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Belowground resprouting potential and nutrient acquisition traits of three perennial grasses during the short dry season in Kenya

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Survival of perennial grasses between wet seasons depends on the maintenance of belowground buds and root systems. Belowground bud and root traits were evaluated in three perennial grasses (*Pennisetum mezianum* (Leeke), *Digitaria macroblephara* (Hack. ex Schinz) Paoli, and *Themeda triandra* (Forssk.) in semi-arid Kenyan rangelands during the short dry season. Bud number remained stablae while bud size declined for all three grass species during the study period. Non-structural carbohydrates in roots and percent root dry matter had increased in all three species by the end of the dry season. *Pennisetum mezianum* had more buds, larger bud sizes, larger average root diameter, lower specific root length (SRL), lower root tissue density (RTD), and the least amount of non-structural carbohydrate (NSC) content when compared to the other two species. Perennial grasses preserved their resprouting capacity during the short dry season through both their stable bud numbers and increasing availability of carbohydrates for resprouting. Further research should be conducted on more range grass species over multiple seasons to better understand how their belowground traits enable the persistence of these species during dry seasons and long-term drought.

Keywords: bud, non-structural carbohydrate, root tissue density, specific root length

Introduction

Globally, grasslands form the major biomes of rangelands and are the main source of forage for domestic and wild ungulates. Livestock production is the main economic activity on rangelands and relies heavily on grasses that have been subjected to overstocking and overgrazing (Piipponen et al. 2022). Consequently, forage availability has been adversely affected, a trend that will most likely continue as climate change takes its toll (Nardone et al. 2010).

Perennial grasses have developed elaborate survival mechanisms to cope with arid and other unfavourable conditions in grasslands during the short dry season (Ott et al. 2019). In particular, the vegetative growth of plants is of great significance, more so the belowground buds, which ensure successive tiller production and compensation for tiller mortality, thus ensuring the persistence of range grasses (Yuan et al. 2020). Belowground buds are the organs that give rise to new tillers in grasses, which replace the ones that have died due to old age or have been grazed. Therefore, buds give rise to the persistence of perennial grasses (Hendrickson and Briske 1997) and the capacity to withstand overgrazing and other environmental disturbances, including droughts (VanderWeide and Hartnett 2015).

Re-growth after disturbance largely depends on activation and subsequent outgrowth of buds when a large proportion of aboveground tissue is removed (Ott et al. 2019). Soluble sugars provide structural materials and energy required to respond to disturbances in an ecosystem (Morkunas and Ratajczak 2014). These non-structural carbohydrate (NSC) reserves are used during periods of moisture deficiency for re-growth and survival by supplying energy to axillary buds to initiate new growth or support ongoing growth, which eventually contributes to new tiller development (Wu et al. 2021). High amounts of soluble sugars ensure that grasses grow rapidly at the onset of the rainy season and that they are well adapted to the erratic rainfall patterns common in many rangelands (Priyadarshini et al. 2016). The NSCs (i.e. sugar and starches) play an important role in regulating key physiological activities of plants, including buffering the plants from adverse environmental conditions (Ji et al. 2020). Physiological activities include nutrient absorption, respiration, organic secretion, and plant growth. In addition, NSCs play an important role in plant defence, metabolism, delaying or preventing plant death, and drought resistance (Ji et al. 2020). Starch is the major reserve carbohydrate for tillering and regrowth of grasses and also acts as a buffer for drought-instigated disparities that occur during resource acquisition by photosynthesis and carbon-sink activities (Muller et al. 2011). In contrast, roots of range grasses respond promptly to variation in soil moisture by adjusting their form, physiology, and structure to compensate for alterations in the availability of resources (Perlikowski et al. 2019).

Recently, the severity and frequency of droughts have significantly increased in regions such as the Horn of Africa,

Sahel Region of Africa, Australia, Western United States, and South Asia (Cervigni and Morris 2016), leading to decreased productivity (Liu et al. 2023). In perennial grasses of rangelands, when the soil moisture conditions ideal for active plant growth are not met, axillary bud production and viability are usually adversely affected and limit the regrowth potential of range grass species (Reichmann and Sala 2014). Consequently, there is a reduction in stand longevity and increased deterioration of rangelands (Ott et al 2019). Therefore, grasses with an extensive belowground bud bank and root system as well as sufficient reserves may be more likely to recover after a disturbance than those species which do not possess these features.

Although the capacity of any grass to withstand moisture deficit is a function of the size of its bud bank, the longevity of existing buds, and the general root dynamics (Ott et al. 2019), comprehensive scientific data on morphological and anatomical responses of subterranean grass parts are lacking. In sub-Saharan Africa, studies on root crown axillary buds have been few, leaving a significant knowledge gap on morphological patterns of bud development, which are crucial in predicting plant community dynamics as a result of external disturbance (Li et al. 2023). More specifically, little is known about the effects of moisture variation on the roots of the common range grass species of East Africa. As climate change continues to unfold, there is an urgent need for plant scientists to have a thorough understanding of how the root systems of grasses respond to fluctuations in soil moisture content (Eshel and Beeckman 2013). Grassroots, crowns, and buds are closely intertwined, and one cannot function without the other. An in-depth understanding of the effect of soil moisture variation on root and bud morphology as well as anatomy, including the bud bank, NSC reserves, and their development, against the backdrop of cyclic patterns of utilisation and re-establishment of root and shoot biomass is paramount when considering the production and persistence of perennial grasses in the plant community. Furthermore, a better understanding of bud bank dynamics will deepen appreciation of the relationship between the formation and maintenance of belowground meristems, which will, in turn, inform a scientific basis for efficient management of key range grass species against the backdrop of the current and future impacts of climatic variability and/or climate change.

A field experiment using three perennial grasses, *Pennisetum mezianum* Leeke (also known as *Cenchrus mezianus* (Leeke) Morrone), *Digitaria macroblephara* (Hack. ex Schinz) Paoli, and *Themeda triandra* Forssk., was carried out to deepen our understanding of the mechanism behind grass species survival during the short dry season in the semi-arid rangelands of Kenya by evaluating their morphological and anatomical changes over three months. This study specifically examined how belowground traits critical to (1) resprouting potential and (2) water and nutrient acquisition shifted during the short dry season and in relation to aboveground growth as measured by tiller height. Resprouting potential was examined by measuring axillary bud numbers and sizes and available non-structural carbohydrates (starch) and total soluble sugars in plant crowns. Water and nutrient acquisition were examined by measuring root traits, including root tissue density, specific root length, root diameter, and root dry matter content. As the dry season progressed, we hypothesised that NSC content would decrease as it was used to support the plant, that bud bank numbers would remain stable, as they are the means by which the plant survives during the dormant season, that bud size would decline as the plants become more water stressed, and that root characteristics would remain unchanged as they would likely not experience active expansion during the dry season. We anticipated that *C. mezianus* would have greater resprouting capacity than *T. triandra* and *D. macroblephara* because it is considered more drought tolerant (Onchangwa 2017). We hypothesised that there would be a positive correlation between tiller height and NSC content as increasing tiller height would indicate increasing NSC storage, while increases in bud size would probably correlate with smaller NSC, as the NSCs are used to continue bud growth.

