Seeing roots from space: aboveground fingerprints of root depth in vegetation sensitivity to climate in dry biomes

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Abstract

With predicted climate change, drylands are set to get warmer and drier, increasing water stress for the vegetation in these regions. Plant sensitivity to drier periods and drought events will largely depend on trait strategies to access and store water, often linked to the root system. However, understanding the role of below-ground traits in enhancing ecological resilience to these climate changes remains poorly understood. We present the results of a study in southern Africa where we analysed the relationship between root depth and the vegetation sensitivity index (VSI) (after Seddon and Macias-Fauria \textit{et al} 2016 \textit{Nature} 531 229–32). VSI demonstrates remotely-sensed aboveground vegetation responses to climate variability; thus our study compares aboveground vegetation responses to belowground root traits. Results showed a significant negative relationship between root depth and vegetation sensitivity. Deeper roots provided greater resistance to climate variability as shown by lower sensitivity and higher temporal autocorrelation in vegetation greenness (as measured by the enhanced vegetation index). Additionally, we demonstrated a link between deeper roots and depth to groundwater, further suggesting that it is the ability of deeper roots to enable access to groundwater that provides ecological resistance to climate variability. Our results therefore provide important empirical evidence that the ability to access deeper water resources during times of lower water availability through deeper roots, is a key trait for dryland vegetation in the face of future climate change. We also show that belowground traits in drylands leave a fingerprint on aboveground, remotely-sensed plant–climate interactions, an important finding to aid in scaling up data-scarce belowground research.

1. Introduction

Plant traits play a fundamental role in mediating vegetation responses to climate change. Recent work has demonstrated that belowground traits (e.g. rooting depth, resprouting ability, belowground storage) might be at least as important as aboveground traits in promoting plant fitness and performance in the face of climate change (Kühn \textit{et al} 2021), enabling plants in dryland biomes to cope with climate and associated environmental changes. The relationship between belowground plant traits and climatic/environmental factors is thus potentially important for determining plant resilience to future change. However, in comparison to other traits, roots are rarely studied due to difficulties in field extraction (Laliberté 2017). Preliminary hypotheses backed up by root research based on a limited global dataset (\(n = 475\)) predict that deeper roots will be more prevalent in arid and semi-arid systems than in humid ones, and more prevalent in certain growth forms (trees from savanna/thorn scrub, or seasonally dry forests) (Schenk and Jackson 2002, Schenk 2005).

Recent collation of existing data in online trait databases (GRooT, FRED, TRY, BIEN) (Enquist \textit{et al} 2009, Kattge \textit{et al} 2011, 2020, Iversen \textit{et al} 2017, Guerrero-Ramírez \textit{et al} 2021) and the advancement of remote root measuring techniques (i.e. isotope
analysis and remote sensing techniques) have supported these hypotheses over large spatial scales. Fan et al. (2017) for example, showed that groundwater plays a key role in driving root depth patterns at both the landscape and global scale. Similarly, deep roots have also been found to strongly correlate with the ability to access deep soil water (Fort et al. 2017, Liu et al. 2021). For example, a recent study in sub-tropical coniferous shrubs showed that during dry seasons the majority of water uptake occurred in deep soil layers (Jiang et al. 2020). Ability to access water from the deeper groundwater table, additional to the rooting zone of soil (Leenaars et al. 2018) through deeper rooting depth (Weigelt et al. 2021), may therefore be an important trait from local (Kühn et al. 2022) to global scales (Laughlin et al. 2021) in times of drought. 

Previous studies on groundwater-dependent ecosystems support the suggestion that certain species are reliant on this deeper groundwater (so called phreatophytes) (Naumburg et al. 2005, Eamus et al. 2015) especially in drier intervals (Gou and Miller 2014). However, the hypothesis of deeper roots mediating plant sensitivity to hydroclimate variability via groundwater access has not yet been widely demonstrated. Furthermore, there is little understanding of whether this relationship is consistent across functionally different biomes within drylands. 

In this study we analysed the relationship between root characteristics and above-ground patterns of vegetation sensitivity to climate variability. The vegetation sensitivity index (VSI; Seddon et al. 2016) quantifies the relationship between anomalies in monthly vegetation greenness (as measured by the enhanced vegetation index (EVI)) and climate anomalies. In the VSI’s multiple regression approach, the month-to-month temporal autocorrelation in EVI (EVI\(^1\rightarrow\)EVI\(^0\)) represents the potential influence of lagged effects on vegetation, which have been found to be key to explain vegetation productivity in drylands (Liu et al. 2018). Greater magnitude in EVI\(^1\rightarrow\)EVI\(^0\) indicates that EVI anomalies are more strongly linked to the previous month’s EVI anomaly than the current climate. Seddon et al. (2016) generated a coarse (5 km), spatially-continuous global map of vegetation sensitivity considering the period 2000–2013. Within this global analysis, southern Africa showed strong variation in vegetation sensitivity to climate variability, with large areas showing high sensitivity to water availability and high temporal autocorrelation in EVI. 

