 2021). We hypothesised that the extent of fire scorching of the *Helichrysum* stems has an effect on their regeneration through resprouting. We also hypothesised that late burning inhibits the regeneration of *Helichrysum* species through seedling recruitment. To test these hypotheses, we conducted an observational study on *Helichrysum* shrubs under fire occurrence in KNP, Tanzania. Our findings will help us understand how fire management affects *Helichrysum* spp. encroachment in grassland systems and provide advice on the timing of fire events.

## 2 | MATERIALS AND METHODS

### 2.1 | Study plant species description

The species identified in KNP were *Helichrysum splendidum*, *Helichrysum odoratissimum*, *Helichrysum forskahlii* and *Helichrysum kirkii* (Mgimba et al., 2024; Table 1).

*Helichrysum* species produce lightweight seeds that are easily dispersed by wind (Chengere et al., 2023). Although a significant portion of the seed bank is located in the surface soil, the density and viability of seeds decrease with increasing soil depth (Wakshum et al., 2018). The vertical distribution of the soil seed bank is influenced by various factors, including soil type, seed size and seed shape (Csontos, 2007). For instance, larger seeds are less likely to penetrate deeper soil layers through movement along fractures or burial by soil-dwelling animals, compared to smaller seeds (Birhanu et al., 2022). Additionally, plant species with seeds that exhibit greater longevity can persist in deeper soil layers (Wakshum et al., 2018). Fires, in addition, have a greater heat effect in soils closer to the surface than deep into the soil (Badía et al., 2017) because soil is a poor conductor of heat (DeBano, 2000). Understanding the impact of fire on *Helichrysum* species is essential for the ecological management, particularly in the National Park grasslands of Tanzania, where *Helichrysum* shrubs are expanding.

### 2.2 | Study area description

The study was conducted in KNP, located in the Southern highlands of Tanzania (09°09'15" S and 33°57'05" E; Figure 1). The park encompasses a plateau at an elevation of 2500 m a.s.l (Lovett & Prins, 1994; URT, 2010) and is characterized by montane grasslands (Nyomora, 2009). The summer period (November–April) is the rainy season, with average annual rainfall ranging from 1500 to 2900 mm and average temperatures of approximately 18°C (Davenport & Marques, 2018). The winter season (May–October) is dry, with average temperatures of approximately 15°C (URT, 2010). Significant temperature fluctuations occur during

winter, with nighttime temperatures occasionally dropping below 0°C (URT, 2020).

Prior to 1965, the grasslands within KNP ecosystem were utilized by local communities for livestock grazing and the cultivation of crops such as *Tanacetum cinerariifolium* (pyrethrum), *Solanum tuberosum* L. (Irish potatoes) and *Triticum aestivum* L. (wheat) (Lovett & Prins, 1994). Commercial cereal and sheep production were phased out in 1968 and 1973, respectively (Lovett & Prins, 1994). Subsequently, only commercial dairy and small-scale crop production continued until the declaration of KNP as a national park in 2005 (Mwinuka and Mushi, pers. comm.).

