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Remotely sensed C3 and C4 grass species aboveground biomass variability in response to seasonal climate and topography

Cletah Shoko[1,2] | Onisimo Mutanga[1] | Timothy Dube[3]

[1]Discipline of Geography, School of Agriculture, Earth & Environmental Sciences, University of KwaZulu Natal, Pietermaritzburg, South Africa

[2]School of Geography, Archaeology and Environmental Studies, University of Witwatersrand, Johannesburg, South Africa

[3]Department of Earth Sciences, Institute for Water Studies, University of the Western Cape, Capetown, South Africa

Correspondence
Cletah Shoko, Discipline of Geography, School of Agriculture, Earth & Environmental Sciences, University of KwaZulu Natal, P. Bag X01, Scottsville, 3209, Pietermaritzburg, South Africa.
Email: kiletashoko@gmail.com

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Abstract

Seasonal climate and topography influence C3 and C4 grass species aboveground biomass (AGB). Climate change further threatens these grasses AGB, thereby compromising their ability to provide ecosystem goods and services. This emphasises the need to monitor their AGB for well-informed management. New-generation sensors, with improved resolution capabilities present an opportunity to explore C3 and C4 AGB. This study therefore investigated the response of remotely sensed C3 and C4 grasses AGB to seasonal climate and topography. Overall, the spatial and temporal responses of AGB due to seasonal climate and topography were observed across the study area. For example, in March, a marked increase in C4 AGB was associated with an increase in rainfall, with the highest significant positive relationship (R^2 = 0.82, p < 0.005). Elevation had very significant positive relationship (R^2 = 0.84; p < 0.005) with C3 and highest negative (R^2 = −0.77; p < 0.005) with C4 AGB. During the winter fall, AGB significantly decreased from averages of 2.592 and 1.101 kg/m^2 in winter (May), to 0.718 and 0.469 kg/m^2 in August, for C3 and C4 grasses, respectively. These findings provide a key step in monitoring rangelands and assessing management practices to boost productivity.

Résumé

Le climat saisonnier et la topographie influencent des espèces de graminées C3 et C4 sur la biomasse aérienne (AGB). Le changement climatique menace davantage ces graminées AGB, compromettant ainsi leur capacité à fournir des biens et services liés à l'écosystème. Cela souligne la nécessité de surveiller leur AGB pour une gestion bien informée. Les capteurs de nouvelle génération, dotés de capacités de résolution améliorées, offrent l'occasion d'explorer les C3 et C4 AGB. Cette étude a donc examiné le résultat des graminées AGB C3 et C4 à télédétection au climat saisonnier et à la topographie. Dans l'ensemble, les résultats spatiaux et temporels de l'AGB en raison du climat saisonnier et de la topographie ont été observés dans la zone d'étude. Par exemple, en mars, une augmentation marquée de l'AGB C4 a été associée à une augmentation des précipitations, avec la relation positive significative la plus élevée (R2 = 0,82, P <0,005). L'élévation a eu une relation positive très significative (R2 = 0,84; P <0,005) avec C3 et la plus négative (R2 = -0,77; P <0,005) avec C4 AGB.

Au cours de l'automne, l'ABG a considérablement diminué, passant de 2,592 kg / m2 et 1,101 kg / m2 en hiver (mai) à 0,718 kg / m2 et 0,469 kg / m2 en août, respectivement pour les graminées C3 et C4. Ces résultats constituent une étape clé dans la surveillance des pâturages et l'évaluation des pratiques de gestion pour à accroître la productivité.

KEYWORDS

climatic effect, productivity, radiation, rainfall, rangeland resources, temporal variability

1 | INTRODUCTION

C3 and C4 grass species aboveground biomass (AGB) directly reflects their level of productivity, structure and functioning. Globally, C4 grasses account for 20%–25% to overall terrestrial productivity (Still, Pau, & Edwards, 2014) and cover large areas in Africa and Australia, when compared to C3. These grasslands also operate as agro-ecosystems, providing forage for livestock (Woodward, Lomas, & Kelly, 2004), which support millions of people, especially in Africa. C4 grasses have also been reported to have better palatability, highly suitable for animal production (Snyman, Ingram, & Kirkman, 2013), compared to C3. C3 and C4 also facilitate nutrient cycling and carbon sequestration. For example, C4 grasses store a substantial amount of carbon, than C3 grasses (Adair & Burke, 2010), and the Intergovernmental Panel on Climate Change (IPCC) has emphasised species AGB as one of the principal carbon pools of terrestrial ecosystems (Eggleston, Buendia, Miwa, Nagara, & Tanabe, 2006; Vashum & Jayakumar, 2012). C3 and C4 AGB also determines the occurrence and intensity of fire regimes (Everson, Everson, & Tainton, 1985) in the management of grassland ecosystems. Most importantly, the seasonal variations in climatic conditions influence C3 and C4 grasses AGB over time, thereby influencing their ability to provide ecosystem goods and services.

Climate and topography influence the spatial and temporal variability of C3 and C4 grasses AGB (Auerswald et al., 2012; Lee, 2011). These factors regulate species biophysical processes and phenological response (Epstein, Lauenroth, Burke, & Coffin, 1997; Ricotta, Reed, & Tieszen, 2003; Saleem, Hassan, Manaf, & Ahmedani, 2009). At different phenological phases, these grasses exhibit variations in their exchange of energy, water and carbon fluxes, as well as in nutrient uptake, storage and release, influencing the productivity of AGB (Adair & Burke, 2010; Jin et al., 2013). The variability in AGB is therefore sensitive to any alterations of the phenological profiles of these grasses due to climatic changes over time. The projected effects of climate change have also been anticipated to influence the productivity of C3 and C4 grass species, with implications on their AGB variability. For example, an increase in warming has been predicted to favour C4 grasses, such that they will improve in productivity, compared to C3 (Bremond, Boom, & Favier, 2012). Climatic changes will therefore, cause significant challenges to the provision of ecosystem goods and services by C3 and C4 grasses. For example, declines in grazing capacity, with significant implications on livestock production and human livelihoods. This emphasises the need to monitor C3 and C4 AGB, to have a better understanding of their state and functioning over time.

Conventional methods have so far been the main sources of characterising C3 and C4 grass species AGB (Auerswald et al., 2012; Epstein et al., 1997; Polley, Derner, Jackson, Wilsey, & Fay, 2014; Taylor et al., 2014). However, these studies were conducted at small geographical coverage (i.e., plot level), at a limited temporal scale. This has been mainly attributed to the high cost, time and labour associated with the use of these methods. Consequently, results obtained lack spatial and temporal aspects of species AGB; hence are insufficient for understanding the dynamics of C3 and C4 AGB. This resulted in uncertainties in the contribution of these species and the effects of climate change. This approach also hinders any prospects to predict the future of C3 and C4 grasses productivity, as well as formulating conclusive management strategies.

Remote sensing provides critical data source for monitoring grass species AGB (Lu, 2005; Zhao et al., 2014). The intrinsic spatial nature of remotely sensed data allows spatial representation of species AGB, which could not be achieved using conventional methods. The spectral capability of remote sensing technology is also crucial in extracting species morphological and phenological characteristics, which influence their AGB variations. Most importantly, emerging sensors offer outstanding opportunities to monitor C3 and C4 grasses AGB (Shoko, Mutanga, & Dube, 2016). For example, the high temporal resolution of emerging sensors (e.g., Sentinel 2 at 5 days) allows multi-temporal analysis of dynamic phenomena like species AGB in a spatially explicit manner. Its large geographical coverage, with a swath width of 195 km at a refined spatial resolution (e.g., 10 m) offers data for large scale monitoring of AGB variations, at a finer spatial resolution. This is also suitable to identify areas in C3 and C4 grasslands, which are most vulnerable to climatic anomalies, under different climate change scenarios. Sentinel 2 is also the first optical sensor of its kind to provide more bands within the red edge domain, noted for extracting key information on vegetation biophysical characteristics (Bruzzone et al., 2017). This represents a substantial improvement, especially with respect to the past, thereby opening a wide range of innovative possibilities of multi-temporal analysis. The present study thus aimed at characterising remotely sensed derived C3 and C4 grasses AGB. Specifically, the study intended to explore the response of C3 and C4 AGB to seasonal climate and topography.