Methods

Study area and species

The study was conducted at a government demonstration farm, 70 km southeast of Nairobi City, Kenya, situated 1°48′ S, 36°47′ E and approximately 1 000 m above sea level (Figure 1), in which ecological zones IV, V and VI are represented. The short rainy season from October to December 2020 received below-average rainfall with an overall mean of 100 mm (KMD 2021). In contrast, the January to March 2021 dry season recorded an average rainfall of only 16 mm, with 25 mm occurring during the first week of February (National Drought Management Authority 2021). The farm is characterised by poorly drained black cotton soils (vertisols), which have a high clay content and a high level of calcium carbonate leading to impeded drainage (Katkar et al. 2019). The natural vegetation of the study area is savanna grassland, dominated by *C. mezianus, T. triandra,* and *D. macroblephara*, with *Acacia* tree species (Ndung'u et al. 2016). The three grass species studied are classified as warm-season C4 species (Boonman 1993), which are known to exhibit greater bud longevity and distinct bud dynamics compared to C3 species (Ott et al. 2019). *Digitaria macroblephara* is a perennial stoloniferous bunchgrass forming open tufts from a knotty rootstock that grows up to 100 cm tall (Clayton et al. 2016), and is common in soils with clay and is primarily found in ecological zones IV and V and rocky areas (Sombroek et al. 1982; FAO 1996). It is dominant in northeast and east Africa and is a relatively palatable species. *Pennisetum mezianum*, also found in ecological zones IV and V, is a perennial tufted grass with a short, stout, woody rhizome that grows up to 120 cm tall (Williams et al. 2016). It has moderate grazing value, can resist excess grazing pressure, and is commonly found in poorly-drained soils. This grass is avoided by grazing animals when senescent or mature because of its wiry or woody structure and low palatability (Odadi et al. 2013). *Themeda triandra* is a perennial tussock with erect culms that extend up to 200 cm high and is widespread in the rangeland ecosystems of Africa, Asia, and Australia (Snyman et al. 2013). It has a high grazing value and is fire-resistant. The grass is common in various soil types and is mainly found in ecological zones III, and IV, and rarely in V and VI (Snyman et al.2013).

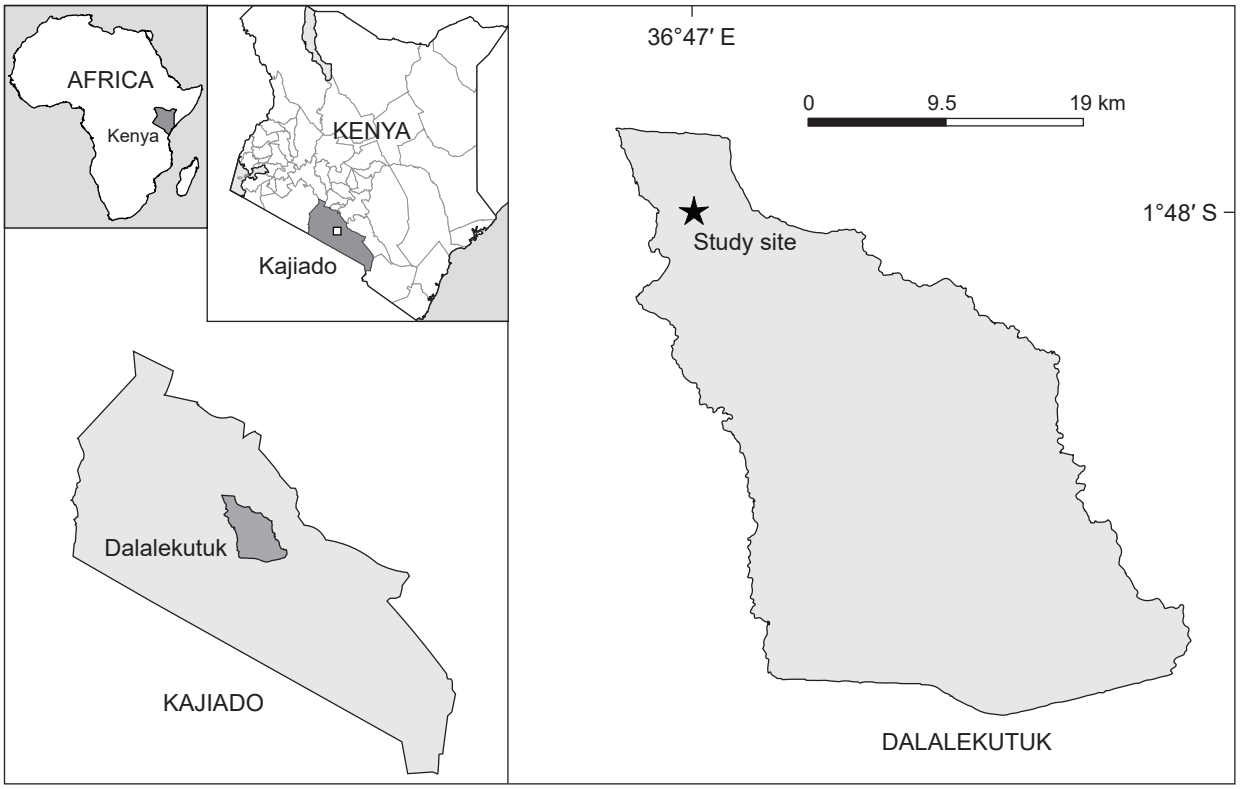

Figure 1: Study location within the Dalalekutuk ward in southeastern Kenya

Experimental design and layout

The experiment was a completely randomised, two-way factorial design comprising three grass species (*P. mezianum, T. triandra,* and *D. macroblephara)* with five sampling dates spaced at approximately 2-week intervals between January and March 2021. A four-week gap occurred between the third and fourth soil moisture sampling events owing to sustained rainfall during that period. Since the study focused on moisture depletion and plant physiological responses during dry conditions, sampling was suspended as minimal changes in soil moisture were expected under wet conditions. A 13 m × 13 m site was identified within the farm, fenced off, cleared of all vegetation, ploughed, and harrowed to a fine tilth. The site was then subdivided into nine plots measuring 3 m × 3 m with a 1 m boundary around each plot. The three grass species were randomly allocated to the nine contiguous plots, resulting in three replications per grass species.

Within each plot, 20 plants of the designated grass species were established using tuft splits obtained from mature grasses within the farm. Planting was done during the October–December short rains. Routine crop husbandry practices such as fertiliser application at planting, and weeding were applied uniformly across the study subplots until all the grasses were well established in all the subplots. Data collection commenced when the plants began flowering.

Sampling

Sampling was conducted in 2021, on 13 and 27 January, 12 February, and 12 and 26 March. On each sample date, an individual plant (genet) was randomly selected from each plot, excavated, placed on a 1 mm wire mesh screen, and the roots thoroughly washed. Plants were placed in plastic bags, stored in a cooler box at 4 °C, and transported to the University of Nairobi's laboratory for analysis. In the laboratory, three tillers were randomly selected from each genet. To determine the number of buds per tiller and their sizes, the tiller crown was placed under a dissecting microscope with magnifications between 7× and 40×. The sheaths were carefully removed to reveal the buds. Only the viable (turgid) buds were counted. Basal bud width was used as a proxy for bud size and measured using a vernier calliper with 0.01 mm precision.

Excavated plant genets were further separated into aboveground and belowground parts in the laboratory by clipping them at the culm base. Roots were scanned on a flatbed scanner to collect images from which root parameters (root diameter, total root length, and volume) were estimated using the software (Image J software, version 1.53). The root materials were then oven-dried at 72 °C for 72 h, and dry weight was determined using a high precision lab scale digital analytical electronic balance with a precision of 0.01 g. From these primary data, root tissue density (RTD) was calculated by dividing the total root dry weight by the root volume (g cm^{-3}). Specific root length (SRL) was calculated by dividing total root length by total root dry weight (m g^{-1}), while percent root dry matter content (RDMC) was calculated by dividing total root dry weight by total root fresh weight.

The average total soluble sugar (TSS) and starch content of the grass species was determined by the Anthrone Method (Yemm and Willis 1954) using approximately 30 mg of the ground root materials. The residue from TSS extraction was

used to estimate the starch content of the root material. Sugar and starch content were estimated by means of mass spectrophotometry at 625 nm (Yemm and Willis 1954). Sugar concentration was calculated using the regression equations based on the standard glucose solutions and starch concentration by multiplying the glucose concentration by a conversion factor of 0.9 (Osaki et al. 1991).

Soil moisture content was determined gravimetrically (Russell 1950). On each sample date, soil samples were obtained from a randomly selected point within the 3 m × 3 m subplot using a hand auger at 0–15 cm depth. The sample was immediately weighed and placed in a can which was tightly closed and transported to the laboratory. Following this, the samples were then dried at 110 °C for 24 hours and weighed again. Soil moisture was expressed as fresh weight divided by dry mass.