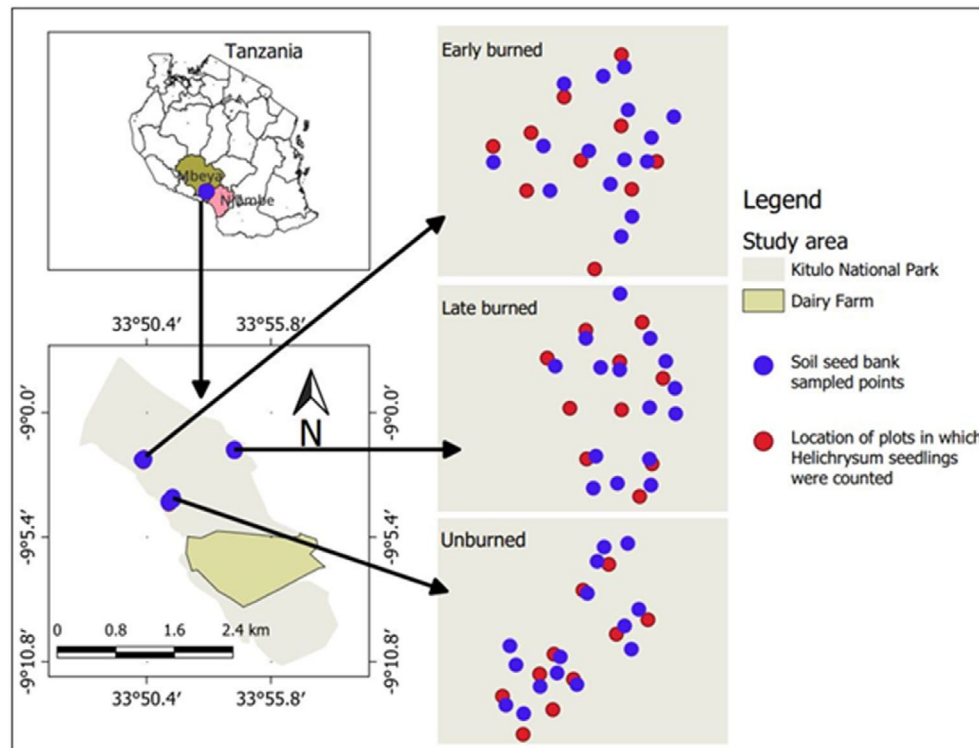
Early fire occurs in KNP occasionally in early June, as prescribed by the management and the wildfires occur occasionally throughout the year but mainly between late August to October. The early fire occurs when vegetation is still green; thus, these fire events are of rather low temperature and low intensity due to the fact that part of the energy released is used to evaporate the remaining humidity of the vegetation (Bloesch, 1999). In contrast, the late fire events are of high temperature and intensity due to the dry organic material which adds to the fuel loads (Bloesch, 1999; Govender et al., 2006).

### 2.3 | Impact of fire on the resprouting of *Helichrysum* individuals

To investigate the impact of fire on the resprouting of *Helichrysum* spp., three 50×50 m plots, set 300 m apart, were permanently marked within an area dominated by *Helichrysum* spp. This site had experienced late burning for two consecutive years, meaning it experienced hot fires as dry vegetation burned readily. The site was late burned again in September 2021, and assessments of resprouting commenced 2 months later, in November 2021. Within each plot, any *Helichrysum* individuals we could identify were categorized based on the extent of fire damage (Morrison, 2002; Vesik & Westoby, 2004). A *Helichrysum* individual was defined as a single rhizome, from which multiple stems may arise (Pljevljakušić et al., 2018). We could not identify all *Helichrysum* species down to species level

**TABLE 1** Ecological description of *Helichrysum* species identified in Kitulo National Park during a field survey in 2022 (Mgimba et al., 2024). Facultative resprouter refers to the characteristic of plants capable of germinating and resprouting after fire (Pausas & Keeley, 2014; Quevedo et al., 2011).

Species	Life form	Regeneration	Anatomy	Reference
<i>H. forskahlii</i>	Perennial herb or shrub	Facultative resprouter	Woody stem, numerous branches	Beentje (2002), Makena et al. (2023)
<i>H. odoratissimum</i>	Perennial herb	Facultative resprouter	Woody stem, erect or sprawling, often with multiple branches	Serabele et al. (2023), Makena et al. (2023)
<i>H. kirkii</i>	Perennial herb	Facultative resprouter	Several erect stems, with simple or few branches, dense leaf cover	Beentje (2000)
<i>H. splendidum</i>	Perennial shrub	Facultative resprouter	Tall, with branches bearing thinly grey woolly leaves	Roux (2003), Steger et al. (2022)



**FIGURE 1** A map depicting unburned, early burned and late burned sites in Kitulo National Park, where soil seed bank samples were collected and newly emerging *Helichrysum* spp. seedlings were observed in the year 2021. The map also indicates the sites where the resprouting of mature *Helichrysum* individuals was monitored among unburned, partially burned and completely burned plots in the year 2021.