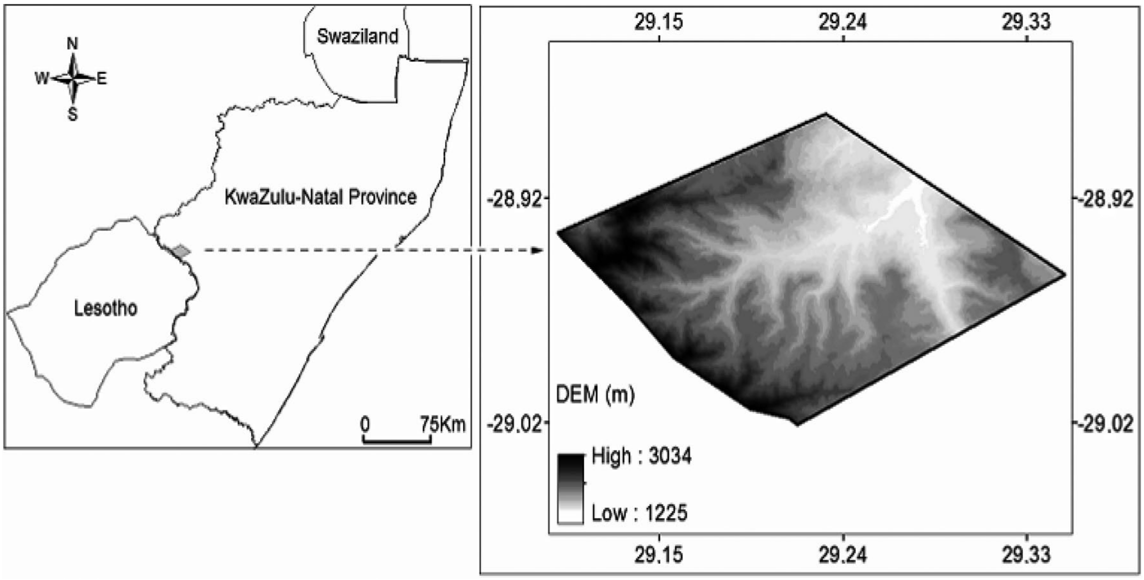

FIGURE 1 Study area location and its elevation variations

2 | MATERIALS AND METHODS

2.1 | Study area

The response of C3 and C4 grass species AGB was explored within the Drakensberg area in KwaZulu-Natal (presented in Figure 1). The study area covered approximately 200 km^2. The area experiences wet humid summers, from November to March and dry, cold winters, from May to August. The summer period is also characterised by high rainfall and high temperatures, whereas in winter, regular frosts and snowfall are typical (Everson & Everson, 2016). Overall, during 2016, the highest total rainfall (263.9 mm) was received in January, whereas the lowest (6.8 mm) was received in July. Temperatures across the study area generally vary, from as low as 5°C in winter, to above 16°C in summer (Mansour, Mutanga, Everson, & Adam, 2012). During the study period, the lowest temperature (6°C) was recorded in July, whereas the highest (26°C) was recorded in December.

2.2 | Data collection and processing

2.2.1 | Grass species AGB data

The present study assessed the response of *Festuca Costata* (C3) and *Themeda triandra* (C4), to seasonal climate and topography. These grasses predominantly occur in the area, which is one of the largest grasslands of South Africa. AGB samples for each grass were collected at summer and winter distinctive seasons. The summer period was represented by data collected in early February and early November, whereas for the winter period, it was early May and end of August 2016. AGB data were collected using random sampling technique, and the random points were generated in ArcGIS 10.2. During each AGB data collection period, three quadrats, measuring 50 cm by 50 cm at each random point were used to collect samples, and these quadrats were demarcated within 100 m^2 (i.e., 10 × 10 m) plot. Ground points where AGB samples were collected were captured by means of a hand held Trimble GEO XH 6000 global position system (GPS). The standing green grass in each quadrat was clipped and weighed in situ; using a weighing scale and this was recorded as fresh AGB in kg/m^2. These AGB samples were oven dried at the University of KwaZulu-Natal grassland facilities, to derive dry AGB and this was expressed as kg/m^2. 240 AGB samples for each grass were collected.

2.2.2 | Climatic and topographic variables

The climatic and topographic variables that were used in this study are provided in Table 1. Rainfall data were delivered as daily point values recorded at eight stations, sufficient for the Cathedral Peak catchment, within which the study area is located. For analysis purposes, the daily rainfall was aggregated to monthly totals and was also interpolated to obtain its spatial variability across the study area. This was performed using ordinary Kriging interpolation method in ArcGIS 10.2. Temperature recordings were available from a station within the study area, and this data were insufficient for analysis; however, the data were used to show the general pattern of temperature variations within the study area. A digital elevation model (DEM) at a spatial resolution of 30 m was also used to derive topographical variables using the surface extension and the hydrological spatial analyst tools in ArcGIS 10.2. Solar radiation recordings were also not available; due to lack of routine observations, hence it was modelled from DEM using radiation modelling tool in ArcGIS 10.2. The use of radiation modelled from DEM has been widely accepted as a reliable data source in ecological modelling (Dube & Mutanga, 2016; Kumar, Skidmore, & Knowles,

TABLE 1 Climatic and topographical variables that were used in this study

Variable	Definition	Source
Aspect	Slope direction measured in degrees (°) or compass direction clockwise from North (0) to North (360)	ASTER DEM
Elevation	Height above sea level, in metres (m)	ASTER DEM
Radiation	Incoming insolation received from the sun, modelled in Watts Hours per square metre (Wh/m^2)	ASTER DEM
Rainfall	Monthly total, in millimetres (mm)	SAEON, SAWS
Slope	Elevation steepness, in degrees (°) from 0 (flat) to 90 (steep)	ASTER DEM
Temperature	Maximum, minimum and average, in degrees Celsius (°C).	SAEON, SAWS
TWI	Wetness condition, which determines the spatial variability of soil water (-)	ASTER DEM

Abbreviation(s): ASTER, advanced spaceborne thermal emission and reflection radiometer; DEM, digital elevation model; SAEON, South African Earth Observation Network; SAWS, South African Weather Services; TWI, total wetness index.

1997; Ruiz-Arias, Tovar-Pescador, Pozo-Vázquez, & Alsamamra, 2009). All derived maps were also standardised to the same resolution using nearest neighbour resampling technique in a GIS environment, to ensure their compatibility and consistency.

2.3 | Remotely sensed derived AGB over space and time

Remotely sensed estimates of C3 and C4 grasses AGB over time were derived using Sentinel 2 variables (presented in Table 2) and the Sparse Partial Least Squares regression (SPLSR) model (Chun & Keles, 2010). The SPLSR is one of the robust and powerful models for estimating species AGB, due to its ability to overcome the challenges of multicollinearity and over-fitting, by transforming the variables to new components (Abdel-Rahman et al., 2014; Sibanda, Mutanga, Rouget, & Kumar, 2017). The detailed explanation on how the SPLSR works in relating species AGB and variables of interest can be found in for example, Sibanda, Mutanga, and Rouget (2015) and Shoko, Mutanga, and Dube (2018).

Sentinel 2 variables corresponding to species AGB for each period were extracted using the GPS points in ArcGIS 10.2. The SPLSR model was first run with grass species ground-based AGB collected during the four different months, with corresponding Sentinel 2 variables. The model generated AGB estimation functions and variables. This was achieved through transformation of the Sentinel 2 variables to a set of components and variables, showing their contribution to estimating species AGB for each period. Secondly, the SPLSR was run to establish the relationship between species AGB and climatic and topographic variables. The climatic and topographic variables are continuous data. Therefore, GPS points corresponding to species AGB were used to extract these variables from climatic and topographic maps. This resulted in species AGB points with corresponding climatic and topographical variables in a spread sheet. The data were also used to generate descriptive statistics.

