Basal bud banks are the primary determinants of survival in woody legume seedlings after clipping

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ARTICLE INFO

ABSTRACT

Disturbances determine the structure of savannas by influencing growth at all stages of a tree's life. Since the seedling stage is such a significant part of a tree's life cycle, greater knowledge of this stage informs woody management and encroachment prevention. In this study, we tested the effect of a suite of seedling functional traits on seedling survival after experimentally-induced disturbance. Twelve mimosoid legume tree species, an important group in African savannas, with different provenances, were grown from seed under experimental conditions. Seedlings were clipped at 1 cm above ground at age 30 days, to simulate disturbance, and their survival recorded. A number of above- and below-ground traits quantifying height, biomass, bud bank and architecture were measured prior to clipping in order to assess what traits could be responsible for post-clipping survival. We also quantified root contraction by calculating the change in height of the lowest bud between the ages of 6 and 60 days. Fire regime and browser biomass of the native range of each species were calculated to test whether these factors predicted seedling survival. Seedling survival was primarily predicted by the whether the plant possessed a bud below 1 cm above ground level, i.e. below the height of clipping. For the first time we report that, in several *Vachellia* species, root contraction occurred, bringing basal buds closer to the ground, and in some cases below the ground, thus increasing seedling survival after clipping. No environmental variables were significant predictors of survival. Our results suggest that, at this young age, buds close to the soil surface are the most important trait predicting seedling survival, while other traits that are important for saplings and adults do not significantly influence the survival of seedlings. At the seedling stage, herbivory and fire are possibly inflicting the same degree of selection pressures and thus little trait differentiation is evident across the environmental gradient.

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1. Introduction

The savanna biome is the largest in Africa, covering more than half the continent (Lehmann et al., 2011; Osborne et al., 2018). Disturbances, particularly fire and herbivory, play a primary role in determining savanna structure, with these disturbances and their impacts varying across the rainfall gradient (Lehmann et al., 2011, 2014). Disturbances result in loss of above-ground biomass, tissue damage and in some cases, top-kill of savanna trees (Holdo, 2006; Hoffmann et al., 2009) and can restrict the woody cover.

Several traits conferring tolerance, avoidance or resistance of disturbances have been identified in savanna trees (Wigley et al., 2020). Tolerance traits do not prevent damage, instead the tree is able to

recover or replace lost and damaged parts post-disturbance. For example, in savanna trees their caged crown architecture (Staver et al., 2012) protects buds from herbivores and reduces herbivore bite size, thus reducing biomass loss (Archibald and Bond, 2003). The presence of spines is a further deterrent to herbivory (Cooper and Owen-Smith, 1986; Gowda, 1996). The ability to resprout after top-kill by burning or herbivore damage as well the ability to fix nitrogen (through the presence of nodules) are also factors considered to confer tolerance after disturbance (Schutz et al., 2009; Pellegrini et al., 2015). Avoidance traits allow trees to escape disturbance either spatially or temporally. For example, taller, rapidly growing trees are better adapted to fire as they quickly reach the fire escape height, which is generally considered to be two meters above ground level (Archibald and Bond, 2003; Botha et al., 2020). Resistance traits minimize the effects of disturbances. An example is thick, fire-resistant bark, enabling trees to circumvent top-kill and limit trunk damage (Pellegrini et al., 2015; Shorrocks and Bates, 2015; Charles-Dominique et al., 2017).

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Trees growing in savannas are likely to be exposed to disturbances such as fire and herbivory and, in some areas, frost, from the early seedling establishment phase (Archibald et al., 2013b; Charles-Dominique et al., 2017). However, much of the work aimed at understanding the relationships between disturbances and tree success has been conducted on saplings and adult trees (Higgins et al., 2000; Pellegrini et al., 2015; Russell et al., 2019; Wigley et al., 2020). This research has demonstrated that top-kill disturbances seldom kill saplings or adult savanna trees (Higgins et al., 2000; Midgley and Bond, 2001; Balfour and Midgley, 2006; Schutz et al., 2009; Wigley et al., 2009; Russell et al., 2019; Atanasso et al., 2021), but they can prevent saplings from recruiting to the adult life stage, keeping them in a sterile non-reproductive life stage where their exposure to repeated disturbances remains high due to their short stature. However, their ability to resprout means that saplings can survive these disturbances (Higgins et al., 2000; Fornara and Du Toit, 2008; Staver et al., 2009; Staver and Bond, 2014). Adult trees, especially tall trees, are far better protected from biomass loss by fire and browsing through adaptations such as thick bark and their large stature (Midgley and Bond, 2001; Balfour and Midgley, 2006).

The effect of top-kill-inducing disturbances on young seedlings and their ability to survive has received comparatively little attention, despite the fact that high mortality at the seedling stage comprises a significant bottleneck in the establishment and persistence of trees within savannas (Archibald et al., 2021). Three known traits are associated with increased seedling (< 1 year age) survival of disturbance: low bud height (Botha et al., 2020), growing taller and thicker stems faster (Cardoso et al., 2016; Archibald et al., 2021), and a high root:shoot ratio indicating investment in below-ground growth and storage of resources (Gignoux et al., 2009; Cardoso et al., 2016; Wigley et al., 2020).