in the assessment of the effect of fire because the four major species that we had identified in an earlier study (Mgimba et al., 2024) were often found coexisting. Their similar phenology at the seedling stage also made identification challenging. The categories we assessed included partially burned, encompassing individuals with fewer than 50% of stems scorched; completely burned, comprising individuals with over 0% of stems scorched and unburned, consisting of individuals that were not scorched. In each category, 10 individuals per plot were sampled ( $N=90$ ). For each sampled individual, any surviving shoots were marked with tape, and the number of resprouts was recorded monthly over a 5-month period, from November 2021 to March 2022.

## 2.4 | Impact of fire on the recruitment of *Helichrysum* seedlings

To evaluate the impact of fire timing on the seeds of *Helichrysum* species, we established sites that had not been burned for more than two consecutive years as observed from remotely sensed fire scar data downloaded (<http://earthexplorer.usgs.gov>). Within these areas, we selected two sites each of 6.7 ha (one for early and the other for late burning), considering that these sites had experienced similar fire occurrences for the past two consecutive years. At each site, ten 5 m × 5 m quadrats dominated by *Helichrysum* spp. were randomly established in February 2022 at a distance of 250 m from one another,  $N=30$  (Guido et al., 2017). The number of *Helichrysum* seedlings were

then recorded in each quadrat. The *Helichrysum* seedlings were defined as young plants <2 cm height (Harris et al., 2022).

## 2.5 | Impact of fire on the soil seed bank of *Helichrysum* species

To understand how the timing of fire events affected the soil seed bank, we collected soil seed bank samples from early burned, late burned and unburned areas (Figure 1). The early burned areas were managed by the Tanzania National Park Authority TANAPA, and the late burned area resulted from accidental wildfires. In each area, we established fifteen 5 m × 5 m quadrats in regions with abundant *Helichrysum* individuals (Guido et al., 2017). We collected the soil sample at three depths: 0–2 cm (surface soil), 2–4 and 4–6 cm (Bekele et al., 2022; Savadogo et al., 2017), taken from the centre and corners of each quadrat, and then combined to form a composite soil sample of approximately 1000 g ( $N=45$ ). The soil samples were dried at 24–27°C for 2 weeks and sieved through a 4 mm sieve to remove debris (Wube et al., 2021). The sieved soil was put in perforated plastic containers placed in an open space and watered every 2 days (Wube et al., 2021). Over a 2-month period, from July 2022 to September 2022, we monitored and identified plant seedling appearance weekly (Harris et al., 2021). Recorded seedlings were discarded to avoid recounting. The *Helichrysum* soil seed bank abundance was estimated based on the cumulative number of emerged seedlings over the entire observation period.

## 2.6 | Statistical analysis

Given that multiple measurements were conducted on the same individual, we included a unique identifier (ID;  $N=10$ ) for each resprout. Resprout ID was nested within the plot ( $N=3$ ) to account for potential differences between experimental plots. We used a generalized linear mixed model with negative binomial (Fahrmeir & Kneib, 2011; Gatecki & Burzykowski, 2013) to compare the total number of resprouts among unburned, partially burned and completely burned shrubs at the end of the experiment (March 2022). Due to strict regulations in the protected area, the fire treatments could not be replicated, resulting in potential issues of pseudo-replication (Hurlbert, 1984). Although the Akaike information criterion (AIC) for the Poisson distribution model was slightly lower than the AIC for the negative binomial dispersion, for both models it was  $>1$  (i.e. 2.6). We assumed that the negative binomial model was more robust than the Poisson model as the former accounts for overdispersion (Hilbe, 2011). We controlled for individual and spatial variation by including resprout ID nested within the plot as a random effect (Fahrmeir & Kneib, 2011). We also illustrated the trend of resprouting under different levels of scorching over time as a possible interaction between fire and month in the model, to investigate whether shrubs affected by different fire treatments generated new resprouts differently over time. We controlled for individual and spatial variation by including the resprout ID nested within the plot as a random effect. To compare the number of *Helichrysum* seeds in the soil seed bank across fire treatments and soil depths, we used a general linear mixed-effects regression model with a negative binomial function (Faraway, 2016) to account for overdispersion, incorporating an interaction between fire treatment and soil layers. Fire timing, soil depth and their interaction were included as fixed effects, while the plot was included as a random factor to control for potential spatial variation between plots.