2.4 | Sentinel 2 variables used to predict grass species AGB

Sentinel 2 variables that were used to predict species AGB were (a) spectral bands (b) vegetation indices (VIs) and (c) combination of indices and spectral bands. The details of these variables are presented in Table 2. The indices that were used in this study were reported to perform well in C3 and C4 grass species AGB estimation, as well as in grassland ecosystems.

TABLE 2 Sentinel 2 variables used to estimate species aboveground biomass (AGB, Shoko et al., 2018)

Data type	Details	Analysis set
Spectral data	Ten spectral bands	i
	Bands 2-8A (Blue, Green, Red, Red edge1-3, NIR, Red edge4)	
	Bands 11 and 12 (Shortwave infrared bands)	
Vegetation Indices (VIs)	EVI, SAVI, NDVI, RDVI, SR, MSR	ii
	Red edge-based NDVI (using red edge bands 1-4)	
	Red edge-based SR (using red edge bands 1-4)	
Image spectral data + VIs	Combined image spectral bands and vegetation indices	iii

TABLE 3 Descriptive statistics of the data collected and extracted

Acquisition month	Variables	Species	Min	Max	Avg.	Stdev
February	AGB	C3	0.524	1.160	0.709	0.115
		C4	0.600	1.276	0.984	0.125
	Aspect	C3	0.0 (N)	358.0 (N)	194.78 (S)	137.9
		C4	0.0 (N)	359.1 (N)	267.7 (W)	99.2
	Elevation	C3	1,375.0	1,462.0	1,397.5	49.1
		C4	1,296.0	1,428.0	1,302.8	21.7
	Radiation	C3	282.20	303.18	297.95	37.6
		C4	289.80	304.35	298.80	37.3
	Rainfall	C3	122.5	129.5	124.3	2.2
		C4	121.0	131.4	125.3	3.7
	Slope	C3	2.4	29.7	17.2	10.6
		C4	0.8	20.9	8.7	4.8
	Temperature	—	12.8	23.5	18.5	—
	TWI	C3	4.47	12.99	7.69	2.92
		C4	4.26	9.39	6.38	1.29
May	AGB	C3	0.460	3.912	1.253	0.719
		C4	0.412	2.592	1.101	0.418
	Aspect	C3	0.0 (N)	358.0 (N)	194.78 (S)	136.4
		C4	0.0 (N)	359.1 (N)	267.7 (W)	102.9
	Elevation	C3	1,375.0	1,462.0	1,398.7	50.5
		C4	1,328.0	1,440.0	1,302.1	19.0
	Radiation	C3	114.83	172.25	143.86	13.65
		C4	116.57	165.41	140.72	13.63
	Rainfall	C3	14.1	17.2	16.1	1.0
		C4	13.5	16.0	15.0	0.9
	Slope	C3	2.4	29.7	15.3	9.6
		C4	0.8	21.9	8.9	4.9
	Temperature	—	10.1	20.3	12.6	—
	TWI	C3	4.47	12.99	7.69	2.92
		C4	4.26	9.39	6.38	1.29
August	AGB	C3	0.376	1.072	0.718	0.306
		C4	0.244	0.668	0.469	0.182
	Aspect	C3	0.0 (N)	358.0 (N)	194.78 (S)	136.4
		C4	0.0 (N)	359.1 (N)	267.7 (W)	102.9
	Elevation	C3	1,375	1,462.0	1,398.7	50.5
		C4	1,328.0	1,440	1,302.1	19.0
	Radiation	C3	122.83	179.85	152.03	13.65
		C4	124.60	173.33	148.91	13.64
	Rainfall	C3	55.8	71.8	61.0	5.2
		C4	58.8	71.4	65.9	5.9
	Slope	C3	2.4	29.7	18.6	9.6
		C4	0.8	20.9	8.9	4.9
	Temperature	—	8.5	20.3	12.9	—
	TWI	C3	4.47	12.99	7.69	2.92
		C4	4.26	9.39	6.38	1.29

(Continues)

TABLE 3 (Continued)

Acquisition month	Variables	Species	Min	Max	Avg.	Stdev
November	AGB	C3	0.226	1.784	0.855	0.355
		C4	0.352	3.208	1.163	0.607
	Aspect	C3	0.0 (N)	358.0 (N)	194.78 (S)	136.4
		C4	0.0 (N)	359.1 (N)	267.7 (W)	102.9
	Elevation	C3	1,375.0	1,462.0	1,398.7	50.5
		C4	1,328.0	1,440.0	1,302.1	18.9
	Radiation	C3	273.58	298.57	293.84	3.63
		C4	284.31	299.50	294.65	3.40
	Rainfall	C3	71.5	86.0	75.4	10.3
		C4	70.6	78.9	74.6	3.3
	Slope	C3	2.4	29.7	21.3	10.1
		C4	0.9	20.9	8.9	4.9
	Temperature	—	9.7	24	16	—
	TWI	C3	4.47	12.99	7.69	2.92
		C4	4.26	9.39	6.38	1.29

Note. Aspect is also indicated in terms of directions, which are represented by N, for North; W, for west; S, for South facing slopes.
Abbreviation(s): Avg, average; Max, maximum; Min, minimum; Stdev, standard deviation; TWI, total wetness index.

2.5 | Statistical analysis

Sparse Partial Least Squares regression model was used to relate seasonal climatic and topographic variables to C3 and C4 AGB. Exploratory analysis was conducted by generating descriptive statistics: to understand species AGB and associated climatic and topographic data that were collected. The one-way Analysis of Variance (ANOVA), at 95% confidence interval was also performed to determine the significant differences among species AGB over time. In addition, the paired *t* test was used to determine the significant differences in AGB between the two species at each period, at 95% confidence intervals.

3 | RESULTS

3.1 | Descriptive statistics of data collected

Table 3 provides the descriptive statistics of AGB, climatic and topographic variables, which indicate variations between C3 and C4 grasses. AGB varied from as low as 0.244 in August (for C4) to 3.912 kg/m^2 in May (for C3).

3.2 | Remotely sensed AGB variability over space and time

Figure 2 illustrates the estimated variability in AGB for the study area, using Sentinel 2 remote sensing dataset. Overall, the area produced noticeable spatial and temporal variations in C3 and C4 grass species AGB. Much of AGB was produced during the summer months. Lower AGB variations were also noted, especially during the winter fall in August and September, where most of the study area showed a decrease in AGB. May had the highest AGB accumulation across the area, whereas the lowest was produced in September. AGB changes across the study area were variable, where some areas experienced notable changes over time, while others remained almost stable, despite seasonal changes. For example, the central and eastern parts show notable changes in AGB over time, when compared to the southern tip and the south-western most parts of the study area.

3.3 | Climate variability over time

Figure 3 shows the general pattern in climatic conditions of the study area in 2016. Overall, climatic conditions showed a temporal variability. Lowest total rainfall (6.8 mm) was recorded in July, whereas January received the highest amount (263.9 mm). Highest temperature (26°C) was recorded in December, whereas July experienced the lowest (6°C). In terms of solar radiation, the highest (185 kWh/m^2) was received in January, whereas the lowest (32.6 kWh/m^2) was received in June.