The different disturbance regimes that species are exposed to may influence their ability to survive disturbances because fire regimes and browser biomass vary in space, timing, intensity, frequency and mode of action. Fires occur more frequently in high rainfall savannas (Archibald et al., 2013b; Ursino, 2013; Lehmann et al., 2014) while browser biomass peaks at intermediate rainfalls (Hempson et al., 2015). Differences in ability to tolerate disturbances are likely explained by the suite of traits that the seedlings possess. The ability of seedlings to survive disturbances may also be affected by their provenance. While seedlings from regions with frequent disturbances may have traits to tolerate top-kill, these traits may differ between areas that experience different disturbance regimes (Staver et al., 2009).

In this study we aim to determine which suite of traits best explains the ability of savanna tree seedlings in the mimosoid clade (Fabaceae: Caesalpinioideae: Mimosoideae; (The Legume Phylogeny Working Group, Bruneau et al., 2013)) to survive top-kill as seedlings

(30 days). The first objective is to understand which traits, above- and below-ground, make it possible for the seedlings to survive a disturbance that results in biomass removal. We hypothesize that seedlings that invest more in growing taller, invest more in below-ground resources and those with a lower bud height will show higher survival in response to clipping.

The second objective is to determine if variation in seedling survival can be explained by the species' biogeography. Because seedlings germinate in the wet season when fire and frost are highly unlikely and herbivory is probably the only disturbance present at this point, we hypothesize that species originating from regions where browser densities are highest will possess traits that facilitate their survival to top-kill and will have the highest survival rates.

2. Materials and methods

2.1. Experimental setup

We compared the relationships between traits and seedling survival in a range of species from one taxonomic group, but from different environmental conditions, whilst accounting for phylogenetic non-independence. We selected twelve southern African tree species from the Mimosoid clade (previously the sub-family Mimosoideae) of the Fabaceae (Table 1). The mimosoids were selected as they are ecologically dominant in many African savannas, are of economic importance (Huntley and Walker, 1982; Shorrocks and Bates, 2015) and occur across gradients of rainfall, fire regimes and herbivory pressure (Ursino, 2013) (Table 1).

Seeds were obtained from a seed supplier (Silverhill Seeds, https://silverhillseeds.co.za/) and from trees planted on the University of Pretoria campus. Seeds were pre-treated and scarified to maximize germination rates (Table 1), and sown into 3.5 L soil bags filled with a 1:1:1 mix of topsoil, river sand and compost. Bags were placed across four greenhouses covered with 40% white shade cloth; the photosynthetically active radiation (measured by ceptometer) ranged from 1239 to 1339 μmol/m²s (mean: 1317). Three greenhouses with six irrigation lines and one greenhouse with three irrigation lines (each line with two rows of 40 seed bags), were used. Each bag received 300 ml of water per day, every second day. Greenhouses are located on the Innovation Africa campus at the University of Pretoria.

Seeds intended for the experiment (270 seeds per species) were scarified the day before sowing using the most effective method (Table 1). Mechanical scarification was done using sandpaper to remove a piece of the seed coat and then leaving seeds in water for a minimum of 12 h. Boiling was done by placing the seeds in a beaker, pouring boiling water over the seeds, and leaving the seeds in this water for a minimum of 12 h. The scarified seeds were sowed every

Table 1
A list of the 12 mimosoid species that were used in this study, the scarification method used that resulted in the most germinations, and the average environmental conditions under which each species naturally occur are included.

Species	Scarification method	Mean annual precipitation (mm/year)	Mean fire intensity/ radiative power (MW)	Herbivore biomass (kg/km²)
Albizia forbesii Benth.	Mechanical	875	116	2864
Dichrostachys cinerea (L.) Wight & Arn	Mechanical	906	140	2405
Senegalia galpinii (Burtt Davy) Seigler & Ebinger	Mechanical	656	153	2760
Senegalia senegal (L.) Britton	Boil	524	125	2240
Vachellia erioloba (E.Mey.) P.J.H.Hurter	Mechanical	387	235	1874
Vachellia exuvialis (I.Verd.) Kyal. & Boatwr.	Mechanical	614	186	2935
Vachellia karroo (Hayne) Banfi & Galasso	Mechanical	581	199	2104
Vachellia nilotica (L.) P.J.H.Hurter & Mabb.	Mechanical	611	123	2506
Vachellia rehmanniana (Schinz) Kyal. & Boatwr.	Mechanical	786	140	2838
Vachellia robusta (Burch.) Kyal. & Boatwr.	Mechanical	770	141	2910
Vachellia sieberiana (DC.) Kyal. & Boatwr.	Boil	921	131	2567
Vachellia swazica (Burtt Davy) Kyal. & Boatwr.	Mechanical	790	200	3171

Table 2

The tree seedling traits that were measured, how they were measured, the ecological significance of the traits, and for which treatments and the age of the seedlings when the traits were measured. Only traits that were used in analyses are included.