Data analysis

An analysis of variance (ANOVA) was performed using R software V4.03 (R Core Team 2020). To assess the effect of grass species and sampling date on bud numbers and sizes, root parameters, tiller height, and NSC, a two-way factorial treatment design with the fixed factors of grass species and sampling date in a completely randomised design was conducted. Tukey's HSD *post hoc* was used to differentiate the means. Pearson's correlation coefficients were calculated to identify relationships among the root morphological parameters, belowground bud parameters, between root parameters and NSC, and between belowground buds and NSC for the three species *C. mezianus, T. triandra, and D. macroblephara* across the sampling dates.

Results

Soil moisture content during the dry season

Soil moisture started at 33.6% and declined by 18.8% during the short dry season. However, a significant rainfall event in the middle of the dry season increased soil moisture significantly ($F_{4,35}$ = 120, p < 0.01) (Figure 2).

Resprouting potential during the short-dry season

The number of buds per tiller varied by species and sample date (Figure 3a). Among the three grass species, *P. mezianum* had a significantly higher number of buds (4.3) per tiller (Figure 3a) than the other two species which had approximately two buds per tiller at the end of the short-dry season. All three grass species maintained relatively stable numbers of buds per tiller over the course of the dry season.

Bud sizes varied significantly across grass species and sampling date. *Pennisetum mezianum* had the largest bud size across all species (Figure 3b), while *T. triandra* had the smallest buds. Bud sizes decreased significantly for *D. macroblephara* and *P. mezianum* as the short dry season lengthened (Figure 3b).

Total non-structural carbohydrates (NSC) increased as the short dry season progressed in all grass species. *Themeda triandra* had the highest NSC content across all sampling dates, with the highest content (483.49 mg g^{-1}) being recorded on the fifth sampling date (Figure 4c). Unlike the other two species which steadily increased their NSC content, the NSC of *T. triandra* dropped during the middle of the dry season but increased at the end of the dry season (Figure 4c). The TSS contents increased as the dry season progressed for all grass species (Figure 4a). Starch content increased in all species; however, their responses to the pulse in soil moisture varied. *Digitaria macroblephara* and *P. mezianum* responded immediately with starch accumulation, whereas *T. triandra* delayed its response until after the rainfall pulse (Figure 4b).

Root trait and aboveground shoot characteristics during the short dry season

Root diameter varied significantly across the three grass species with *P. mezianum* having the highest root diameter across all sampling dates (Table 1). *Themeda triandra* consistently had a larger root diameter than *D. macroblephara* except on the first sampling dates. Overall, *D. macroblephara* had a significantly higher root tissue density than the other two grass species. Root tissue density remained stable for each species across the sampling dates except for *T. triandra* at the first two sampling dates. Differences in specific root length (SRL) were significant among the grass species, with *D. macroblephara* having the highest SRL and *P. mezianum* having the lowest on all sampling dates. Generally, an increase in SRL for *D. macroblephara* occurred as the season progressed, especially after the mid-dry season precipitation event. Sampling date had a significant effect on the root dry matter, with the lowest being observed when soil moisture was highest on the third sampling date and higher values occurring at the end of the short dry season when soil moisture content was lowest.

Average tiller heights were significantly different between the first two sampling dates. All three species grew during the short dry growing season but mainly between the first and second sampling dates, with only *T. triandra* showing a large shoot height gain following the soil moisture pulse in the middle of the dry season. Of the three grass species, *T. triandra* was the tallest (Table 1).

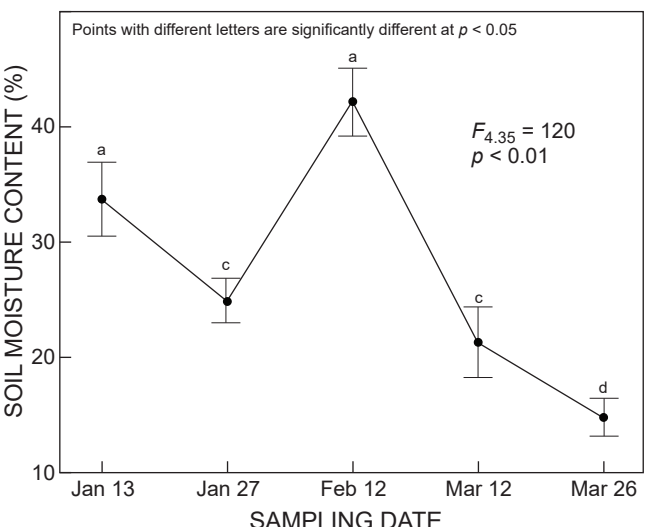

Figure 2: Mean soil moisture content (%) across five sampling dates (n = 3). Points are means ± standard deviation

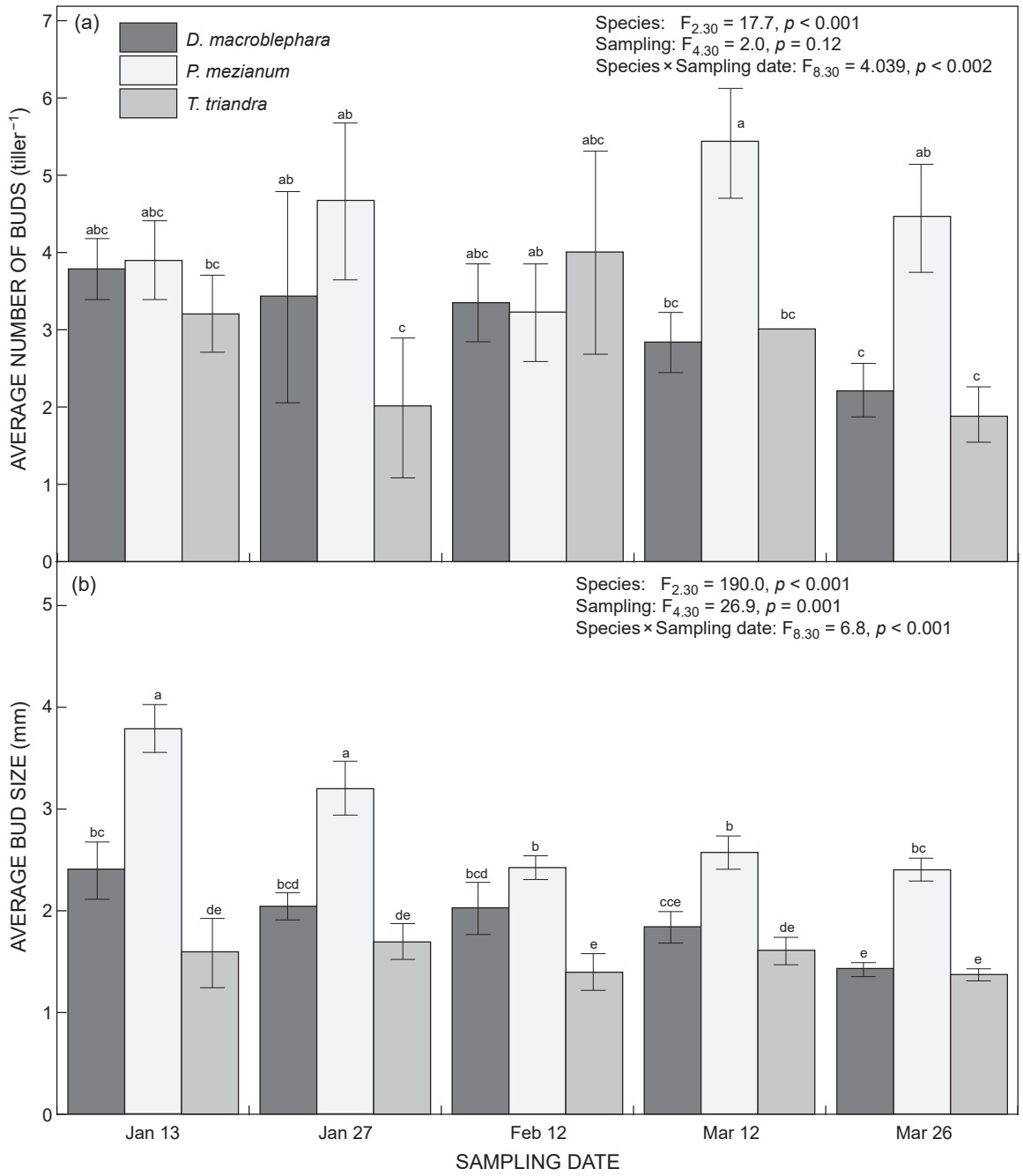

Figure 3: (a) Average number of buds per tiller, and (b) average bud size (mm) of the three grass species studied over time (n = 3). Points are means ± standard deviation