3.4 | Spatial variability in climatic and topographic variables

Figure 4a–f shows the spatial variability in climatic and topographic variables within which C3 and C4 grass species AGB was explored. High rainfall (Figure 4a) was received at the southern tip, compared to most parts of the area. The southern, western and eastern parts also received more radiation, compared to the central and north eastern parts. The elevation (Figure 4c) was quite variable, ranging between 1,225, in the central and north eastern parts, and 3,034 m above sea level, in the western and southern parts. Similarly, slope

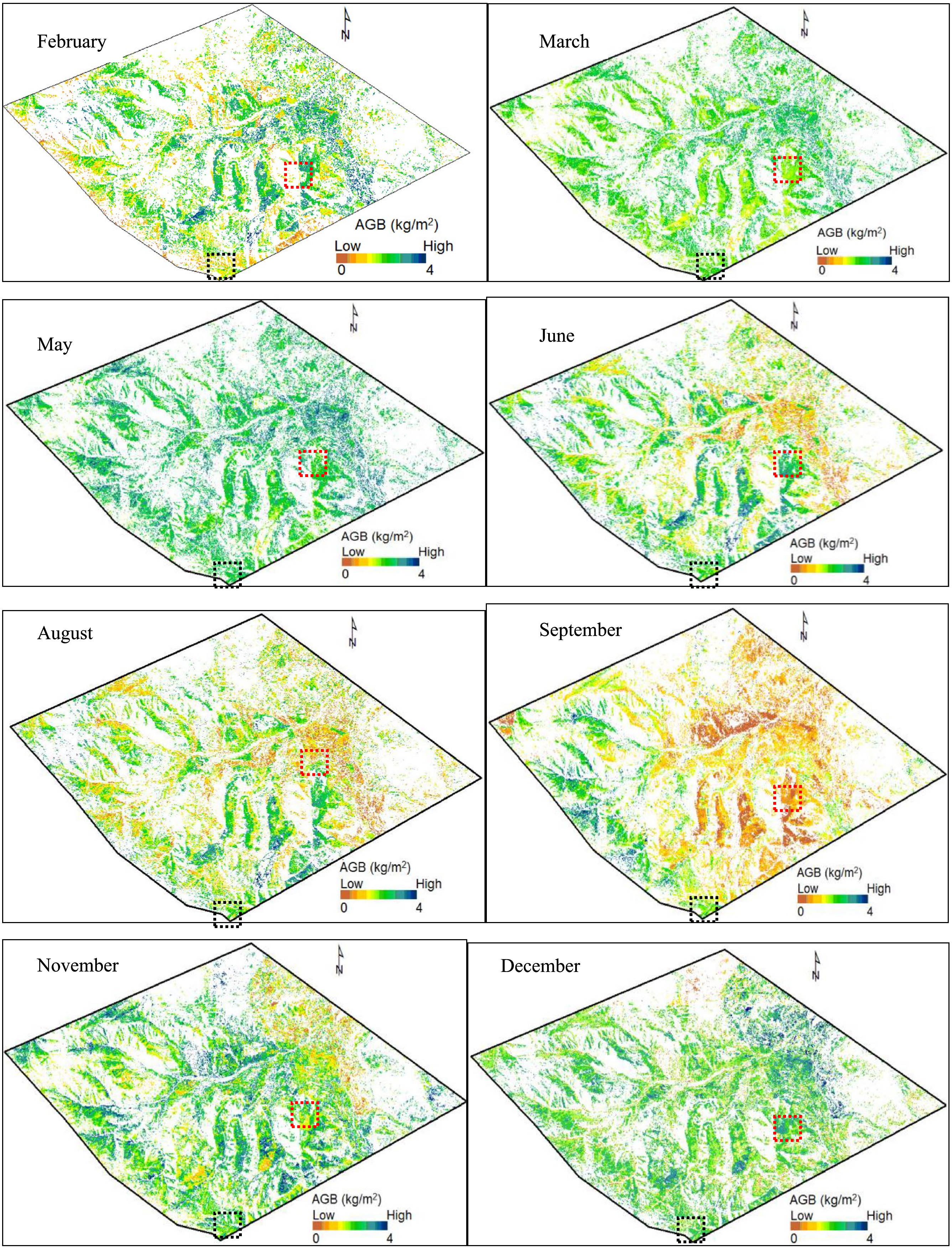

FIGURE 2 The variability in aboveground biomass (AGB) over time. Areas bounded in red were unstable in AGB, whereas those in black remain stable [Colour figure can be viewed at wileyonlinelibrary.com]

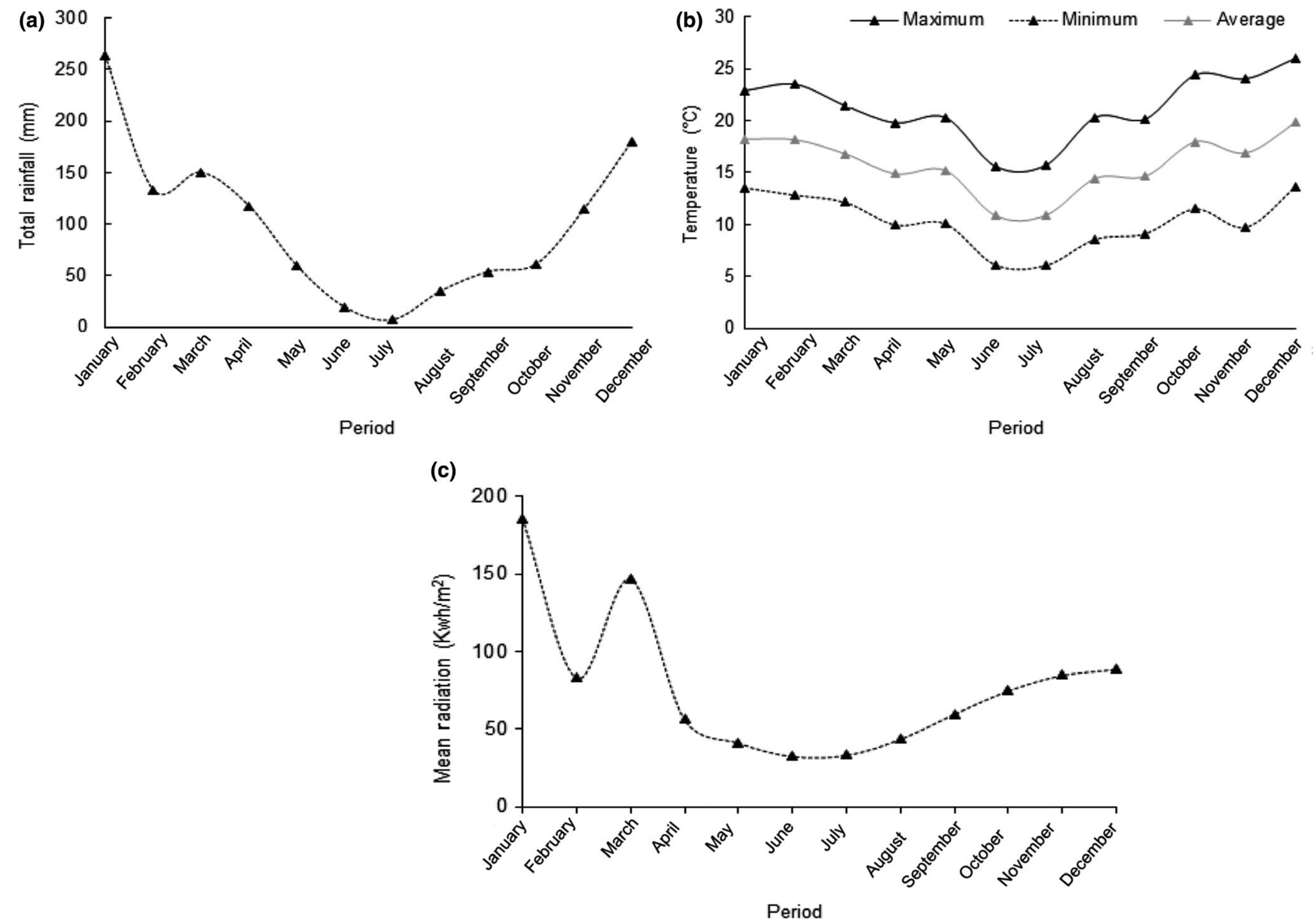

FIGURE 3 The general (a) rainfall, (b) temperature and (c) radiation variability over time

(Figure 4d) varies from 0 to 70.4°, with high slopes for most parts of the area, except for the central and north eastern parts. The aspect (Figure 4e) of the area was found to be heterogeneous, constituting slopes facing different directions, whereas the TWI (Figure 4f) indicates that the majority of the area has low soil water potential, except for the central and north eastern parts.