Finally, we used a general linear mixed-effects regression model with the Poisson link function to compare seedling abundance (count variable) across sites exposed to different fire timing. To account for potential variation within experimental plots and subplots, we included subplots nested within the plot as a random effect. We used R (version 4.1.3) and the vegan package (Sengupta, 2001) for data analysis and Origin Pro software version 2019 (9.65) (Speight, 2005) for plotting graphs.

## 3 | RESULTS

### 3.1 | Regeneration of *Helichrysum* through resprouting after fire events

The mixed-effects model showed that resprouting among *Helichrysum* stems scorched by fire differed significantly. *Helichrysum* individuals that were partially or even completely scorched by fire showed almost twice the regenerative capacity through resprouting than unburned individuals (Table 2; Figure 2A).

**TABLE 2** The results of the generalized mixed model for the effects of partial and complete burning of *Helichrysum* stem on resprouting ability, compared to the unburned stems as observed in the field study within Kitulo National Park from November 2021 to March 2022. We used the unburned results as a reference for comparisons. Complete damage refers to individuals with over 0% of stems scorched, while partial damage means individuals with fewer than 50% of stems scorched.

	Estimate	SE	z	p
(Intercept)	0.475	0.064	7.375	<0.001
Complete damage	0.255	0.086	2.969	0.003
Partial damage	0.222	0.086	2.565	0.010*

\* $p < 0.05$ .

Two months post-fire, the number of resprouts in unburned shrubs was approximately half that in both completely burned and partially burned ( $t=13.0$ ,  $df=58$   $p < 0.001$ ;  $t=10.7$ ,  $p < 0.001$ ,  $df=58$ ; Figure 2A). This proportion remained similar until March, that is, 5 months post-fire, with resprout numbers in unburned shrubs being approximately three times lower than in completely burned shrubs ( $t=-2.4$ ,  $p=0.05$ ,  $df=58$ ; Figure 2B). In December, that is, 3 months after the fire, the mean number of resprouts from completely burned shrubs was approximately four times higher than in unburned shrubs ( $z=5.0$ ,  $p < 0.001$ ). However, the number of new resprouts decreased markedly over time across all treatments (Figure 3).

### 3.2 | *Helichrysum* soil seed bank abundance

The *Helichrysum* seed numbers in soil of unburned sites were twice as high as that in the early burned sites and 10 times higher than in the surface soil layer in late burned sites (Table 3; Figure 4).

Our soil seed bank incubation showed that the number of seeds in soil that had been subjected to early and late burning emerged only in half the cases compared to the ones in unburned soils. This effect was most strongly visible for the seeds in the surface soil layer compared to the deeper soil layers (Table 4). At both early burned and late burned sites, the seed bank abundance per plot (25 m<sup>2</sup>) did not differ significantly across soil depths, except for the unburned site (Figure 5). In the unburned site, the seed bank abundance in the surface soil was almost three times higher than in lower soil depths, with the 2–4 and 4–6 cm layers having nearly equal seed bank abundances (Figure 5).