Pearson correlation coefficients for root, TSS, buds, and NSC parameters

There was a consistent negative correlation between the number of buds per tiller and bud sizes with tiller height (r = −0.52 and r = −0.68, respectively) and SRL (r = −0.58 and r = −0.63, respectively) (Table 2). Bud sizes were negatively correlated with NSC (r = −0.8), while NSC was positively correlated with tiller height and RDMC (r = 0.73 and r = 0.52, respectively). The RTD and SRL were negatively correlated to root diameter (RD) (r = −0.81 and r = −0.88, respectively).

Discussion

Resprouting potential changes during the dry season

The resprouting capacity of all three species was maintained during the short dry season with stable bud numbers and increasing available carbohydrates for resprouting despite declines in bud size. Bud numbers remained stable for all three species during the short dry period, demonstrating drought adaption where bud banks serve as meristem reservoirs during dormant periods for plants to continue

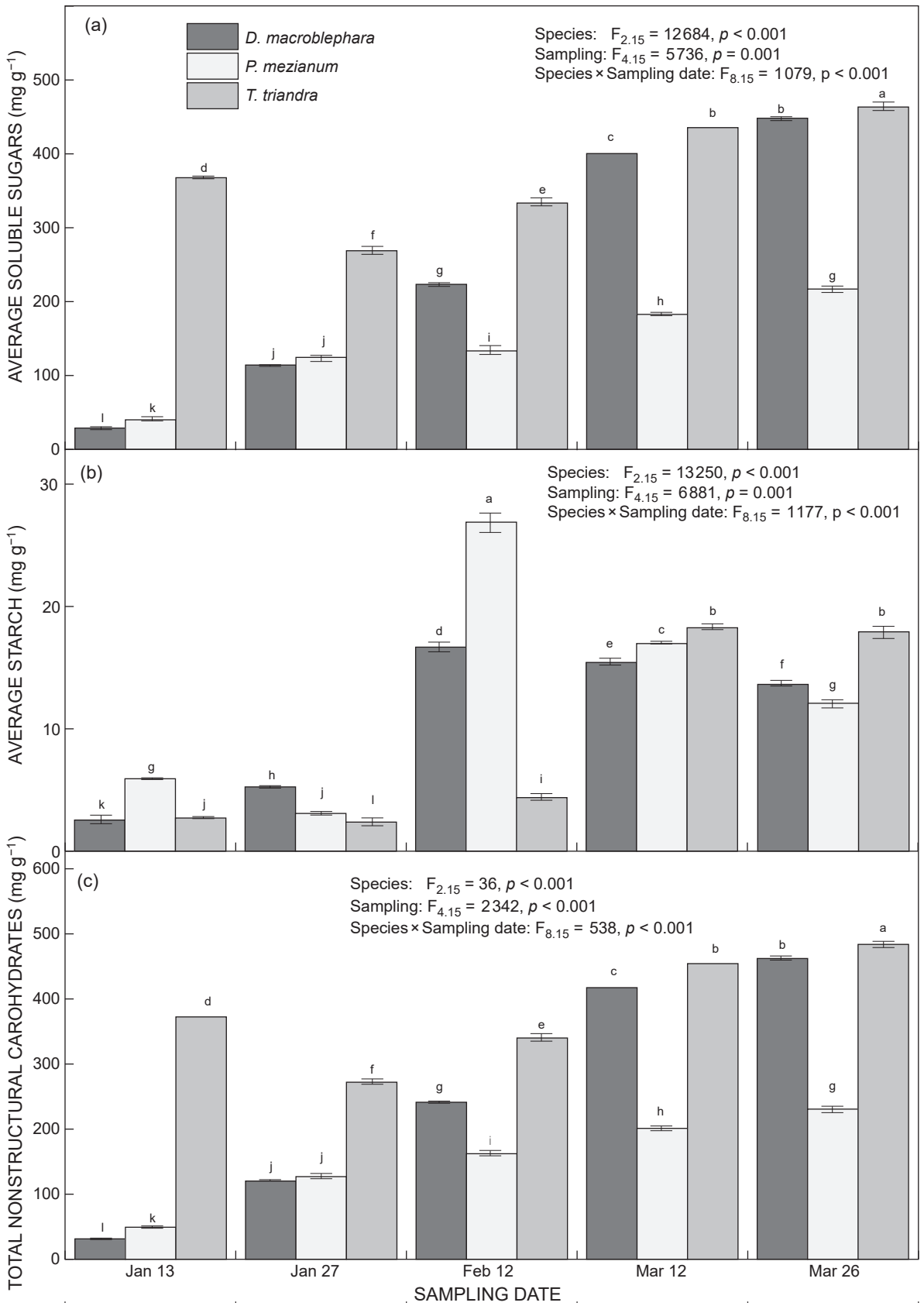

Figure 4: (a) Soluble sugars, (b) starch, and (c) non-structural carbohydrates (the sum of soluble sugars and starch) across grass species and different soil moisture deficits (n = 3). Bars with different letters are significantly different at $p < 0.05$. Points are means ± standard deviation.

Table 1: Average root diameter (mm), root tissue density (g cm^{-3}), specific root length (m g^{-1}), root dry matter content (%), and tiller height (cm) of three grass species across five sampling dates (n = 3)