3.5 | The response of remotely sensed species AGB to climate variability over time

Figure 5 shows the response of C3 and C4 target grass species AGB to monthly: (a) total rainfall; (b) average temperature; and (c) average radiation, over time. These results were based on the collected GPS point-based AGB and corresponding climatic values extracted. The findings revealed that seasonal climatic factors had a significant influence on C3 and C4 AGB over time. For example, a marked increase in AGB (e.g., in February and March) was noted with an increase in total rainfall (Figure 5a), whereas dry months were associated with a decrease in AGB. During the summer months (February, March, November and December), species AGB showed a gradual increase with an increase in radiation. Between April and June, peak species AGB was reached; however, this period indicated a sharp decrease in radiation.

Figure 6 also zoomed in to highlighted areas (Figure 2) which show the spatial variations of AGB over time. Random points were generated within these areas and AGB values and corresponding climatic values were extracted using these points. Generally, the unstable areas were mostly dominated by C4 (*Themeda*), whereas the stable tip was dominated by C3 (*Festuca*), although species co-existence occurs. In C3-dominated areas, high radiation was associated with lower species AGB, for example in March (Figure 6a(i)). High fluctuations in AGB were also observed for C3, despite rainfall and radiation changes over time. On the other hand, C4 (Figure 6b) showed sharp or immediate response (either decreasing or increasing) to rainfall (ii) and radiation (i) variations, especially in November and December.

Tables 4 and 5 illustrate the correlation between species AGB with climatic and topographic variables. Overall, C4 AGB showed better positive correlations with rainfall and radiation, than C3 AGB. C4 AGB also had the highest significant positive association with rainfall ($R^2 = 0.82$; $p < 0.05$). However, C3 AGB showed the highest significant positive correlation with elevation ($R^2 = 0.84$; $p < 0.05$). Positive correlations between C3 AGB and topographical variables were also found, whereas for C4 AGB, there were mixed findings. For example, C4 was negatively correlated with elevation and slope, while responded positively to aspect and TWI. Elevation had the highest positive correlation with C3 AGB and highest negative correlation with C4. The highest positive correlation for C4 AGB was with TWI, whereas the lowest was found with aspect.

It was also found that AGB varied significantly ($F_{1.14} = 2.31$, $p < 0.05$) over time, between C3 and C4 grasses, based on ANOVA. On the other hand, the *t* test results have highlighted that the two species AGB were significantly different in February ($p = 0.032$), August ($p = 0.024$) and November ($p = 0.011$), whereas in May it was not significantly different ($p = 0.26$), at 95% confidence intervals.

4 | DISCUSSION

Results from this study have indicated the spatial and temporal AGB variations derived using multi-temporal Sentinel 2 remote sensing images. These findings indicate the potential of using freely available emerging sensors for monitoring the dynamics of C3 and C4 AGB. This has been a limitation in monitoring C3 and C4 grass species, especially considering the anticipated climate change effects on their productivity. Species AGB differed significantly between C3 and C4 target grasses over time, except in May. This finding may be attributed to the phenology of the target species. Possibly, both grasses experienced maximum productivity in May, which contributed to less variation in AGB.

The spatial representation of AGB over time has shown that AGB variations across the study area were variable. For example, summer months produced high AGB for most parts of the study area, until May, whereas a decrease in AGB was noted from June to September. The spatial and temporal variations observed in this study indicated not only the influence of seasonal climatic, but also that of spatial heterogeneity in terms of topography. For example, topographical derivatives maps have shown that the area is predominantly high elevated, with steep slopes of varying aspects, facing all the different campus direction. These variations influence, for example, the intensity of radiation received, soil moisture and temperature. These topographical influence on species growth and AGB productivity have also been identified, for example by Måren, Karki, Prajapati, Yadav, and Shrestha (2015).

Significant spatial changes in AGB were also observed across the study area, over time. However, changes in AGB over time were not uniform across the study area. Instead, some areas experienced rapid changes, whereas others remained almost stable, despite changes in climatic conditions. This possibly occurred because of the climatic and topographical heterogeneity of the area, which exert difference influence on C3 and C4 grasses AGB over time. However, in August and September, the majority of the study area showed a marked decrease in AGB. This is an indication that the period, which is winter fall, did not offer favourable conditions

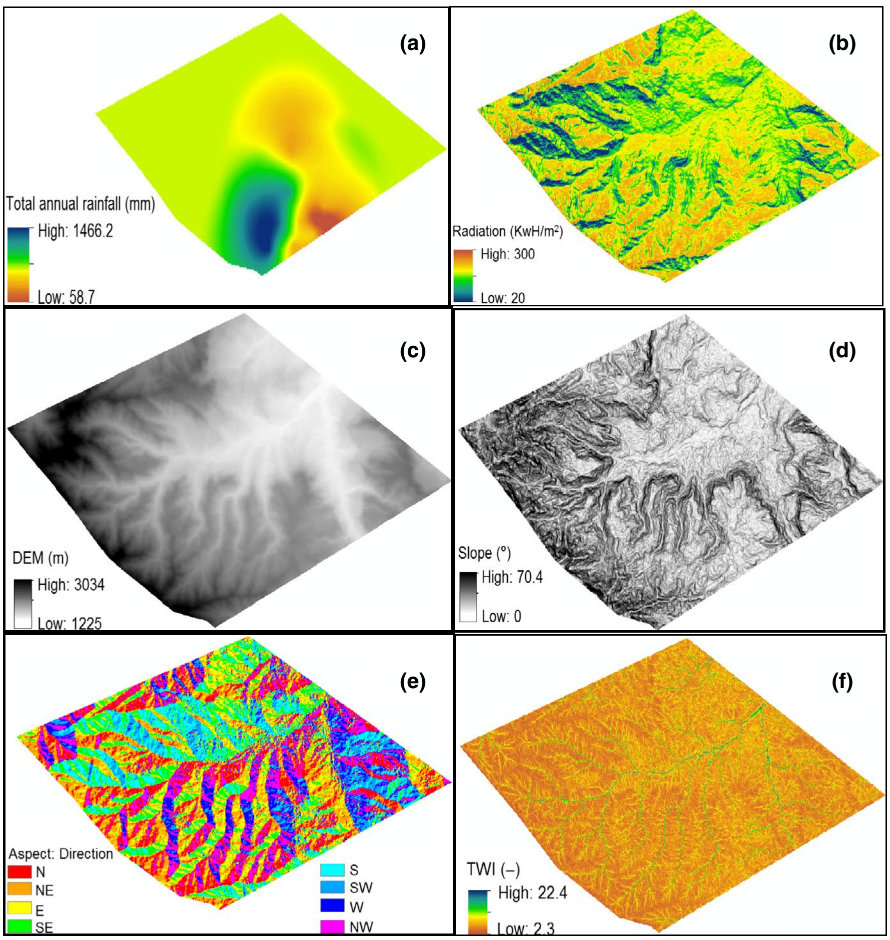

FIGURE 4 Spatial variability in: (a) mean annual radiation, (b) rainfall, (c) elevation, (d) slope, (e) aspect and (f) TWI [Colour figure can be viewed at wileyonlinelibrary.com]