Trait	How it is measured	Ecological significance	Clipping	Harvest	Control
Stem length	Stem is gently straightened, and length taken from soil surface to highest bud	Taller trees escape fire (Wigley et al., 2020)	Day 30	Day 30	Day 6, 30, 60
Height of lowest bud	Distance between lowest bud (leaf, cotyledon or branch) and soil surface	Buds closer to the surface are better protected (Klimešová et al., 2019; Botha et al., 2020)	Day 30	Day 30	Day 6, 30, 60
Stem diameter at 1 cm	At 1 cm above the soil surface the diameter of the stem is taken using callipers	Insulation, storage and protection against fire (Wigley et al., 2020)	Day 30	Day 30	Day 6, 30, 60
Stem tip count	Number of apical buds	Indicative of branching architecture (Wigley et al., 2020)	Day 30	Day 30	Day 6, 30, 60
Depth of stem-root transition	Measured from the point where stem is clipped at soil surface to the start of the root	The depth of the stem and where the root starts, how protected the stem buds are		Day 30	
Taproot length	Root is gently straightened and measured from where it starts to the very end	Rooting depth and ability to avoid competition with grasses (Wigley et al., 2020)		Day 30	
Root diameter at 1 cm	Taken at 1 cm from the start of the root using callipers	Indicator of investment in below-ground biomass (Wigley et al., 2020)		Day 30	
Presence/absence of nodulation	Are there any nodules on the roots	Potential ability to acquire additional nutrients (Shorrocks and Bates, 2015)		Day 30	
Survival	Yes or no, based on the presence or absence of green material	Derived trait, used to assess ability to recover from clipping (Shaw et al., 2002)	End of Experiment		
Above:below- ground dry mass	Ratio of above- to below-ground dry mass. The above- and below-ground material was separated by clipping at the soil surface, and the , harvest was dried at 65 °C for a minimum of three days and then weighed on a micro-scale	Derived trait, indicator of investment in above or below- ground growth (Wigley et al., 2020)		Day 30	
Stem diameter: stem length	Ratio of stem diameter to stem length	Derived trait, indicator of trade-off between growing tall *vs* wide	Day 30	Day 30	Day 6, 30, 60
Bud below 1 cm (Y/N)	Record the presence/absence of leaves or cotyledons below 1 cm	Derived trait, below clipping height thus protected	Day 30	Day 30	Day 6, 30, 60

second day between 2 and 12 December 2020. Two seeds of the same species were sown in each bag in case one seed did not germinate. The species were planted in their replicates (1−135), with the order of species within each replicate randomized.

Seedling germinations were recorded every second day until 24 December 2020. A seed was considered to have germinated when any green tissue was visible above ground. If both seeds in a bag germinated, the seedling that germinated later was removed and if two seedlings germinated on the same day, the smaller seedling was removed. Due to unexpected deaths or failure to germinate, a second round of plantings of 47 seedlings from 11 species occurred on 27 January 2020 in the same manner as described above.

2.2. Seedling measurements

Seedlings were assigned to one of two treatments: control and, to represent top-kill, clipping. Additionally, five seedlings of each species were set aside for measuring below-ground traits (see below). Twelve individuals per species were assigned to the clipping treatment. Seedlings assigned to this treatment were measured and clipped at 30 days old. Above-ground traits were measured on these individuals prior to clipping (Table 2) and thereafter, the stem of the seedling was clipped at a height of one centimetre above the ground. Clipped biomass was placed in a drying oven and its dry mass measured (Table 2).

To assess the below-ground traits of seedlings at 30 days old (before clipping) seedlings were "harvested". It was not possible to measure below-ground traits of the clipped seedlings prior to clipping without killing them. Instead, harvested seedlings were removed from their soil bags at 30 days old (i.e., the same age at which clipping occurred) and average trait values of their below-ground traits calculated from five individuals per species. All other traits measured at 30 days were also measured per species. Averaged traits represent species-level traits (Table 2).

Several other relevant traits, such as above-ground:below-ground dry mass, were calculated based on primary traits measured during the experiment (Table 2).

Eight seedlings per species were control seedlings. Traits of these seedlings (Table 2) were remeasured several times throughout the duration of the experiment. Several above-ground traits were measured at 6, 30 and 60 days (Table 2).

At the end of the experiment (1 April 2021), when most seedlings were between 104 and 118 days old but four seedlings were between 65 and 70 days old, the clipped seedlings were re-measured to determine their survival. Individuals were considered to have survived if they had any green tissue (Table 2).