Sampling dates	1	2	3	4	5
Root diameter (mm) Species: $F_{2, 30}$ = 233.2, p < 0.001 Sampling: $F_{4, 30}$ = 2.98, p < 0.05 Species×Sampling date: $F_{8, 30}$ = 2.98, p < 0.05					
D. macroblephara	$0.68^{cdef} \pm 0.03$	$0.58^{def} \pm 0.03$	$0.52^{f} \pm 0.03$	$0.55^{ef} \pm 0.06$	$0.51^{f} \pm 0.03$
C. mezianus	$1.33^{a} \pm 0.14$	$1.39^{a} \pm 0.10$	$1.24^{a} \pm 0.06$	$1.18^{a} \pm 0.17$	$1.15^{ab} \pm 0.09$
T. triandra	$0.63^{cdef} \pm 0.05$	$0.88^{bc} \pm 0.08$	$0.80^{cde} \pm 0.10$	$0.83^{cd} \pm 0.14$	$0.76^{cdef} \pm 0.08$
Root tissue density (g cm^{-3}) Species: $F_{2, 30}$ = 46.83, p < 0.001 Sampling: $F_{4, 30}$ = 2.24, p < 0.001 Species×Sampling date: $F_{8, 30}$ = 8.4, p < 0.001					
D. macroblephara	$0.4697^{ab} \pm 0.061$	$0.5604^{a} \pm 0.0388$	$0.4159^{ab} \pm 0.1666$	$0.4428^{ab} \pm 0.1471$	$0.5910^{a} \pm 0.1356$
C. mezianus	$0.0772^{c} \pm 0.0364$	$0.0562^{c} \pm 0.0308$	$0.2453^{bc} \pm 0.0711$	$0.2286^{bc} \pm 0.0210$	$0.2625^{bc} \pm 0.0319$
T. triandra	$0.6818^{a} \pm 0.069$	$0.0972^{c} \pm 0.0830$	$0.2236^{bc} \pm 0.1259$	$0.2807^{bc} \pm 0.0489$	$0.4667^{ab} \pm 0.114$
Specific root length (m g^{-1}) Species: $F_{2, 30}$ = 292.18, p < 0.05 Sampling: $F_{4, 30}$ = 13.33, p < 0.05 Species×Sampling date: $F_{8, 30}$ = 7.9, p < 0.001					
D. macroblephara	$347.89^{cde} \pm 39.32$	$422.61^{bc} \pm 14.66$	$392.39^{cd} \pm 39.48$	$504.11^{ab} \pm 3.12$	$551.68^{a} \pm 39.40$
C. mezianus	$163.67^{g} \pm 30.43$	$217.57^{fg} \pm 12.92$	$168.28^{g} \pm 10.06$	$197.07^{g} \pm 46.02$	$209.29^{fg} \pm 30.32$
T. triandra	$306.33^{de} \pm 31.66$	$348.51^{cde} \pm 42.77$	$324.32^{de} \pm 11.80$	$287.92^{ef} \pm 13.15$	$326.94^{de} \pm 4.93$
Root dry matter (%) Species: $F_{2, 30}$ = 0.15, p = 0.86 Sampling: $F_{4, 30}$ = 242.08, p < 0.001 Species×Sampling date: $F_{8, 30}$ = 2.4, p < 0.05					
D. macroblephara	$20.27^{d} \pm 1.57$	$38.61^{c} \pm 3.41$	$25.19^{d} \pm 3.21$	$52.04^{b} \pm 5.52$	$69.50^{a} \pm 4.52$
C. mezianus	$24.30^{d} \pm 4.21$	$40.42^{bc} \pm 2.07$	$23.99^{d} \pm 4.27$	$44.38^{bc} \pm 4.82$	$76.32^{a} \pm 1.40$
T. triandra	$21.93^{d} \pm 1.83$	$44.86^{bc} \pm 7.73$	$19.95^{d} \pm 1.46$	$50.89^{b} \pm 5.43$	$70.92^{a} \pm 1.97$
Tiller height (cm) Species: $F_{2, 30}$ = 133.62, p < 0.001 Sampling: $F_{4, 30}$ = 28.67, p < 0.001 Species×Sampling date: $F_{8, 30}$ = 3.5, p < 0.001					
D. macroblephara	$69.3^{e} \pm 5.27$	$97.7^{cd} \pm 6.46$	$99.2^{cd} \pm 9.05$	$98.9^{cd} \pm 13.83$	$101.4^{c} \pm 2.61$
C. mezianus	$76.6^{de} \pm 1.08$	$83.3^{cde} \pm 12.07$	$81.2^{cde} \pm 8.04$	$97.6^{cd} \pm 10.15$	$96.2^{cd} \pm 4.19$
T. triandra	$95.1^{cd} \pm 13.72$	$137.2^{ab} \pm 7.96$	$127.6^{b} \pm 5.72$	$146.2^{ab} \pm 4.62$	$151.6^{a} \pm 3.9$

Means within the same row and column with different superscripts are significantly different at p < 0.05

Values are presented as mean ± Standard Deviation, calculated using an R statistical model

Table 2: Pearson correlation coefficients for root morphological parameters, below ground bud parameters, between root parameters and NSC, and between below ground and NSC

	NSC	Tiller height	Average root diameter	Buds/tiller	Bud sizes	Root tissue density	Specific length	RDMC
NSC		0.7333**	−0.4976	−0.5861	−0.8042***	0.3860	0.4863	0.5277*
Tiller height			−0.2702	−0.527*	−0.6873**	−0.0156	0.1984	0.4258
Average root diameter				0.5752*	0.7580**	−0.8139***	−0.8860***	−0.0577
Buds/tiller					0.6269*	−0.3897	−0.5836*	−0.2682
Bud sizes						−0.5798*	−0.6343*	−0.2811
Root tissue density							0.6472*	0.0971
Specific root length								0.2453
RDMC								

growth in the subsequent season. Steady numbers of buds per tiller even under severe soil moisture deficit agrees with the findings of VanderWeide and Hartnett (2015) on grasses and forbs of tallgrass prairie during a two-year drought and Busso et al. (2011) under moderate to heavy defoliation of *Poa ligularis* grass species. Bud dormancy may fluctuate over the course of the dry season (Ott et al. 2019). Even though buds are present, they remain in a dormant state, preventing their recruitment to tiller.

For *P. mezianum*, the low TSS content can explain its slow growth rate. The increase in TSS with the increase in soil moisture deficit was expected as the plant prioritises storing more sugars in the roots for the next growing season. Roots are the primary nutrient-acquiring and storing organs, and as such, the reserved carbohydrates will increase as soil moisture content decreases (Snyman 2009). The stored sugars ensure the emergence of new tillers at the onset of rain (Guo et al. 2020) and their rapid growth, even

when there was limited soil moisture a few days prior. Increase in soluble sugars has been interpreted as a way of increasing osmotic potential under moisture deficit conditions (Hasibeder et al. 2015). Similar results were reported by Guo et al. (2020), who in their study on perennial ryegrass seedlings, reported increased sugar levels in roots under moisture deficit conditions. Our results are in agreement with those of Priyadarshini et al. (2016), who looked at the interactions between trees and perennial grasses on root characteristics of range grasses in the Arid and Semi-Arid Lands (ASALs) of South Africa. Their study found that soluble sugars formed a significant portion of NSC in the roots of C4 grasses.

Starch levels were low in our study and formed a small fraction of the NSC. Similar results were reported by Guo et al. (2020) who found that starch content did not change significantly in roots but significantly decreased in shoots under drought conditions, possibly because the grasses allocated more carbon for storage in roots in addition to the amount required for growth. Despite the low starch content in NSC, it is crucial for long-term storage, especially when there is an extended period of moisture deficit (Busso et al. 1990).

Themeda triandra had the highest NSC content throughout the short dry season, which might partially explain its relatively fast growth rate. Ji et al. (2020) observed that plants with thinner root diameters had higher levels of soluble sugars than roots with a thicker diameter, as in the case of *T. triandra* and *D. macroblephara* in our study. The NSC increased gradually in all three grass species as the moisture deficit increased. Under moisture deficit, NSC in roots has been shown to increase at the expense of the amount in shoots, which is thought to facilitate the emergence of new tillers at the onset of rains (Guo et al. 2020). Where carbon (C) uptake is severely limited, priority has been given to belowground carbon storage over aboveground storage (Bahn et al. 2013). This paradigmatic shift is necessitated by the preparation for the next season's growth, when resources will be used to activate bud outgrowth into new tillers until leaf development and photosynthesis can enable the tiller to be self-sustaining. Oosthuizen and Snyman (2003) reported high levels of NSC in *T. triandra* with an increase of up to 25% under moisture deficit. Busso et al. (1990), in their study with North American grass species, reported an increase of up to seven times in belowground NSC in both clipped and unclipped plants under severe moisture deficit. It was theorised that the rise in belowground NSC was in preparation for rapid initial regrowth once favourable soil moisture conditions resumed (Hasibeder et al. 2015). Level of NSC have been shown to remain relatively high in the early days after the cessation of drought, thus ensuring the successful formation of new tillers (Guo et al. 2020).

Species differences

The average number of buds varied among the three grass species, which may be explained by their different growth morphologies. *Pennisetum mezianum* is rhizomatous, *D. macroblephara* has horizontal extravaginal stolons, and *T. triandra* is a tufted perennial grass characterised by upright bud growth (intravaginal outgrowth), resulting in many new shoots next to the parent plant (Williams et al. 2016). Rhizomatous grasses, with their individual tillers more disbursed from one another, may prioritise maintenance of more buds at the base of the tillers than stoloniferous and tufted growth forms. Bud production per tiller of these three grasses was similar to bud production numbers of perennial grasses of the Kalahari sandveld region of Botswana (Hartnett et al. 2006; Dalgleish et al. 2012). Among grasses of the same genus with similar growth characteristics, the average number of buds per tiller lies within the same range. Dalgleish et al. (2012) reported that *P. macrourum* (now *Cenchrus caudatus* (Schrad.) Kuntze as per WFO Plant List), had, on average, a relatively higher number of buds per tiller (3.0), higher than many other species (*Aristida* species, *E. cylindriflora*, *P. squarrosa* and *P. patens*). In the same study, *Digitaria eriantha* had 2.5 buds per tiller, similar to the number of buds in *D. macroblephara*.