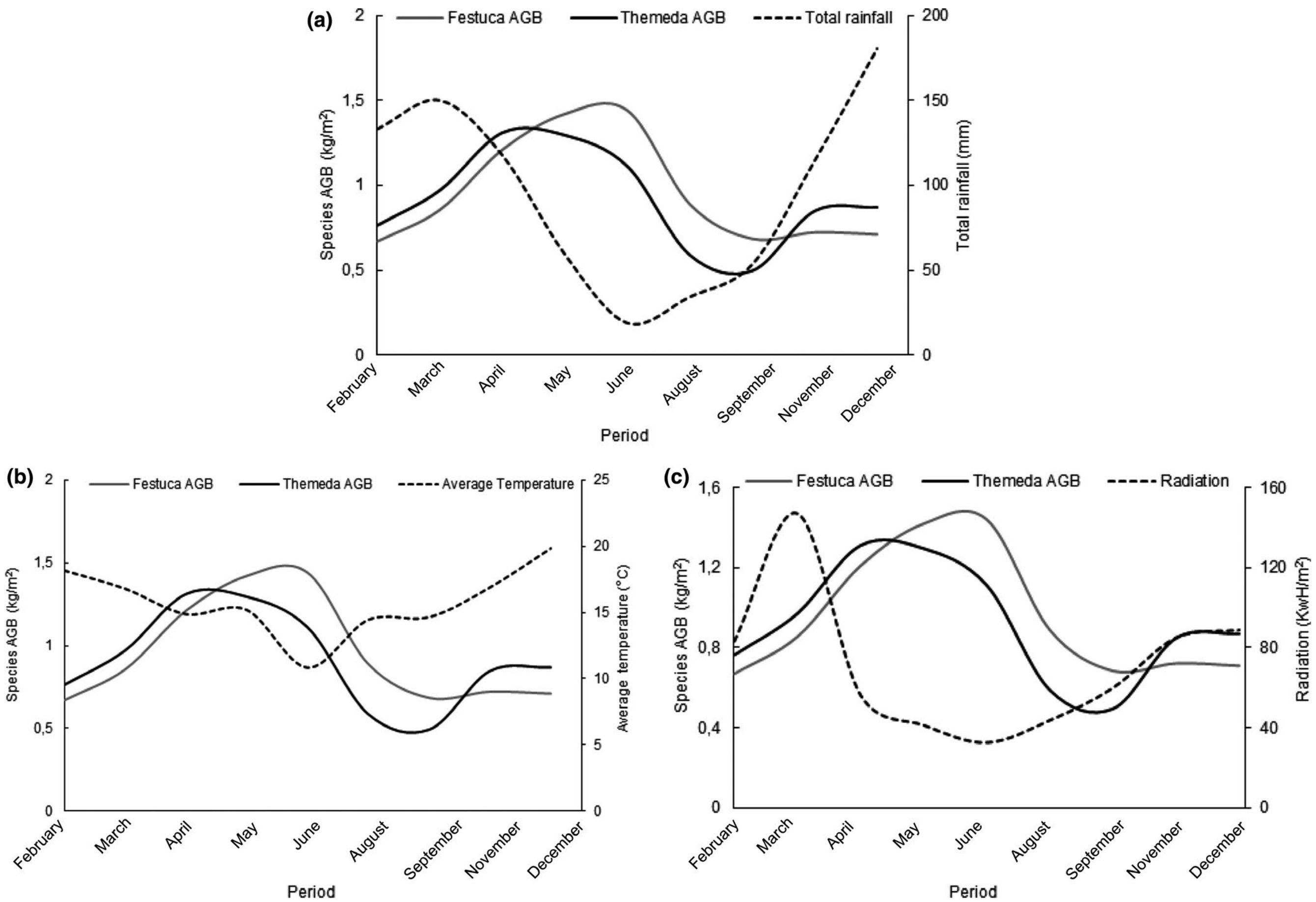

FIGURE 5 The response of individual species aboveground biomass (AGB) to (a) rainfall, (b) temperature and (c) radiation over time

for both species AGB. For example, C3 grasses are active under cooler climatic conditions, particularly during winter. Possibly, during winter fall, rise in temperatures expectedly impacted negatively to C3 AGB. Different studies (Adjorlolo, Mutanga, Cho, & Ismail, 2012; Auerswald et al., 2012) have also indicated that C3 grasses require higher moisture content, and this is not sufficient during the dry period of August and September, hence they become less active. Similarly, it is expected that rise in temperatures associated with dry conditions reduces the rate of activity of C4 negatively, impacting its AGB. C4 grasses prefer warm environments, with sufficient rainfall, hence as conditions becomes dry in August and September, their productivity is constrained and AGB decreases. Possibly, the activity of C3 and C4 grasses and AGB production significantly decreases if the conditions are above their optimal or below their optimal requirements. For instance, August and September marked the end of winter, which is preferred by C3 and it does not fall within the summer period, which is favourable to C4.

It was also found that rainfall, temperature and radiation influence species AGB over time. For example, C4 AGB had positive correlation with rainfall, where high AGB values were observed with an increase in rainfall during the summer months. The same trend was observed during dry period in winter with lowest rainfall, where C4 AGB showed a sharp decrease. These trends can be considered intuitively sound. Rainfall within the study area is received during the summer period; this coincided with the growth of C4 grasses, thereby influencing their AGB variations. In addition, the response of selected areas, predominated by C4 grass has indicated a close association between AGB and rainfall pattern over time. In agreement, it has been long established that summer rainfall typically benefits the growth of C4 grasses, thereby increasing their relative contribution to AGB accumulation (Carmel & Kadmon, 1999). This observation also concurs with previous studies (Epstein et al., 1997; Måren et al., 2015; Polley et al., 2014) which have indicated that rainfall boost the growth and AGB accumulation of C4 grasses. For example, the studies done during the summer period in United States by Epstein et al. (1997) found that mean annual rainfall explained 81% of C4 AGB in the great plains, whereas Polley et al. (2014) reported that C4 AGB increased significantly with an increase in rainfall in Texas. For C3 grass species, although a positive correlation was found with rainfall, its AGB remained high in winter, despite a noted decrease in rainfall. Similarly, the selected area predominated by C3, that showed almost stable response in AGB over time has indicated the same trend. It is likely that C3 AGB remained high in winter due to cool conditions, associated with winter period. In agreement with this notion, June had the lowest average temperature and this corresponded with the highest estimated C3 AGB. As temperatures drop, cool conditions occur, which favour C3 grasses; hence their AGB remained stable despite a decrease in rainfall.