## 4 | DISCUSSION

### 4.1 | Effect of fire on the resprouting ability of *Helichrysum* species

Contrary to our expectations, we found that completely burned *Helichrysum* shrubs exhibited a greater number of resprouts compared to partially burned and unburned shrubs. We expected that unburned *Helichrysum* plants would demonstrate more

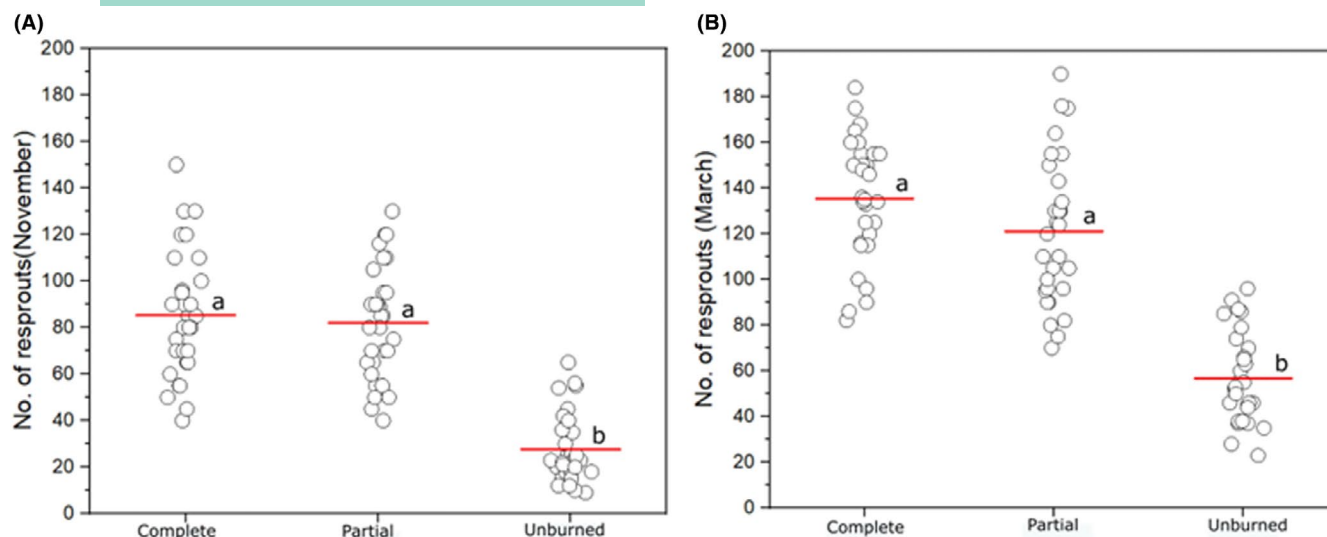


FIGURE 2 The mean (red line) total number of resprouts counted for unburned, partially burned and completely burned *Helichrysum* shrubs at the beginning (November) and the end (March) of the fire experiment (A and B, respectively). 'Complete' referred to plants individuals where over >50% of stems scorched while 'Partial' meant partial damage to individuals where fewer than 50% of stems scorched. Different letters denote groups that are significantly different at  $p < 0.05$  according to Bonferroni's post hoc test.

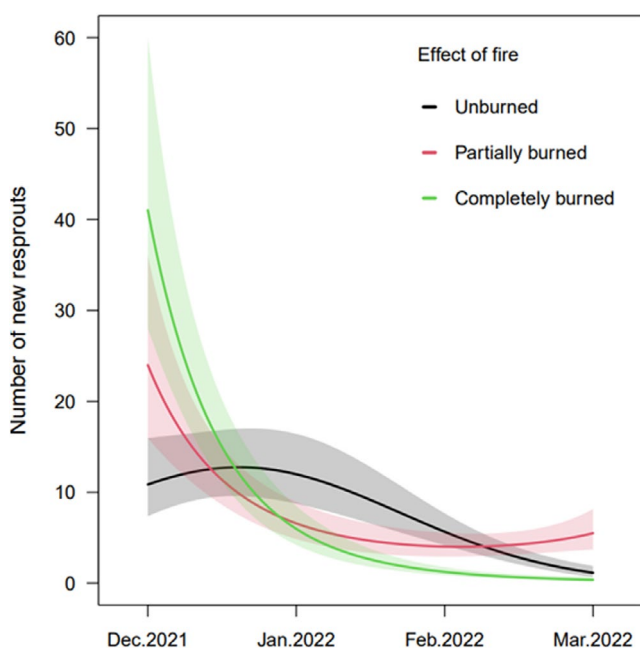


FIGURE 3 The number of new *Helichrysum* species resprouts emerging from unburned, partially burned and completely burned shrubs (see Figure 2 for descriptions of categories) as was monitored from December 2021 to March 2022. The lines represent the predicted response according to our regression model and the shaded area denotes the 95% confidence interval.