The higher number of buds per tiller found in *P. mezianum* implies a higher resilience to the vagaries of nature than its contemporaries since it is able to more rapidly replace tillers that have been removed. More belowground buds also can increase the dominance of that particular species in its habitat by producing a high number of new tillers when conditions are favourable due to their ability to capitalise on periods of high resource availability. In addition, large numbers of buds are a natural adaptive mechanism against environmental variability since they enhance the growth of grasses after grazing (Hartnett et al. 2006). For species that do not maintain large belowground bud banks, such as *D. macroblephara* and *T. triandra,* tiller recruitment is slow and limits their ability to respond to disturbances (Russell et al. 2015). For such grass species, the ability to recover from stresses imposed by drought, fire, or grazing may be limited.

Large bud sizes, as demonstrated by *P. mezianum,* have been associated with a well-developed and active vascular connectivity with the polar auxin transport system (PATS), which increases auxin export and nutrient import into the bud (Waldie et al. 2010). More resources are likely to be stored in these buds, ensuring a higher survival rate and competitiveness during the early phase of ontogenesis (Wu et al. 2021). Grass species with larger buds could also have longer bud longevity, leading to a large bud bank comprising multiple-year cohorts (Ott et al. 2019). The decrease in bud size with increasing water deficit may be attributed to a reduction in water supply to buds, which could result in decreased growth and turgor pressure. Our results reflect those of Pembleton et al. (2010), who showed that species that experienced moisture deficit had smaller buds.

Pennisetum mezianum had a greater number of buds per tiller and larger bud sizes than the other two species but also the lowest soluble sugars and nonstructural carbohydrates, which may indicate that carbohydrate reserves were used to create and maintain its buds. However, bud construction and metabolic costs are modelled to be low (Vesk and Westoby 2004). In addition, stem bases can also be sources of non-structural carbohydrate storage (Richards and Caldwell 1985). Therefore, there may be other reasons for the lowered levels of carbohydrates in *P. mezianum* roots apart from axillary bud costs.

Effects of soil moisture variability on tiller height

Tiller heights differed among the grass species, most likely due to their inherent genetic and morphological differences.

Fast-growing species with erect culms are usually taller than the slow-growing species with semi-erect culms and have been shown to have a competitive advantage over others, as they use resources more efficiently (Mganga 2009). However, the tall, erect *T. triandra* is more likely to be grazed first due to its palatability when there is overgrazing. Nevertheless, *T. triandra's* rapid growth rate enables it to out-compete other species for water, light, and nutrients (Dunning et al. 2017).

The progressive increase in tiller height with grass maturity was expected since it is a function of growth and development (Machogu 2013; Koech et al. 2016; Kamau 2020). The negative relationship between tiller height, number of buds per tiller, and bud sizes observed in our study suggests that when plants invest a greater proportion of their resources in increasing bud numbers and sizes, fewer resources are available for rapid growth and plant biomass. This was also supported by the negative relationship between NSC in roots and bud sizes in our study. Bud banks are highly resource-dependent, and the reserves stored in the buds are used for resprouting and supporting the parent plant (Bell and Ojeda 1999).

Root characteristics during short dry seasons

Differences in root diameters (RD) among the three grasses were expected due to their distinct genetic differences. However, grass species with a larger RD have a higher resource storage capacity, transport more water, and have a stronger soil-penetrating ability to access deeper layers in drying soil conditions than those with smaller RDs (Davies and Bacon 2003). In addition, thicker roots generally have a lower turnover rate, longer lifespan, and larger cross-sectional areas, making them more resistant to external stress factors (Gu et al. 2011). In contrast, species with a large RD have been shown to have a low instantaneous moisture uptake (Roumet et al. 2011). However, they can maintain high cumulative water uptake over a longer time and, hence, survive with less water during dry seasons (Ji et al. 2020). *Digitaria macroblephara* and *T. triandra*, with smaller root diameters, were observed to be laterally oriented, meaning that they were best adapted to utilise soil moisture content in the upper soil profile. Grasses with small RD tend to acquire resources faster, which is advantageous under soil moisture deficit conditions (Fort et al. 2013). These grasses also have a high nutrient uptake, rendering them more adaptable to rapid growth and establishment at the onset of the rains. Similar to this study, several previous studies have reported a marginal decrease in RD with increased soil moisture deficit; this is attributed to improved nutrient and water acquisition (Fuentealba et al. 2015; Ma et al. 2018).

Root tissue density (RTD) is a fundamental trait in comparative root ecology, being increasingly used as an indicator of plant species resource use strategy. Low RTD has been associated with fast-growing species in nutrient-rich habitats (Wahl and Ryser 2000). Contrary to our expectations, *P. mezianum* (a slow-growing species) had the lowest RTD among the three grass species. This was attributed to several characteristics of its roots. First, *P. mezianum* roots were found to have a relatively thick outside coat, which increased their volume. Second, the low RTD could be accounted for by the relatively high water content in its roots (Kakusu 2022). For *T. triandra* and *D. macroblephara,* the slight increase in RTD with an increase in moisture deficit meant that resources were being directed toward root development. This also means that when there is sufficient moisture, these grasses develop low-density roots, which are formed relatively fast and result in rapid aboveground biomass development. However, as soil moisture deficit increases, more focus is given to more dense roots with longer lifespans.

Specific root length (SRL) is the ratio between root length and root mass and reflects the root's efficiency in exploring the soil in search of nutrients and water (Hernández et al. 2010). In this study, *T. triandra* and *D. macroblephara* had the highest SRL. In contrast, *P. mezianum* had the lowest SRL, suggesting that *T. triandra* and *D. macroblephara* had more efficient water acquisition strategies. A high SRL (thinner roots) facilitates better exploration of the soil profile for water, leading to increased overall root hydraulic conductance (Hernández et al. 2010). This was further supported by the negative relationship between RD and SRL in this study. Specific root length has also been associated with higher nitrogen uptake rates (Reich et al. 1998), root respiration (Liu et al. 2020), and shorter root lifespan (Ryser 2006). High SRL is generally recorded in fast-growing plant species, which is closely associated with a high root turnover, root elongation rate, and high nutrient uptake, which is a function of the root surface area (Leuschner et al. 2013; Freschet et al. 2015). Similar results were reported by Fort et al. (2013) in their study of root and leaf functional traits of eleven perennial temperate grasses. The less drought-tolerant species were found to have a high SRL and high N uptake, while the more drought-tolerant species had a low SRL. As *P. mezianum* had a lower SRL, this meant that the root turnover was low, and a higher investment of resources per unit length was needed to ensure the longevity of the current season's roots (Eissenstat et al. 2000). In other words, the root growth strategy of *P. mezianum* was more resource-conservative due to thicker roots, which enhanced soil penetration as the profile dried up (Davies and Bacon 2003). Low SRL, however, meant that less soil volume was explored for water and nutrient acquisition.

In *D. macroblephara,* SRL increased with an increase in soil moisture deficit, while *T. triandra* and *P. mezianum* maintained a constant SRL with an increase in soil moisture deficit. Kadam et al. (2015) reported conflicting findings from their study on rice and wheat tolerance to water deficit. In rice, the SRL increased with an increase in water deficit, but in wheat, the opposite was true. A significant decrease in SRL in wheat cultivars was attributed to an increase in average root thickness and total root weight density. Similarly, de Vries et al. (2016), in their study on grassland species under controlled conditions, reported a decrease in SRL with increased moisture deficit in *Anthoxanthum odoratum* L. and *Leontodon hispidus* L., while SRL increased in *Rumex acetosa* L. and remained constant in *Dactylis glomerata* L.