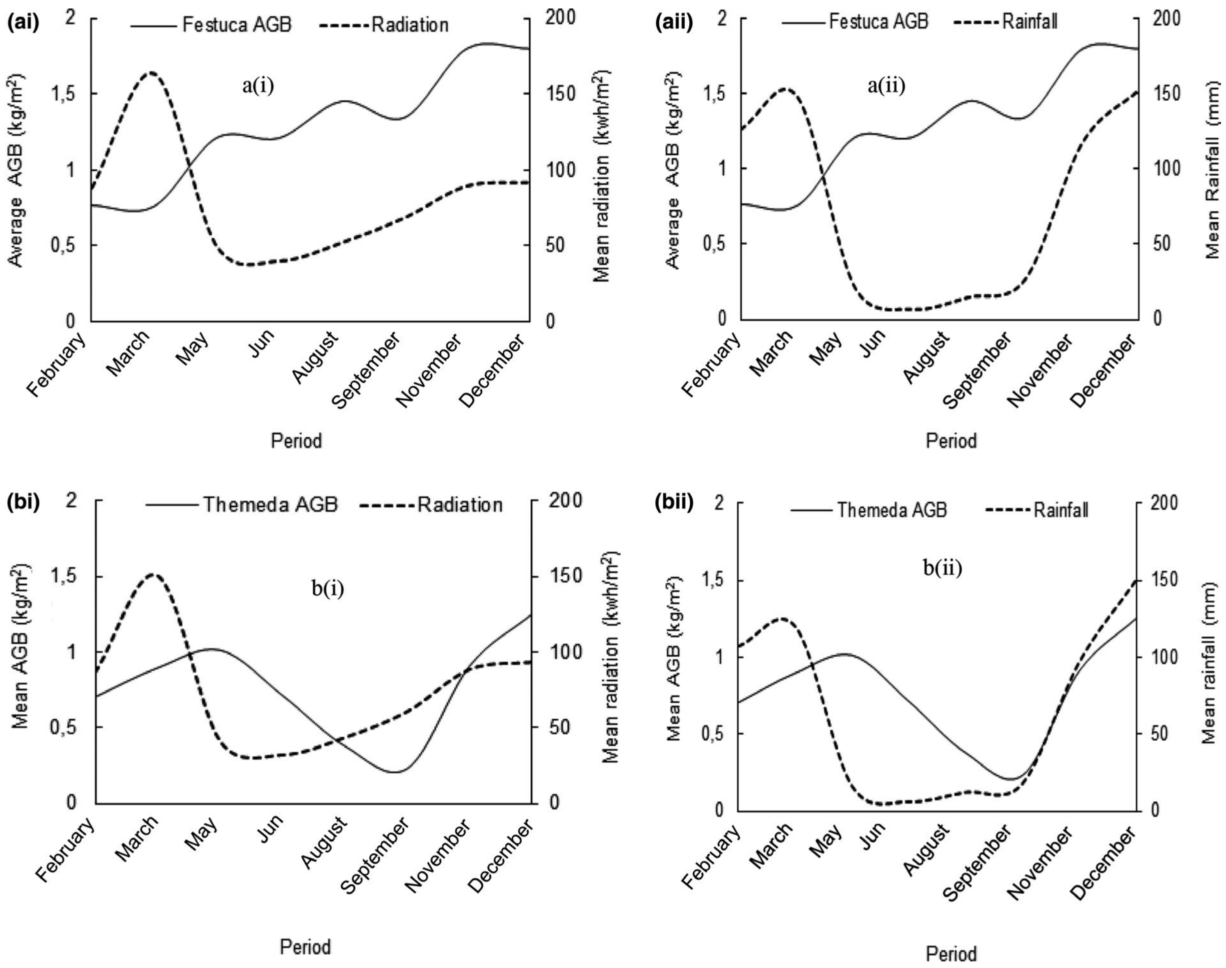

FIGURE 6 The response of (a) *Festuca* and (b) *Themeda* aboveground biomass (AGB) to (i) radiation and (ii) rainfall over time

The influence of solar radiation was also detected on C3 and C4 AGB over time. C4 AGB responded positively with radiation variations over time; this was most apparent during the summer months, like February, March, November and December. C4 grass species have been identified to require high solar radiation (Adjorlolo et al., 2012), this condition promote their AGB production. Solar radiation is the primary source of energy that regulates physical, chemical and biological processes (e.g., photosynthesis and evapotranspiration) of terrestrial ecosystems (Dubayah & Rich, 1995; Ruiz-Arias et al., 2009). Consequently, it determines species growth rate and productivity of AGB. For C3 AGB, highest AGB was associated with low radiation, for instance, in winter (May and June). This is because C3 grass species prefer low radiation (Adjorlolo et al., 2012), which is received during the winter period.

Topography also influenced species AGB; however, this was variable between C3 and C4 species. For instance, elevation, aspect, slope and TWI were positively related with C3 AGB. C3 AGB production favours conditions at high elevated and steep slopes, as well as with high potential of soil moisture. The influence of elevation on C3 AGB might be attributed to the fact that the study area forms part of the Drakensburg mountain range, which promote cool conditions favourable to the growth and AGB accumulation of C3, hence changes in elevation significantly result in AGB changes. In agreement, it is well accepted that high elevated areas are typically cool and C3 species generally favour cool conditions (Adjorlolo et al., 2012; Yan & de Beurs, 2016). Yan and de Beurs (2016) found the importance of elevation in the distribution and abundance of C3 grasses at three varying temporal scale, using

TABLE 4 Correlation between species aboveground biomass (AGB) and climatic factors over time

	Festuca (C3) AGB				Themeda (C4) AGB			
Climatic variables	Feb	May	Aug	Nov	Feb	May	Aug	Nov
Radiation	0.44	0.49	0.42	0.54	0.63	0.54	0.46	0.79
Rainfall	0.57	0.52	0.31	0.59	0.79	0.61	0.70	0.82

TABLE 5 Correlation between species aboveground biomass (AGB) and topography

Topographical variables	Festuca (C3) AGB	Themeda (C4) AGB
Aspect	0.64	0.55
Elevation	0.84	−0.80
Slope	0.78	−0.77
TWI	0.74	0.69

Abbreviation(s): TWI, total wetness index.

random forest algorithm. For C4 species, high elevated and steep areas promote cool conditions, which do not favour their growth and AGB production. This explained why C4 AGB was negatively correlated with elevation and slope in this study. TWI was positively correlated with both C3 and C4 AGB. The index determines the spatial variability in soil moisture conditions (Wilson et al., 2016), which boost vegetation cover, growth and productivity; this possibly explains it had a positive association with species AGB in this study. The influence of TWI on species cover and growth was also reported by Pei et al. (2010) and Seutloali, Dube, and Mutanga (2017) in modelling erosion, using topographical derivatives. They noted that areas associated with high TWI had more vegetation cover and density.

5 | CONCLUSION

This study examined the response of C3 and C4 grass species AGB to seasonal climate and topography, within the montane grasslands of South Africa. It can be concluded that topography and climatic variations exert considerable influence on C3 and C4 grasses AGB over time. However, changes in species AGB over time were not uniform across the study area. Some areas experienced rapid changes, whereas others remained almost stable, despite changes in climatic conditions over time. This indicates the spatial and temporal heterogeneity of C3 and C4 dominated areas, which exert varying changes to AGB and ecosystem goods and services over time. These findings provide a key step in detecting the productivity of rangelands, their response to environmental changes, fire occurrences and assessing management practices to boost productivity and fire regimes.

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DATA AVAILABILITY

The data that support the findings of this study are available from [third party]. Restrictions apply to the availability of these data, which were used under license for this study. Data are available [from the authors at URL] with the permission of [third party].

ORCID

Cletah Shoko https://orcid.org/0000-0003-4222-3539

Timothy Dube https://orcid.org/0000-0003-3456-8991

REFERENCES

Abdel-Rahman, E. M., Mutanga, O., Odindi, J., Adam, E., Odindo, A., & Ismail, R. (2014). A comparison of partial least squares (PLS) and sparse PLS regressions for predicting yield of Swiss chard grown under different irrigation water sources using hyperspectral data. *Computers and Electronics in Agriculture*, *106*, 11–19. https://doi.org/10.1016/j.compag.2014.05.001

Adair, E. C., & Burke, I. C. (2010). Plant phenology and life span influence soil pool dynamics: *Bromus tectorum* invasion of perennial C3–C4 grass communities. *Plant and Soil*, *335*, 255–269. https://doi.org/10.1007/s11104-010-0413-3

Adjorlolo, C., Mutanga, O., Cho, M. A., & Ismail, R. (2012). Challenges and opportunities in the use of remote sensing for C3 and C4 grass species discrimination and mapping. *African Journal of Range & Forage Science*, *29*, 47–61.

Auerswald, K., Wittmer, M. H. O. M., Bai, Y., Yang, H., Taube, F., Susenbeth, A., & Schnyder, H. (2012). C4 abundance in an inner Mongolia grassland system is driven by temperature–moisture interaction, not grazing pressure. *Basic and Applied Ecology*, *13*, 67–75. https://doi.org/10.1016/j.baae.2011.11.004

Bremond, L., Boom, A., & Favier, C. (2012). Neotropical C3/C4 grass distributions–present, past and future. *Global Change Biology*, *18*, 2324–2334. https://doi.org/10.1111/j.1365-2486.2012.02690.x

Bruzzone, L., Bovolo, F., Paris, C., Solano-Correa, Y. T., Zanetti, M., & Fernández-Prieto, D. (2017). *Analysis of multitemporal Sentinel-2 images in the framework of the ESA Scientific Exploitation of Operational Missions*. 2017 9th International Workshop on the Analysis of Multitemporal Remote Sensing Images (MultiTemp).

Carmel, Y., & Kadmon, R. (1999). Effects of grazing and topography on long-term vegetation changes in a Mediterranean ecosystem in Israel. *Plant Ecology*, *145*, 243–254.