This makes the region a suitable case study to test if water-related traits such as root depth play a role in determining vegetation sensitivity to climate change as observed by the aboveground VSI patterns. Further, this offers the opportunity to analyse whether belowground traits can be estimated by analysing the variability in EVI of aboveground vegetation. 

We recomputed the VSI at a finer spatial resolution (1 km) and analysed the relationship between root depth and sensitivity to climate variability for the 20 year period comprising 2000–2019 in the biodiverse dryland biomes of southern Africa to test the following hypotheses: 

(a) Deeper roots are found in areas with lower VSI (thus deeper roots result in greater ecological resistance to drought events). 

(b) Deeper roots are also found in areas that demonstrate greater temporal autocorrelation in EVI (EVI\(^1\rightarrow\)EVI\(^0\)) (thus suggesting previous state, mediated by belowground traits, are more important in determining EVI anomalies than month-to-month climate variability). 

(c) The relationships apparent in (a) and (b) are regulated by overall growth form and vegetation characteristics captured by biome type. 

(d) We expect a positive relationship between root depth and groundwater depth and a negative relationship between root depth and soil water holding capacity, in agreement with the proposed mechanism that deeper roots enables access to deeper groundwater resources.

2. Methods 

2.1. Study site and climate 

We conducted our analysis in southern Africa, including all land area between 20° S and 40° S and 11° E and 35° E. This area encompasses 11 biomes, with varying vegetation types and growth forms (figure 1 and see supplementary table S1).

Most of southern Africa experiences a colder dry season (April–October) and a warmer wet season (November–March). However, in the south-western tip of the region (covering Fynbos and Succulent Karoo biomes), the seasons are reversed, with dry summers and wet winters produced by mid-latitude cyclones. Observed past climate change in southern Africa indicates warming of 0.4 °C per decade between 1961 and 2014, making it one of the regions experiencing the greatest warming in Africa (Davis and Vincent 2017). This warming has resulted in greater evapotranspiration. Further, the region has shown declining trends in rainfall, resulting in an aridification trend that is predicted to continue, with increased frequency and intensity of droughts implying even greater future water stress across the region (Davis and Vincent 2017, Naik and Abiodun 2019). 

2.2. Trait data 

Root depth data and their geographical coordinates from the study area in southern Africa were collated from existing datasets from published literature and online trait databases, resulting in 88 records. These data are collected using a range of methods including root excavations, isotopic analysis, and borehole inspections. In addition, 12 more records were randomly subset (see methods section 2.6) from root depth data collected via excavation by a prior study (Kühn et al. 2022) (n = 124). In total, 100 records of
root depth across biomes and growth forms were collated from existing datasets (see supplementary table S2). These covered six out of the 11 biomes in the study region, with the most data points in Savanna ($n=67$) and Fynbos ($n=22$) and fewer in Succulent Karoo (5), Nama Karoo (3), Azonal Vegetation ($n=2$), Grassland ($n=1$). Four growth forms were considered: trees ($n=64$); shrubs ($n=30$); graminoids ($n=4$); and non-graminoid herbaceous plants ($n=2$).

2.3. Climate and vegetation data
Climate data used in this study were obtained from the satellite Moderate Resolution Imaging Spectroradiometer (MODIS) 8 day composite ratio of actual vs potential evapotranspiration (Running et al 2019). These were obtained at a 0.5 km resolution over 2000–2019, along with MODIS daily cloudiness (Vermote and Wolfe 2020) at 1 km resolution over 2000–2019, which was calculated following the methodology outlined by Wilson and Jetz (2016). In addition, we obtained Climatologies at high resolution for the earth’s land surface areas, CHELSA monthly timeseries of maximum temperature at 1 km resolution (period 2000–2019) (Karger 2018, Karger et al 2017), as well as data from the MODIS monthly EVI (Didan 2015) at 1 km resolution over the period 2000–2019. All outputs were then calculated using layers at a spatial resolution of 1 km.

2.4. Vegetation sensitivity to climate variability and temporal autocorrelation in EVI
The VSI was calculated at a spatial resolution of 1 km over the time period 2000–2019, using the methodology developed by Seddon et al (2016). This involved modelling the relationship between monthly anomalies in EVI and monthly anomalies in climate variables (evapotranspiration, cloudiness, temperature), together with the EVI anomaly of the previous month for the whole period. The details of the algorithm are described in the supplementary material and in Seddon et al (2016). Higher values of VSI indicate greater sensitivity to month-to-month climate variability. As part of the multiple regression approach to estimate VSI, the temporal autocorrelation in the EVI of the previous month is estimated (hereafter temporal autocorrelation in EVI ($\text{EVI}_{t-1}$)). This represents the contribution of the previous month’s state to the anomalies in the EVI. Higher values of $\text{EVI}_{t-1}$ indicate greater association of past EVI with current EVI anomalies.