As expected, root dry matter content (RDMC) increased with an increase in soil moisture deficit. Being a ratio of dry weight: fresh weight, it was expected that the moisture content in plants would decrease as it decreased in the soil. Liu et al. (2020) reported an increase in root carbon allocation with increase in moisture deficit, which contributed to an increase in RDMC. In addition, increased RDMC was

attributed to an increase in NSC, which increased as the moisture deficit increased. This was confirmed by the positive relationship between NSC and RDMC in our study. High RDMC has been linked to high inorganic N, which would cause high N availability in the soil due to decreased uptake from the soil (de Vries et al. 2016). Pérez-Ramos et al. (2012) reported a positive correlation between RDMC, leaf thickness, and leaf dry matter content. They linked the high RDMC to water use efficiency and low SRL.

Conclusion

Although soil moisture deficits can have negative impacts on plant growth, perennial grasses preserved their resprouting capacity during the short dry season with stable bud numbers and increasing available carbohydrates for resprouting despite declines in bud size for some species. This study also showed that grasses can respond to moisture deficit by having thicker roots with longer lifespans and more penetrating power. Further, NSC in underground parts is likely to increase when there is some form of moisture deficit in grasses in preparation for the next season's growth. Belowground buds and roots play an important role in aboveground vegetation dynamics, with patterns of variability in these belowground organs being associated with changes in soil moisture content. Findings from this study contribute to our understanding of how roots and buds are expected to change with climate change and their role in the changing composition and dynamics of grasslands.

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References

Bahn M, Lattanzi FA, Hasibeder R, Wild B, Koranda M, Danese V, Bruggemann N, Schmitt M, Siegwolf R, Richter A, 2013. Responses of belowground carbon allocation dynamics to extended shading in mountain grassland. *New Phytologist* 198: 116–126.

Bell TL, Ojeda F. 1999. Underground starch storage in Erica species of the Cape Floristic Region–differences between seeders and resprouters. *New Phytologist* 144: 143–152.

Boonman G. 1993. *East Africa's grasses and fodders: their ecology and husbandry*. Dordrecht: Springer.

Busso CA, Gittins C, Becker GF, Ghermandi L. 2011. Tiller hierarchy and defoliation frequency determine bud viability in the grass *Poa ligularis*. *Ecological Research* 26: 985–997.

Busso CA, Richards JH, Chatterton NJ. 1990. Nonstructural carbohydrates and spring regrowth of two cool-season grasses: interaction of drought and clipping. *Rangeland Ecology and Management* 43: 336–343.

Cervigni R, Morris M (eds). 2016. Confronting drought in Africa's drylands: Opportunities for enhancing resilience. World Bank Publications.

Clayton WD, Vorontsova MS, Harman KT, Williamson H. 2016. *GrassBase: the online world grass flora*. https://www.kew.org/data/grasses-db.html

Dalgleish HJ, Ott JP, Setshogo MP, Hartnett DC. 2012. Inter-specific variation in bud banks and flowering effort among semi-arid African savanna grasses. *South African Journal of Botany* 83: 127–133.

Davies WJ, Bacon MA. 2003. .Adaptation of roots to drought. In *Root Ecology*. Berlin, Heidelberg: Springer Berlin Heidelberg. pp 173–192.

De Vries FT, Brown C, Stevens CJ. 2016. Grassland species root response to drought: consequences for soil carbon and nitrogen availability. *Plant and Soil* 409: 297–312.

Dunning LT, Liabot AL, Olofsson JK, Smith EK, Vorontsova MS, Besnard G, Simpson KJ, Lundgren, MR, Addicott E, Gallagher RV, Chu Y, Pennington RT, Christin P-A, Lehmann CER. 2017. The recent and rapid spread of *Themeda triandra*. *Botany Letters* 164: 327–337.

Eissenstat DM, Wells CE, Yanai RD, Whitbeck JL. 2000. Building roots in a changing environment: implications for root longevity. *New Phytologist* 147: 33–42.

Eshel A, Beeckman T (eds). 2013. *Plant roots: the hidden half*. CRC press.

FAO. 1996. Agro-ecological Zoning Guidelines. *FAO Soils Bulletin 73*. Rom. www.fao.org

Fort F, Jouany C, Cruz P. 2013. Root and leaf functional trait relations in Poaceae species: implications of differing resource-acquisition strategies. *Journal of Plant Ecology* 6: 211–219.

Freschet GT, Swart EM, Cornelissen JH. 2015. Integrated plant phenotypic responses to contrasting above-and below-ground resources: Key roles of specific leaf area and root mass fraction. *New Phytologist* 206: 1247–1260.

Fuentealba MP, Zhang J, Kenworthy KE, Erickson JE, Kruse J, Trenholm LE. 2015. Root development and profile characteristics of bermudagrass and zoysiagrass. *HortScience* 50: 1429–1434.

Gu J, Yu S, Sun Y, Wang Z, Guo D. 2011. Influence of root structure on root survivorship: an analysis of 18 tree species using a minirhizotron method. *Ecological Research* 26: 755–762.

Guo T, Tian C, Chen C, Duan Z, Zhu Q, Sun LZ. 2020. Growth and carbohydrate dynamic of perennial ryegrass seedlings during PEG-simulated drought and subsequent recovery. *Plant Physiology and Biochemistry* 154: 85–93.

Hartnett DC, Setshogo MP, Dalgleish HJ. 2006. Bud banks of perennial savanna grasses in Botswana. *African Journal of Ecology* 44: 256–263.

Hasibeder R, Fuchslueger L, Richter A, Bahn M. 2015. Summer drought alters carbon allocation to roots and root respiration in mountain grassland. *New Phytologist* 205: 1117–1127.

Hendrickson JR, Briske DD. 1997. Axillary bud banks of two semiarid perennial grasses: occurrence, longevity, and contribution to population persistence. *Oecologia* 110: 584–591.

Hernández EI, Vilagrosa A, Pausas JG, Bellot J. 2010. Morphological traits and water use strategies in seedlings of Mediterranean coexisting species. *Plant Ecology* 207: 233–244.

Ji L, Attaullah K, Wang J, Yu D, Yang Y, Yang L, Lu Z. 2020. Root traits determine variation in nonstructural carbohydrates (NSCs) under different drought intensities and soil substrates in three temperate tree species. *Forests* 11: 415.

Kadam NN, Yin X, Bindraban PS, Struik PC, Jagadish KS. 2015. Does morphological and anatomical plasticity during the vegetative stage make wheat more tolerant of water deficit stress than rice? *Plant Physiology* 167: 1389–1401.

Kakusu EM. 2022. Effects of Soil Moisture Variability on Morphological and Anatomical Attributes of Roots and Buds of Selected Rangeland Grasses of Southern Rangelands of Kenya. MSc Thesis, University of Nairobi, Nairobi, Kenya.

Kamau HN. 2020. Evaluation of twenty three indigenous grass species suitability for rehabilitation of degraded semi-arid rangeland in Suswa, Kenya. MSc Thesis, University of Nairobi, Nairobi, Kenya.

Katkar RN, Kharche VK, Konde NM. 2019. Characterization and problems of saline/sodic vertisols and their management options. *Research Developments in Saline Agriculture:* 357-368.

KMD (Kenya Meteorological Department). 2021. *State of the climate – Kenya 2020*. Nairobi: Kenya Meteorological Department. https://meteo.go.ke/resources/downloads/state-climate-report-kenya-2020

Koech OK, Kinuthia RN, Karuku GN, Mureithi SM, Wanjogu R. 2016. Irrigation levels affects biomass yields and morphometric characteristics of range grasses in arid rangelands of Kenya. *SpringerPlus* 5: 1–15.

Leuschner C, Gebel S, Rose L. 2013. Root trait responses of six temperate grassland species to intensive mowing and NPK fertilisation: a field study in a temperate grassland. *Plant and Soil* 373: 687–698.