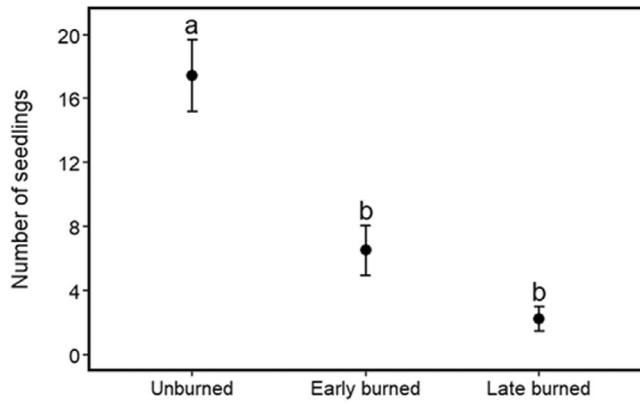
resprouting vigour than burned ones and that complete scorching would result in few or no resprouts as fires strongly suppressed resprouting in other plant species, for example, *Manilkara sansibarensis* and *Baphia kirkii* (Mligo, 2019). Similar to our findings, Strydom et al. (2020) assessed survival and resprouting vigour post-fire in relation to fire severity and found that fire severity had

TABLE 3 The results of the generalized mixed model for the effects of late burning and no burning on the *Helichrysum* seed bank compared to the early burned sites in Kitulo National Park as assessed in 2022. We used the early burned results as a reference for comparisons.

	Estimate	SE	z	p
Intercept	1.828	0.120	15.184	<0.001
Late burned	-1.083	0.142	-7.626	<0.001
Unburned	0.987	0.084	11.787	<0.001

a positive effect on resprouting shoot count of thicket shrubs in South Africa. Further, Schafer and Just (2014) found that 95% of shrubby plants resprouted following complete burning and removal of aboveground biomass in a study in North Carolina. Similarly, woody plant species in prescribed burned and unburned sites revealed higher resprouting abilities in burned than in unburned Mediterranean areas of North East Spain (Quevedo et al., 2007). The removal of aboveground biomass reallocated stored carbohydrates in plant roots towards the production and growth of new stems (Clarke et al., 2013; Diaz-Toribio & Putz, 2021).

Our findings show that the completely scorched stems of *Helichrysum* shrubs had a high abundance of resprouts compared to the partially and unburned stems. While the present study determined the resprouting ability of individuals of *Helichrysum* species that were differently affected by fire, a study by Quevedo et al. (2011) determined the effect of fire regime across different plant species. The findings from the previous study revealed that individuals of *Acer* sp. which were completely burned all of them resprouted, while individuals of *Juniperus communis* and *Juniperus phoenicea* that were less severely burned showed low resprouting ability (Quevedo et al., 2007). Moreover, the findings from the



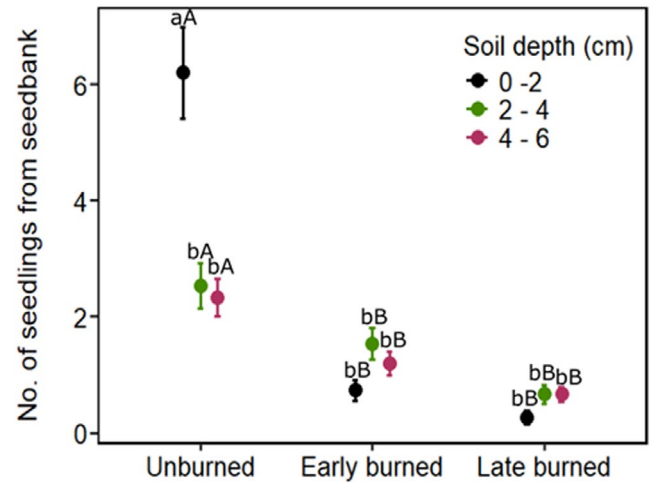
**FIGURE 4** *Helichrysum* seedling numbers that emerged after different fire timings as counted in the field at unburned, early burned (June, 2021) and late burned (September, 2021) sites at Kitulo National Park during our field work. Different letters denote groups that are significantly different at  $p < 0.05$  according to Bonferroni's post hoc test.