2.5. Comparison of all VSI data across biomes
Biome maps from The Vegetation Map (SANBI 2018), the Atlas of Namibia Project (Directorate of Environmental Affairs Ministry of Environment and Tourism 2002), and World Wildlife Fund (WWF) Ecoregions maps (Olson et al 2001) were merged and rasterised using the ‘raster’ package in R (Hijmans 2012). Mean and median VSI and $\text{EVI}_{t-1}$ values were calculated for each biome to facilitate comparison of their central tendencies. One-way analysis of variance (ANOVA) and Tukey honestly significant difference (HSD) tests (with a 95% confidence interval) were performed on a 10% random subsample of pixels for each biome to compare whether VSI and $\text{EVI}_{t-1}$ differed across biomes.
2.6. Statistically exploring the relationship between VSI and EVI_{t-1} vs root depth

We tested the relationship between VSI and EVI_{t-1} (response variables vs root depth, biome and growth form using generalised least squares models. This approach was used to account for heteroskedasticity and correlation between residuals. VSI and EVI_{t-1} values were extracted for each of the 1 km pixels where root depth data were present (n = 100 in total).

These relationships can be summarised by the following functions:

\[
\text{VSI} = \alpha_{\text{VSI}} + \beta_{\log(root depth)} \times \log(root depth) + \beta_{\text{biome}} \times \text{Biome} + \beta_{\text{growth form}} \times \text{growth form} + \epsilon
\]

\[
\text{EVI}_{t-1} = \alpha_{\text{EVI}_{t-1}} + \beta_{\log(root depth)} \times \log(root depth) + \beta_{\text{biome}} \times \text{Biome} + \beta_{\text{growth form}} \times \text{growth form} + \epsilon
\]

where \(\alpha\) is the estimated random intercept and \(\beta\) is the estimated regression coefficient associated with each of the explanatory variables, given by the subscript. The \(\alpha\) and \(\beta\) parameters are estimated separately in two models, one with VSI and the other with EVI_{t-1} as the response variable, again indicated by the subscripts. The error terms are captured by \(\epsilon\), and all model assumptions were verified using diagnostic plots (supplementary figure S1). Models were run both with the full set of root depth data as well as without an extreme value of root depth found to be deeper than modelled depth to groundwater (section 2.7) to ensure the results were robust to uncertainty in the root depth measurements (supplementary table S3).

This analysis assumes that the rooting depth value is representative of the 1 km² pixel in which it was collected. This assumption is supported by the fact that rooting depths were collected from dominant vegetation in the landscape (Higgins et al 1987, Obakeng 2007, Zhou et al 2020). Of the 100 root depths collected, 21% were outside the time period of our remote sensing data (2000–2019). We chose to retain these points in our analysis as we assume that areas where vegetation had deep roots in the earlier time periods of collected data (pre-2000) are likely to have deep roots now.

2.7. Depth to groundwater and root zone plant-available water holding capacity

To determine whether access to deeper groundwater (beyond shallow rooting zone water) via deeper roots was a potential mechanism underlying the relationships found between root depth and VSI, we regressed root depth against modelled groundwater depth (at 5 km resolution) (MacDonald et al 2012) and root zone plant-available water holding capacity (at 1 km resolution) (Leenaars et al 2018) (see supplementary material for further details). Depth to groundwater used in this analysis is defined as the maximum depth from the ground surface to the phreatic water table. Further, VSI was regressed against these metrics in order to compare published climate responses obtained using hydrological modelling to connect climate drivers to belowground water resources (Gao et al 2014, de Boer-euser et al 2019, Bouaziz et al 2022) against our approach of connecting aboveground climate-mediated vegetation responses to belowground traits.