2.3. Analyses

All analyses were run in R *v.* 4.0.5 using these packages: blme 1.0−5 (Chung et al., 2013), rcompanion 2.4.1 (Mangiafico, 2021), bestglm 0.37.3 (McLeod et al., 2020), stats 4.0.2 (R Core Team, 2020), jtools 2.1.3 (Long, 2020), car 3.0−10 (Fox and Weisberg, 2019), ggplot2 3.3.5 (Wickham, 2016), Rcpp 1.0.8.3 (Eddelbuettel and Francois, 2011; Eddelbuettel, 2013; Eddelbuettel and Balamuta, 2018), rgdal 1.5−31(Bivand, 2022), raster 3.5−15 (Hijmans, 2022), and maptools 1.0−2 (Bivand and Lewin-Koh, 2020).

Before any models were run, a correlation matrix for all traits was constructed; if two traits were highly correlated (correlation > |0.7|), one of the traits was removed from further analysis (Table A1). One analysis assessing the effects of traits on seedling survival was run at the level of individual seedling (details below). For this analysis, presence of leaves below 1 cm and cotyledons below 1 cm were combined into one trait, namely 'buds below 1 cm', as they were highly correlated. No other traits were highly correlated. Another analysis assessing the effects of traits on survival was run at species-level. For this model, the following predictors were removed prior to analysis due to high collinearity: average height of the lowest bud, average above-ground dry mass, average below-ground dry mass, average stem length and average stem diameter (Table A2). Finally, for the analysis assessing the effect of provenance on disturbance response, mean fire return interval (MFRI) and herbivore biomass were highly correlated, so MRFI was removed (Table A3).

A binomial generalized mixed effects model was run to test whether seedling survival was predicted by their above-ground traits measured

Table 3
A summary of results of all the models that were run for analyses. Models were determined using a best subset method and all retained only one predictor variable. The first model was run with individual seedlings as replicates, and the estimate is for the main effect ('bud below 1 cm); while all other models were run with species as replicates.

Model	Predictor estimate	Predictor p-value	Model p-value	R^2 value	Akaike value	Degrees of freedom
Survival (Y/N) ∼ bud below 1 cm (Y/N) + (1|Species) + (1|Greenhouse)*	6.715 (Y>N)	3.49×10^{-5}	3.49×10^{-5}	0.795	82.500	133
% Survival ∼ proportion leaves below 1 cm	3.573	0.089	0.055	0.640	10.737	10
% Survival ∼ Fire intensity	0.025	0.324	0.324	0.188	15.905	10
% Buds below 1 cm ∼ avg change height in lowest bud	−0.042	0.003	0.003	0.569	4.155	10
% Survival ∼ avg change height in lowest bud	−0.390	2.57×10^{-6}	2.57×10^{-6}	0.890	−18.618	10

* Random effects variance/SD for species 1.704/1.305 and greenhouse 0.426/0653.

immediately prior to clipping. Only the trait measurements of the clipped individuals (i.e., above-ground traits) were used as predictors (Table 2), and greenhouse number and species were included in the model as random variables. The best model was determined through backwards step-wise selection as the one with the lowest AIC value.

Because below-ground traits could not be obtained for individual clipped seedlings due to the destructive nature of below-ground trait collection, the ability of both above and below-ground traits to predict proportional survival of seedlings could only be conducted at the species level. Therefore, all above and below-ground traits at 30 days were averaged per species and the proportion of seedling survival after clipping calculated per species (Table 2). A binomial generalized linear model was run to test the effect of average trait values on proportion survival and a best subset function was used to determine the model with the lowest AIC value.

Over the course of the experiment, we noticed that the height of the lowest bud appeared to be decreasing for some species, and, during the final measurements, some seedlings had thorns and leaves below the ground, suggesting the roots had contracted (Fensham et al., 2009; Klimešová et al., 2019). Thus, we chose to carry out an analysis of the change in the height of the lowest bud between day six and day 60 for all control individuals. The change in the height of the lowest bud was averaged per species. Two generalized additive models were run to test a) whether species that showed a greater decrease in bud height with age also showed a higher incidence of holding their buds below 1 cm, and b) whether species that showed greater root contraction, i.e. a greater decrease in height of the lowest bud, had a higher survival after clipping.

To assess relationships between survival traits and biogeography, GBIF locality records of each species were downloaded for South Africa and Eswatini. Locality records were randomly subsampled to one locality record per one degree cell to remove spatial bias (Beck et al., 2014) . Three disturbance variables were used to calculate the average disturbance conditions for each species within the study area. The variables used were fire intensity (fire return power, (Archibald et al., 2013a)), fire frequency (fire return interval, (Archibald et al., 2013b)) and herbivore density (Hempson et al., 2015). Herbivore density represents reconstructed densities from a time before humans had major influences on herbivore biomass (Hempson et al., 2015). Only browser and mixed feeder density were used to calculate herbivore density, as grazers are unlikely to have an adaptive influence on trees. To calculate herbivore biomass per species, browser biomass and half the mixed feeder biomass were summed per grid cell. The values of the three disturbance variables were extracted per locality record, and their averages calculated per species. To determine if species survival was influenced by the disturbance regime of their provenance, a generalized linear model with binomial distribution was run. A best subset function was used to determine the model with the lowest Akaike value.