**TABLE 4** The statistical comparison of the effect of fire on the *Helichrysum* seed bank abundance across the soil layers (0–2, 2–4 and 4–6 cm) against the seed bank abundance in the surface soil (0–2 cm) from the early burned site. Early burned referred to the burning that occurred at the beginning of the dry season in May and June in 2021, and late burning occurred between August and October 2021.

	Estimate	SE	z	p
(Intercept)	-0.065	0.258	-0.250	0.803
Late burned (0–2 cm)	-1.609	0.632	-2.545	0.011*
Unburned (0–2 cm)	2.425	0.270	8.979	<0.001
Early burned (2–4 cm)	0.065	0.365	0.177	0.860
Late burned (2–4 cm)	-0.852	0.483	-1.763	0.078
Unburned (2–4 cm)	0.615	0.324	1.895	0.058
Early burned (4–6 cm)	-1.034	0.516	-2.002	0.045*
Late burned (4–6 cm)	-1.545	0.632	-2.443	0.015*
Unburned (4–6 cm)	-0.446	0.422	-1.058	0.299

\* $p < 0.05$ .

present study showed that unburned shrubs produced fewer resprouts compared to the complete and partially burned shrubs, likely because they allocated their resources more evenly across both existing old shoots and new resprouts (Clarke et al., 2013; Guo et al., 2022). The strong resprouting capability of completely scorched *Helichrysum* shrubs demonstrates their ability to recuperate despite extreme fire conditions. This compensatory response indicates that these *Helichrysum* shrubs are highly adapted to



**FIGURE 5** Average abundance ( $\pm$ SE) of *Helichrysum* seeds in the soil seed bank at unburned, early burned and late burned sites (see Figure 4 for explanation of categories) at soil depths of 0–2, 2–4 and 4–6 cm, where the soil was collected and propagated ex situ. Different lowercase and uppercase letters denote significant differences in the means of seed bank abundance of *Helichrysum* species across soil depths and within treatments, respectively, at  $p < 0.05$  according to Bonferroni's post hoc test.

fire-prone settings, potentially complicating efforts to manage their expansion. The compensatory growth response of *Helichrysum* following high-intensity fires may promote the proliferation of these species through resprouting, challenging management strategies intended to limit their spread in vulnerable environments. The number of resprouts reached a maximum in December, just 3 months after fire, reflecting the resprouting ability of the shrubs after fire, but then decreased significantly over time. This pattern of resprouting reflects the regeneration trend of facultative resprouters in the fire-prone environment (Underwood et al., 2023). The gradual decline in the number of resprouts over time might be due to the dual allocation of resources between seedling and resprouting establishment, which is a common phenomenon in the facultative resprouters (Paula & Ojeda, 2006).

#### 4.2 | Effect of fire on the regeneration of *Helichrysum* species soil seed bank

The late and early burned areas exhibited low levels of seedling recruitment compared to the unburned areas. This finding aligns with studies conducted in other regions (Cury et al., 2020; Lipoma et al., 2018; Shi et al., 2022), which reported that unburned sites exhibited the highest levels of seedling recruitment from the soil seed bank, with a decrease in recruitment at greater soil depths. This finding suggests that *Helichrysum* seeds lack a protective mechanism against fire, unlike other shrubby species such as *Erica coccinea* L. subsp. *Coccinea* (Bell & Ojeda, 1999). According to Steger et al. (2022), the papery texture of *Helichrysum* seeds indicates their primary presence in surface soil, rendering them vulnerable

to fire damage. Therefore, late burning can effectively reduce the *Helichrysum* encroachment as most of the *Helichrysum* seeds are vulnerable to destruction by fire.