Chun, H., & Keles, S. (2010). Sparse partial least squares regression for simultaneous dimension reduction and variable selection. *Journal of Royal Statistical Society: Series B (Statistical Methodology)*, *72*(1), 3–25. https://doi.org/10.1111/j.1467-9868.2009.00723.x

Dubayah, R., & Rich, P. M. (1995). Topographic solar radiation models for GIS. *International Journal of Geographical Information Systems*, *9*, 405–419. https://doi.org/10.1080/02693799508902046

Dube, T., & Mutanga, O. (2016). The impact of integrating WorldView-2 sensor and environmental variables in estimating plantation forest species aboveground biomass and carbon stocks in uMgeni Catchment, South Africa. *ISPRS Journal of Photogrammetry and Remote Sensing*, *119*, 415–425. https://doi.org/10.1016/j.isprsjprs.2016.06.017

Eggleston, S., Buendia, L., Miwa, K., Nagara, T., & Tanabe, K. (2006) *IPCC guidelines for national greenhouse gas inventories*. Volume 4-Agriculture, forestry and other land use. IGES, Japan.

Epstein, H., Lauenroth, W., Burke, I., & Coffin, D. (1997). Productivity patterns of C3 and C4 functional types in the US Great Plains. *Ecology*, *78*, 722–731.

Everson, C. S., & Everson, T. (2016). The long-term effects of fire regime on primary production of montane grasslands in South Africa. *African Journal of Range & Forage Science*, *33*, 33–41. https://doi.org/10.2989/10220119.2015.1124922

Everson, C. S., Everson, T. M., & Tainton, N. M. (1985). The dynamics of *Themeda triandra* tillers in relation to burning in the natal Drakensberg. *Journal of the Grassland Society of Southern Africa*, *2*, 18–25.

Jin, C., Xiao, X., Merbold, L., Arneth, A., Veenendaal, E., & Kutsch, W. L. (2013). Phenology and gross primary production of two dominant savanna woodland ecosystems in Southern Africa. *Remote Sensing of Environment*, *135*, 189–201. https://doi.org/10.1016/j.rse.2013.03.033

Kumar, L., Skidmore, A. K., & Knowles, E. (1997). Modelling topographic variation in solar radiation in a GIS environment. *International Journal of Geographical Information Science*, *11*, 475–497. https://doi.org/10.1080/136588197242266

Lee, J.-S. (2011). Combined effect of elevated CO2 and temperature on the growth and phenology of two annual C3 and C4 weedy species. *Agriculture, Ecosystems & Environment*, *140*, 484–491. https://doi.org/10.1016/j.agee.2011.01.013

Lu, D. (2005). Aboveground biomass estimation using Landsat TM data in the Brazilian Amazon. *International Journal of Remote Sensing*, *26*, 2509–2525. https://doi.org/10.1080/01431160500142145

Mansour, K., Mutanga, O., Everson, T., & Adam, E. (2012). Discriminating indicator grass species for rangeland degradation assessment using hyperspectral data resampled to AISA Eagle resolution. *ISPRS Journal of Photogrammetry and Remote Sensing*, *70*, 56–65. https://doi.org/10.1016/j.isprsjprs.2012.03.006

Måren, I. E., Karki, S., Prajapati, C., Yadav, R. K., & Shrestha, B. B. (2015). Facing north or south: Does slope aspect impact forest stand characteristics and soil properties in a semiarid trans-Himalayan valley? *Journal of Arid Environments*, *121*, 112–123.

Pei, T., Qin, C.-Z., Zhu, A.-X., Yang, L., Luo, M., Li, B., & Zhou, C. (2010). Mapping soil organic matter using the topographic wetness index: A comparative study based on different flow-direction algorithms and kriging methods. *Ecological Indicators*, *10*, 610–619. https://doi.org/10.1016/j.ecolind.2009.10.005

Polley, H. W., Derner, J. D., Jackson, R. B., Wilsey, B. J., & Fay, P. A. (2014). Impacts of climate change drivers on C4 grassland productivity: Scaling driver effects through the plant community. *Journal of Experimental Botany*, *65*(13), 3415–3424. https://doi.org/10.1093/jxb/eru009

Ricotta, C., Reed, B., & Tieszen, L. (2003). The role of C3 and C4 grasses to interannual variability in remotely sensed ecosystem performance over the US Great Plains. *International Journal of Remote Sensing*, *24*, 4421–4431.

Ruiz-Arias, J. A., Tovar-Pescador, J., Pozo-Vázquez, D., & Alsamamra, H. (2009). A comparative analysis of DEM-based models to estimate the solar radiation in mountainous terrain. *International Journal of Geographical Information Science*, *23*, 1049–1076. https://doi.org/10.1080/13658810802022806

Saleem, A., Hassan, F., Manaf, A., & Ahmedani, M. (2009). Germination of *Themeda triandra* (Kangaroo grass) as affected by different environmental conditions and storage periods. *African Journal of Biotechnology*, *8*, 4094–4099.

Seutloali, K. E., Dube, T., & Mutanga, O. (2017). Assessing and mapping the severity of soil erosion using the 30-m Landsat multispectral satellite data in the former South African homelands of Transkei. *Physics and Chemistry of the Earth, Parts A/B/C*, *100*, 296–304. https://doi.org/10.1016/j.pce.2016.10.001

Shoko, C., Mutanga, O., & Dube, T. (2016). Progress in the remote sensing of C3 and C4 grass species aboveground biomass over time and space. *ISPRS Journal of Photogrammetry and Remote Sensing*, *120*, 13–24. https://doi.org/10.1016/j.isprsjprs.2016.08.001

Shoko, C., Mutanga, O., Dube, T., & Slotow, R. (2018). Characterizing the spatio-temporal variations of C3 and C4 dominated grasslands aboveground biomass in the Drakensberg, South Africa. *International Journal of Applied Earth Observation and Geoinformation*, *68*, 51–60.

Sibanda, M., Mutanga, O., & Rouget, M. (2015). Examining the potential of Sentinel-2 MSI spectral resolution in quantifying above ground biomass across different fertilizer treatments. *ISPRS Journal of Photogrammetry and Remote Sensing*, *110*, 55–65. https://doi.org/10.1016/j.isprsjprs.2015.10.005

Sibanda, M., Mutanga, O., Rouget, M., & Kumar, L. (2017). Estimating biomass of native grass grown under complex management treatments using WorldView-3 spectral derivatives. *Remote Sensing*, *9*, 55. https://doi.org/10.3390/rs9010055

Snyman, H. A., Ingram, L. J., & Kirkman, K. P. (2013). *Themeda triandra*: A keystone grass species. *African Journal of Range & Forage Science*, *30*, 99–125.

Still, C. J., Pau, S., & Edwards, E. J. (2014). Land surface skin temperature captures thermal environments of C3 and C4 grasses. *Global Ecology and Biogeography*, *23*, 286–296.

Taylor, S. H., Ripley, B. S., Martin, T., De-Wet, L. A., Woodward, F. I., & Osborne, C. P. (2014). Physiological advantages of C4 grasses in the field: A comparative experiment demonstrating the importance of drought. *Global Change Biology*, *20*, 1992–2003.

Vashum, K. T., & Jayakumar, S. (2012). Methods to estimate above-ground biomass and carbon stock in natural forests-A review. *Journal of Ecosystem & Ecography*, *2*, 1–7.

Wilson, N. R., Norman, L. M., Villarreal, M., Gass, L., Tiller, R., & Salywon, A. (2016). Comparison of remote sensing indices for monitoring of desert cienegas. *Arid Land Research and Management*, *30*, 460–478. https://doi.org/10.1080/15324982.2016.1170076

Woodward, F., Lomas, M., & Kelly, C. (2004). Global climate and the distribution of plant biomes. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, *359*, 1465–1476. https://doi.org/10.1098/rstb.2004.1525

Yan, D., & de Beurs, K. M. (2016). Mapping the distributions of C3 and C4 grasses in the mixed-grass prairies of southwest Oklahoma using the Random Forest classification algorithm. *International Journal of Applied Earth Observation and Geoinformation*, *47*, 125–138. https://doi.org/10.1016/j.jag.2015.12.007

Zhao, F., Xu, B., Yang, X., Jin, Y., Li, J., Xia, L., … Ma, H. (2014). Remote sensing estimates of grassland aboveground biomass based on MODIS Net Primary Productivity (NPP): A case study in the Xilingol grassland of Northern China. *Remote Sensing*, *6*, 5368–5386. https://doi.org/10.3390/rs6065368

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