3. Results

The best model that predicted individual seedling survival retained only one trait, namely buds below 1 cm above ground level

(agl), as a predictor variable (Table 3). Individuals with buds below 1 cm agl were significantly more likely to survive clipping; 98% of individuals with buds below 1 cm agl survived, 29% of seedlings without buds below 1 cm agl survived (Fig. 1). This was observed for almost all species (Fig. 2). Only seedlings of *Dichrostachys cinerea* and *Vachellia sieberiana* had high survival despite having no or very few individuals with buds below 1 cm agl (Fig. 2).

The best model that predicted proportion survival at species level (Table 3) retained only proportion leaves below 1 cm agl as a predictor variable. Proportion survival of each species increased as the proportion of leaves below 1 cm increased (Table 3); this relationship was marginally significant.

We observed bud banks being pulled closer to the ground as seedlings aged in seven *Vachellia* species. For these species, the height of the lowest bud at day 60 was lower (on average 2−7 mm lower) than the height of the lowest bud at day six (Fig. 3). As the height of the lowest bud decreased, the proportion of seedlings with buds below 1 cm increased (those with a negative average change in height of the lowest bud had more than 50% of individuals with buds below 1 cm, Fig. 3). This suggests that root contraction does, indeed, result in buds being held close to the ground. Additionally, species that showed the greatest decrease in lowest bud height with age had the highest survival after clipping (species with an average negative change in height had survival rates greater than 80%, Fig. 3), suggesting that root contraction increases seedling survival by pulling buds closer to the ground. . *Vachellia sieberiana* was the only *Vachellia* species in this study for which bud height did not decrease with age; no *V. sieberiana* seedlings had buds below 1 cm, but most (58%) survived clipping (Fig. 2). In *D. cineria* 40% of the clipped individuals survived clipping, despite only 10% having a bud below 1 cm (Fig. 2).

There was no relationship between the fire and herbivory regime of the regions from which the seedlings originated and their survival.

4. Discussion

We show that seedling survival in the face of disturbance is best explained by seedlings having buds below 1 cm. The presence of this trait was the overriding explanation of survival, as no relationships between survival, other traits and biogeography were revealed in this study. We also showed that many of the high-surviving trees, specifically seven of the eight *Vachellia* species, likely enhance this trait by pulling their buds closer to the ground as the seedling grows.