### 4.3 | Effect of late and early burning on the regeneration of *Helichrysum* through seedlings across soil depth

We found that the impact of fire on seeds diminishes at soil depths greater than 2 cm, which confirms that soil temperatures likely decrease with increasing depth during a fire (Afolayan et al., 1997; Williams et al., 2004; Xu et al., 2022). Another study on the effect of fire on seed germination showed that while an intermediate heat level of 110°C reduces seed germination of *Daucus carota* L, the same heat intensity increases *Helichrysum foetidum* (L.) Moench and *Oenothera glazioviana* Micheli seed germination (Riveiro et al., 2019).

We conclude that fire might negatively affect seed germination and establishment of *Helichrysum* species in both early and late burned areas. However, we also point out that established *Helichrysum* stands are likely resilient to fire and can resprout post-fire, potentially producing multiple new stems, even in late burned sites. Although this study covered only a short period of time following the fire, it provides valuable insights into the effects of fire on *Helichrysum* regeneration, an area that so far shows limited empirical studies. Most existing literature on the genus *Helichrysum* and its fire ecology has focused on controlled environments (Afolayan et al., 1997; Giovannini et al., 2008; Makena et al., 2023; Mott, 1972; Riveiro et al., 2019), while our study included both field observations and ex-situ studies. Our findings provide a further understanding of the potential responses of *Helichrysum* species phenology and population expansions as other species such as *Helichrysum petiolare* and *H. foetidum* have been triggered by wildfire in their expansion into new habitat (Prunera-Olivé et al., 2019). The findings of this study underscore both early and late fire burning as one of the ecological management tools that can inhibit *Helichrysum* shrub encroachment in grassland ecosystems.

## 5 | CONCLUSION

We conclude that both early and late burning can be effective management approaches for inhibiting the expansion of *Helichrysum* shrubs into grasslands, primarily due to the low seed germination we found under fire events. As we reported the highest numbers of *Helichrysum* seeds in the surface soil compared to deeper soil layers, we claim that these seeds will be most susceptible to fire destruction. We propose that both early and late burning reduce the potential for long-term *Helichrysum* shrub encroachment as both burning events negatively affected *Helichrysum* seed germination. However, we also point out that neither early nor late burning might be sufficient to eliminate already established *Helichrysum* shrubs in KNP, since we found the shrubs were rather resilient to fire, particularly through

their resprouting ability. This suggests that fire alone may not suffice as a long-term control strategy for this shrub species. Therefore, we propose that future management strategies should consider both the timing and phenological stage of the encroaching *Helichrysum* plants. Given that this study only covered a 5-month period post-fire, we recommend a longer-term monitoring study to investigate additional fire aspects, such as the effect of fire frequency on the regeneration ability of *Helichrysum* and other shrubs in KNP.

### AUTHOR CONTRIBUTIONS

Christopher A. Mgimba: Literature review, conceptualization, data analysis, writing original draft and editing; Issakwisa B. Ngondya: Conceptualization, methodology, reviewing and editing; Anna C. Treydte: Conceptualization, methodology, reviewing and editing.

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### CONFLICT OF INTEREST STATEMENT

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

### PEER REVIEW

The peer review history for this article is available at <https://www.webofscience.com/api/gateway/wos/peer-review/10.1002/2688-8319.70037>.

### DATA AVAILABILITY STATEMENT

The authors confirm that all data underlying the findings are fully available without restriction. The data generated during and/or analysed during the current study will be made available via Zenodo at <https://doi.org/10.5281/zenodo.15032986> (Mgimba, 2025).

### RELEVANT GREY LITERATURE

You can find related grey literature on the topics below on Applied Ecology Resources: [Shrub](#), [Late burn](#), [Grassland](#), [Prescribed fire](#), [Wildfire](#), [Soil](#), [Seed bank](#).

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