Li Y, Bao G, Zhang P, Feng X, Ma J, Lu H, Liu K. 2023. Changes in bud bank and their correlation with plant community composition in degraded alpine meadows. *Frontiers in Plant Science* 14: 1259340.

Liu Y, Li P, Wang T, Liu Q, Wang W. 2020. Root respiration and belowground carbon allocation respond to drought stress in a perennial grass (*Bothriochloa ischaemum*). *Catena* 188: 104449.

Liu Z, Zhu J, Xia J, Huang K. 2023. Declining resistance of vegetation productivity to droughts across global biomes. *Agricultural and Forest Meteorology* 340: 109602.

Ma Z, Guo D, Xu X, Lu M, Bardgett RD, Eissenstat DM, Hedin LO. 2018. Evolutionary history resolves global organization of root functional traits. *Nature* 555: 94–97.

Machogu C. 2013. A comparative study of the productivity of Brachiaria hybrid cv. Mulato II and native pasture species in semi-arid rangelands of Kenya. MSc thesis, University of Nairobi, Nairobi, Kenya.

Mganga KZ. 2009. Impact of grass reseeding technology on rehabilitation of degraded rangelands: A case study of Kibwezi district, Kenya. MSc Thesis, University of Nairobi, Nairobi, Kenya.

Morkunas I, Ratajczak L. 2014. The role of sugar signaling in plant defense responses against fungal pathogens. *Acta Physiologiae Plantarum* 36: 1607–1619.

Muller B, Pantin F, Génard M, Turc O, Freixes S, Piques M, Gibon Y. 2011. Water deficits uncouple growth from photosynthesis, increase C content, and modify the relationships between C and growth in sink organs. *Journal of Experimental Botany* 62: 1715–1729.

Nardone A, Ronchi B, Lacetera N, Ranieri MS, Bernabucci U. 2010. Effects of climate changes on animal production and sustainability of livestock systems. *Livestock Science* 130: 57–69.

National Drought Management Authority. 2021. Kajiado County drought monitoring and early warning bulletin March 2021. *NDMA-KnowledgeWeb*

Ndung'u PLN, Wasonga OV, Mnene WN, Koech OK, Elhadi YAM. 2016. Community perception of importance, trends, and variations of indigenous grasses in Southern Kenya. Fifth RUFORUM Biennial Regional Conference, 14: 807 – 817.

Odadi WO, Karachi MK, Abdulrazak SA, Young TP. 2013. Protein supplementation reduces non-grass foraging by a primary grazer. *Ecological Applications* 23: 455–463.

Onchangwa AM. 2017. Suitability of selected drought tolerant grass species as trap plants for chilo partellus (swinhoe) in Kisumu county, Kenya. Doctoral Dissertation, Kenyatta University, Kenya.

Oosthuizen IB, Snyman HA. 2003. Impact of water stress on growth reserves and re-growth of *Themeda triandra* (Forssk) following defoliation. *African Journal of Range and Forage Science* 20: 41–45.

Ott JP, Klimešová J, Hartnett DC. 2019. The ecology and significance of below-ground bud banks in plants. *Annals of Botany* 123: 1099–1118.

Osaki M, Shinano T, Tadano T. 1991. Redistribution of carbon and nitrogen compounds from the shoot to the harvesting organs during maturation in field crops. *Soil Science and Plant Nutrition* 37: 117–128.

Pembleton KG, Volenec JJ, Rawnsley RP, Donaghy DJ. 2010. Partitioning of taproot constituents and crown bud development are affected by water deficit in regrowing alfalfa (Medicago sativa L.). *Crop Science* 50: 989–999.

Pérez-Ramos IM, Roumet C, Cruz P, Blanchard A, Autran P, Garnier E. 2012. Evidence for a 'plant community economics spectrum' driven by nutrient and water limitations in a Mediterranean rangeland of southern France. *Journal of Ecology*. 100: 1315–1327.

Perlikowski D, Augustyniak A, Masajada K, Skirycz A, Soja AM, Michaelis Ä, Kosmala A. 2019. Structural and metabolic alterations in root systems under limited water conditions in forage grasses of Lolium-Festuca complex. *Plant science*. 283: 211–223.

Piipponen J, Jalava M, de Leeuw J, Rizayeva A, Godde C, Cramer G, Kummu M. 2022. Global trends in grassland carrying capacity and relative stocking density of livestock. *Global Change Biology*. 28: 3902–3919.

Priyadarshini KVR, de Bie S, Heitkönig IM, Woodborne S, Gort G, Kirkman KP, Prins HH. 2016. Competition with trees does not influence root characteristics of perennial grasses in semi-arid and arid savannas in South Africa. *Journal of Arid Environments*. 124: 270–277.

R Core Team. 2020. R: a language and environment for statistical computing.

Reich PB, Walters MB, Tjoelker MG, Vanderklein D, Buschena C. 1998. Photosynthesis and respiration rates depend on leaf and root morphology and nitrogen concentration in nine boreal tree species differing in relative growth rate. *Functional Ecology*. 12: 395–405.

Reichmann LG, Sala OE. 2014. Differential sensitivities of grassland structural components to changes in precipitation mediate productivity response in a desert ecosystem. *Functional Ecology*. 28: 1292–1298.

Richards JH, Caldwell MM. 1985. Soluble carbohydrates, concurrent photosynthesis and efficiency in regrowth following defoliation: A field study with *Agropyron* species. *Journal of Applied Ecology*. 22: 907–920.

Roumet C, Urcelay C, Diaz S. 2011. Suites of root traits in species growing differ between the and perennial. *New Phytologist*. 170: 357–367.

Russell J. 1950. *Soil conditions and plant growth.* London: Longmans, Green.

Russell ML, Vermeire LT, Ganguli AC, Hendrickson JR. 2015. Season of fire manipulates bud bank dynamics in northern mixed-grass prairie. *Plant Ecology*. 216: 835–846.

Ryser P. 2006. The mysterious root length. *Plant and Soil*. 286: 1–6.

Snyman HA. 2009. Root studies on grass species in a semi-arid South Africa along a soil-water gradient. *Agriculture, Ecosystems and Environment*. 131: 247–254.

Snyman HA, Ingram LJ, Kirkman KP. 2013. *Themeda triandra*: a keystone grass species. *African Journal of Range and Forage Science* 30: 99-125)

Sombroek WG, H. Braun MH, Van der Pouw BJA. 1982. *Exploratory soil map and agro-climatic zone map of Kenya, 1980. Scale 1: 1,000,000*. Kenya Soil Survey.

VanderWeide BL, Hartnett DC. 2015. Belowground bud bank response to grazing under severe, short-term drought. *Oecologia*. 178: 795–806.

Vesk PA, Westoby M. 2004. Funding the bud bank: a review of the costs of buds. *Oikos*. 106: 200–208.

Wahl S, Ryser P. 2000. Root tissue structure is linked to ecological strategies of grasses. *New Phytologist*. 148: 459–471.

Waldie T, Hayward A, Beveridge CA. 2010. Axillary bud outgrowth in herbaceous shoots: how do strigolactones fit into the picture? *Plant Molecular Biology*. 73: 27–36.

Williams EV, Ntandu JE, Ficinski P, Vorontsova M. 2016. Checklist of Serengeti ecosystem grasses. *Biodiversity Data Journal*. 4: e8286

Wu J, Chen X, Xu L, Qian J, Liu Z. 2021. The spatial pattern of the belowground bud bank and its responses to soil water status in the interdune lowlands of active sand dunes of Inner Mongolia, China. *Restoration Ecology*. 29: e13223.

Yemm EW, Willis AJ. 1954. The estimation of carbohydrates in plant extracts by anthrone. *Biochemical Journal* 57: 508–514.

Yuan J, Li H, Yang Y. 2020. The compensatory tillering in the forage grass Hordeum brevisubulatum after simulated grazing of different severity. *Frontiers in plant science*. 11: 524216.

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