A bud bank close to the ground increases savanna seedling survival. At this low height, the buds are much less likely to be damaged by or lost to a disturbance by top-kill (Klimešová et al., 2019). Low bud banks appear to protect seedlings from fire damage; experiments where seedlings were exposed to fire showed minimal damage to the lowest part of the main stem (Supplementary material) and seedlings with the greatest number of basal leaf buds (below 1 cm) had the highest survival (Botha et al., 2020). Browsers are also unlikely to be able to damage the bud banks as they cannot crop shoots on the soil surface (pers. obs. M. Greve). Protecting bud banks from disturbance means that following top-kill, the seedlings can rapidly initiate photosynthesis (Wigley et al., 2009) without having to heavily rely on
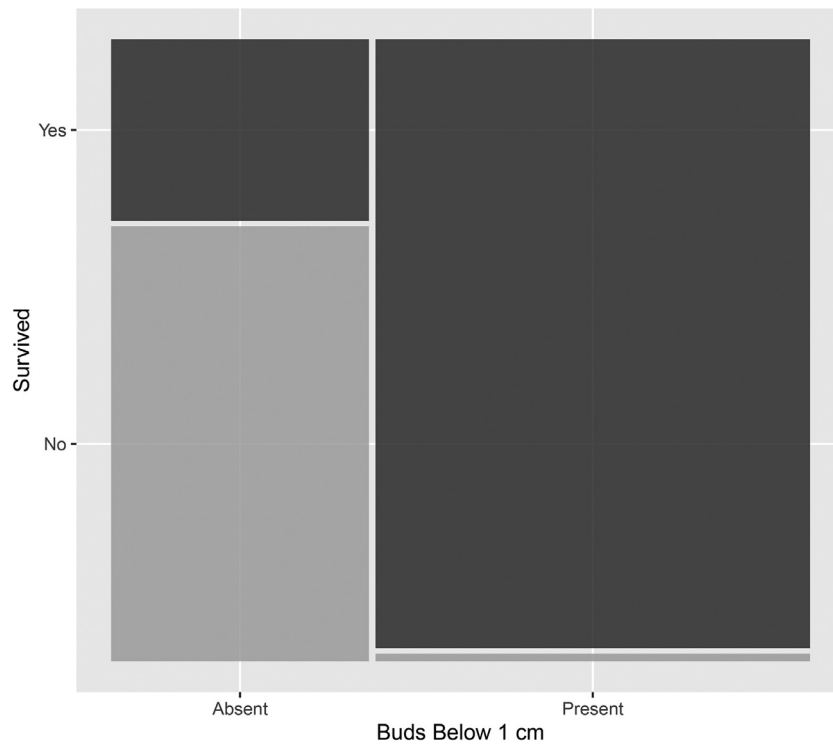
Fig. 1. Results of the individual seedling analyses. Proportion individuals with buds below 1 cm and proportion that survived clipping at day 30.
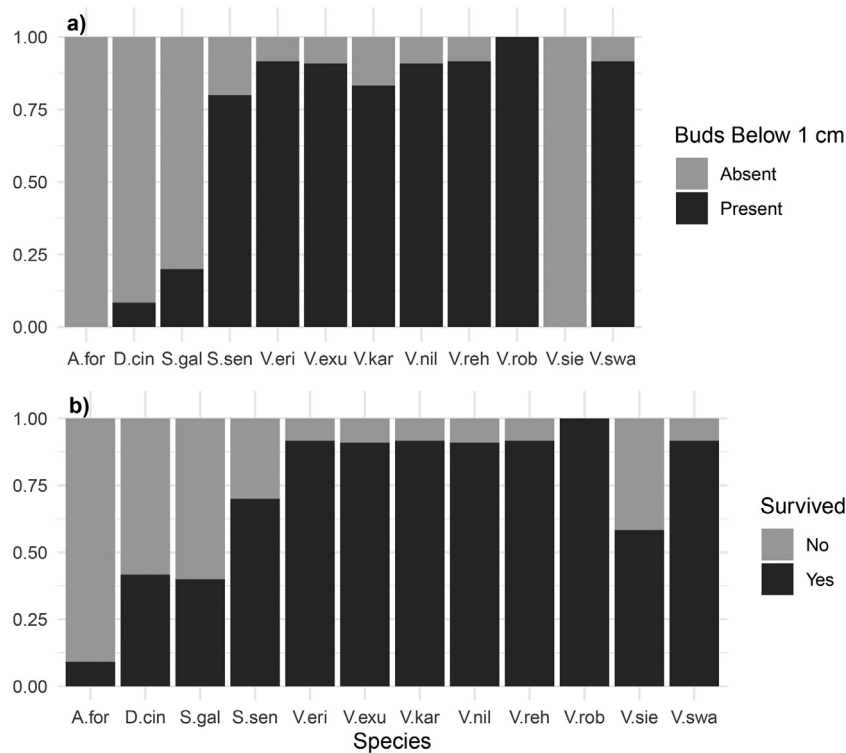

Fig. 2. Results of the individual seedling analyses grouped by species. Proportion of individuals of each species with a) buds below cm and b) survived the day 30 clipping treatment. Only the first three letters of each species' name is included in the figure; see Table 1 for the full species names.

root reserves, which are likely very low in newly established seedlings (Gignoux et al., 2009; Schutz et al., 2009; Wigley et al., 2009). Even if the leaf or cotyledon is damaged by herbivory or fire, the presence of pre-existing buds means they are still able to resprout instantly (Wigley et al., 2009; Charles-Dominique et al., 2015).

We observed that several *Vachellia* species actively brrought buds closer to, or even below, the soil surface, probably through root contraction (Fig. 4). The action of contracting roots repositions buds to a lower height, thus decreasing exposure to disturbances (Fisher, 2008). Repositioning the height of a bud to below the soil allows the
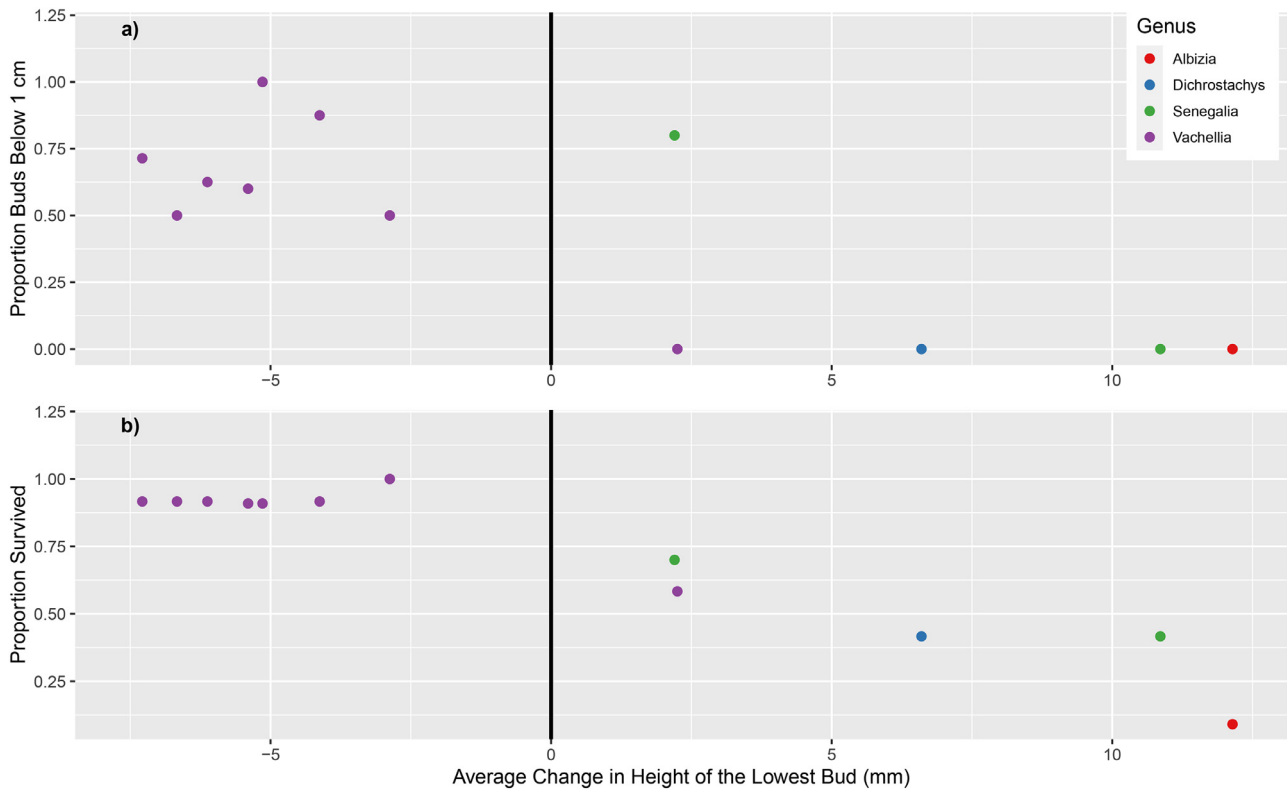
Fig. 3. The relationships between the average change in height of the lowest bud and a) proportion survived and b) the proportion of buds below cm for each species. The black represents no change in bud height. Points on the left side of the black line are species that showed an average decline in height of lowest bud. Points are colour-coded according to genus.

Fig. 4. Image of a *Vachellia* seedling's below-ground parts during final measurements. This seedling had been cut at the soil surface so that all tissues seen here were below the soil surface. Note spines and leaves that were found below the soil surface.

soil to act as a protective barrier for the buds (Klimešová et al., 2019) against large herbivores, fire or frost (Pausas et al., 2018). To our knowledge, this is the first time root contraction has been recorded in *Vachellia* seedlings, though it has been reported in other Fabaceae species (Fisher, 2008). The root contracting mechanisms in these Fabaceae involves the use of G-fibres (gelatinous or tension wood fibres), causing roots to contract or bend along their vertical axis (Fisher, 2008). We propose that this ability to contract roots and ultimately provide some form of bud protection at so young an age could be a key trait in the success of *Vachellia* species across African savannas where they are widely prevalent, especially where disturbance is frequent (Huntley and Walker, 1982).

Two species had fairly high survival despite having few buds below 1 cm, i.e. the height at which seedlings were clipped: *Vachellia sieberiana* and *Dichrostachys cinerea*. The survival of these species is likely driven by a trait that is not linked to establishment of buds. Both species are encroachers in South Africa (Department Environmental Affairs, 2019), so knowing how they are both able to survive

disturbance during this bottleneck life stage is an important avenue for further research.

We suggest that at 30 days post-germination, bud position is the most important trait predicting seedling survival. Seedlings at this young age have not had time to accumulate enough resources to develop other strategies and therefore have to rely on this resistance trait to enhance survival. As seedlings age and transition into the sapling and adult stage, the ability of a woody individual to survive disturbances increases (Gignoux et al., 1997; Botha et al., 2020; Archibald et al., 2021). It is likely that the role of other traits in surviving disturbance-prone savannas will increase. Other resprouting traits may gain in importance; for example, more root reserves increase resprouting ability in saplings (Schutz et al., 2009) and better bud protection, determined by the position of the buds in the bark, and the bark's thickness, protects trees from fire (Charles-Dominique et al., 2015). For adults, tree size can be instrumental in escaping disturbances (Staver and Bond, 2014) and investment in cagey architecture decreases exposure to herbivory (Staver et al., 2012). Thus, if the

seedlings were older, they would perhaps display more than one disturbance adaptation.

Contrary to our original hypothesis, no environmental variables significantly predicted percentage survival. Savanna trees germinate during the wet season when fire is highly unlikely to occur naturally, therefore it is speculated that they would all only be exposed to herbivory at this age, regardless of biogeography. Herbivory intensity would vary across the environmental gradients but would still inflict similar damage (complete loss of biomass above 1 cm) to the various seedlings. It could be that biogeography did not predict survival of seedlings because the effects of different disturbance agents on seedlings do not differ much at this age.

This study provides insight into the influence of above-ground disturbances on demographic bottlenecks in the seedling stage and therefore has implications for savanna management, encroachment prevention and conservation.

Declaration of Competing Interest

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.

Acknowledgments

Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.sajb.2023.05.017.

Appendix

Tables A1, A2 and A3

Table A1
Correlation matrix of traits for individual-level analyses. Only continuous traits are shown. Underlined values were significant (p-value < 0.05).

	Stem length	Stem diameter:length	Stem diameter	Stem tip count
Stem length	1.00	−0.53	0.66	0.05
Stem diameter/length	−0.53	1.00	0.18	−0.06
Stem diameter	0.66	0.18	1.00	0.06
Stem tip count	0.05	−0.06	0.06	1.00

Table A2
Correlation matrix of all traits measured for species-level analyses. Red text indicates correlations with |r| > 0.7. Variables that were removed from analyses are indicated in bold. Significant correlations are underlined (p-value < 0.05). Ave = Average; Prop = Proportion.

	Prop leaves below 1 cm	Prop cotyledons present	Prop cotyledons below 1 cm	Ave below-ground dry mass	Ave above-ground dry mass	Prop nodulation present	Ave tap root diameter	Ave tap root length	Ave stem-root transition depth	Ave stem tip count	Ave stem length	Ave stem diameter	Ave lateral branches	Ave height of the lowest bud	Ave above-/below-ground dry mass	Ave stem diameter/length
Prop leaves below 1 cm	1.00	0.32	0.84	0.04	−0.21	−0.03	−0.09	0.42	0.00	−0.62	−0.51	−0.24	−0.62	−0.87	0.22	0.71
Prop cotyledons present	0.32	1.00	0.57	0.63	0.17	0.13	0.11	0.01	0.63	−0.33	−0.15	−0.28	−0.33	−0.52	0.14	−0.01
Prop cotyledons below 1 cm	0.84	0.57	1.00	0.18	−0.02	0.11	0.00	0.14	0.14	−0.49	−0.33	−0.18	−0.49	−0.76	0.35	0.50
Prop nodulation present	0.04	0.63	0.18	1.00	0.14	0.06	0.15	0.15	0.61	0.09	0.07	0.00	0.09	−0.45	0.08	−0.04
Ave below-ground dry mass	−0.21	0.17	−0.02	0.14	1.00	0.95	0.90	0.18	0.27	0.15	0.83	0.74	0.15	0.04	0.36	−0.38
Ave above-ground dry mass	−0.03	0.13	0.11	0.06	0.95	1.00	0.88	0.18	0.19	0.13	0.75	0.76	0.13	−0.06	0.51	−0.27
Ave tap root diameter	−0.09	0.11	0.00	0.15	0.90	0.88	1.00	0.12	0.28	0.14	0.63	0.57	0.14	−0.05	0.23	−0.15
Ave tap root length	0.42	0.01	0.14	0.15	0.18	0.18	0.12	1.00	−0.05	−0.46	0.20	0.35	−0.46	−0.56	0.11	0.19
Ave stem-root transition depth	0.00	0.63	0.14	0.61	0.27	0.19	0.28	−0.05	1.00	0.16	−0.01	−0.23	0.16	−0.35	0.24	−0.21
Ave stem tip count	−0.62	−0.33	−0.49	0.09	0.15	0.13	0.14	−0.46	0.16	1.00	0.36	0.18	1.00	0.43	0.34	−0.52
Ave stem length	−0.51	−0.15	−0.33	0.07	0.83	0.75	0.63	0.20	−0.01	0.36	1.00	0.88	0.36	0.32	0.38	−0.65
Ave stem diameter	−0.24	−0.28	−0.18	0.00	0.74	0.76	0.57	0.35	−0.23	0.18	0.88	1.00	0.18	0.17	0.33	−0.28
Ave lateral branches	−0.62	−0.33	−0.49	0.09	0.15	0.13	0.14	−0.46	0.16	1.00	0.36	0.18	1.00	0.43	0.34	−0.52
Ave height of lowest bud	−0.87	−0.52	−0.76	−0.45	0.04	−0.06	−0.05	−0.56	−0.35	0.43	0.32	0.17	0.43	1.00	−0.33	−0.51
Ave above-/below-ground dry mass	0.22	0.14	0.35	0.08	0.36	0.51	0.23	0.11	0.24	0.34	0.38	0.33	0.34	−0.33	1.00	−0.37
Ave stem diameter/length	0.71	−0.01	0.50	−0.04	−0.38	−0.27	−0.15	0.19	−0.21	−0.52	−0.65	−0.28	−0.52	−0.51	−0.37	1.00

Table A3

Correlation matrix of disturbance predictor variables. Red text indicates correlations with |r| > 0.7. Variables that were removed from analyses are indicated in bold. Significant correlations are underlined (p-value < 0.05).

	Fire Intensity	Fire Frequency	Herbivore Biomass
Fire Intensity	1	0.27	−0.28
Fire Frequency	0.27	1	−0.89
Herbivore Biomass	−0.28	−0.89	1

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