2.8. Savanna biome root depth prediction

To further explore the biome with the most comprehensive root depth data, we used a linear model to test the relationship between VSI and root depth in the Savanna biome (n = 63):

\[
\text{VSI}_{\text{Savanna}} = \alpha_{\text{VSI(Savanna)}} + \beta_{\log(root depth)} \times \log(root depth)_{\text{Savanna}} + \epsilon
\]

A further motivation for this step was that if the above regression on VSI-only works, it has the potential to produce a spatially comprehensive map of predicted root depth over the savanna for the region. We cross-evaluated the model to ensure its generalisability by randomly partitioning the data into a training and a test set in a 70:30 ratio over 1000 iterations. After checking for model robustness, the relationship was then inverted, treating root depth as the response variable, which enabled us to predict root depth using the spatially continuous map of VSI. We ran the model and the root prediction map for trees only, as most of the data (94%) was for trees. To ensure that there was no bias in the prediction for high or low root depth values, we compared observed vs predicted values of tree root depth for the region. To assess the applicability of our model for the range of tree cover of this study region, we also compared tree cover density of the study region vs our empirical root data using MOD44B version 6 vegetation continuous fields yearly product (DiMiceli et al 2015), where we used the per cent tree cover in each pixel in 2020. The final spatial prediction of root depth was limited to pixels whose VSI values were within the range of values in pixels covering our calibration root depth observation dataset.

3. Results

3.1. Vegetation sensitivity varies across biomes

Vegetation sensitivity differed across southern Africa (figure 2(a)) and significantly among biomes (supplementary figure S2(a), table S4) \((F = 14.033, \text{DF} = 11, p < 2 \times 10^{-16}; \text{one-way ANOVA})\): all biomes were significantly different in their mean VSI values from
Figure 2. (a) VSI, (b) temporal autocorrelation in EVI (EVI$_{-1}$), which shows higher values in areas where current EVI anomalies have a greater association with past EVI anomalies, i.e. a stronger effect on vegetation sensitivity than that of climate variability and (c) climate weights of VSI across our study extent in southern Africa. Areas with EVI < 0.1 were excluded due to very low vegetation cover and show as no-data in white. Grey denotes sea.
Table 1. Generalised least squares model parameter estimates, standard error, confidence interval, test statistic (t-value), p-value (bold values indicate significance at p<0.05) and R² for VSI and EVIₜ₋₁ models. Although growth form alone is deemed non-significant, it is nonetheless required in the best model.

| Parameters                  | VSI          | EVIₜ₋₁       |
|-----------------------------|--------------|--------------|
| Parameter estimates         | Std. error  | CI           | Test statistic | p      | Parameter estimates | Std. error  | CI           | Test statistic | p      |
| α (intercept)               | 21.87        | 3.75         | 14.52−29.22  | 5.83   | <0.001            | 70.34       | 8.38         | 53.91−86.77  | 8.39   | <0.001          |
| βgrowth form [depth]        | −2.45        | 0.45         | −3.33−1.57   | −5.45  | <0.001            | −73.83      | 9.53         | −92.51−55.16 | −7.75  | <0.001          |
| βbiome [African Savanna]    | 18.09        | 4.26         | 9.73−26.45   | 4.24   | <0.001            | 37.86       | 6.73         | −51.06−24.66 | −5.62  | <0.001          |
| βbiome [Fynbos]             | 7.62         | 3.01         | 1.71−13.52   | 2.53   | 0.013             | −11.91      | 4.95         | −21.61−4.28  | 2.41   | 0.018           |
| βbiome [Nama Karoo]        | 22.13        | 4.41         | 13.50−30.77  | 5.02   | <0.001            | −77.90      | 9.85         | −97.21−58.60 | −7.91  | <0.001          |
| βbiome [Grassland]         | 13.62        | 7.37         | −0.83−28.06  | 1.85   | 0.068             | −63.55      | 16.47        | −95.83−31.27 | −3.86  | <0.001          |
| βbiome [Azonal Vegetation] | 11.91        | 4.95         | 2.21−21.61   | 2.41   | 0.018             | −47.87      | 11.06        | −69.55−26.18 | −4.33  | <0.001          |
| βgrowth form [herb]         | −1.08        | 5.16         | −11.18−9.03  | −0.21  | 0.835             | −6.93       | 11.52        | −29.51−15.66 | −0.60  | 0.549           |
| βgrowth form [shrub]        | 4.11         | 3.29         | −2.34−10.55  | 1.25   | 0.215             | 8.58        | 7.35         | −5.82−22.98  | 1.17   | 0.246           |
| βgrowth form [tree]         | 7.56         | 4.45         | −1.16−16.29  | 1.70   | 0.093             | 11.98       | 9.95         | −7.51−31.48  | 1.21   | 0.231           |
| Observations                | 100          | 0.607        |              |        | 100               | 0.607       |              |              |        |
| R²                          |              |              |              |        |                  |              |              |              |        | 0.665           |

one another (except Desert, which was not significantly different from Nama Karoo nor from Indian Ocean Coastal Belt) (supplementary figure S2(a) for results from Tukey’s HSD test for multiple comparisons). Notably, the Succulent Karoo biome showed the lowest sensitivity.

Month-to-month temporal autocorrelation in EVI (EVIₜ₋₁) also differed significantly among biomes (figure 2(b), see supplementary figure S2(b)) (F = 105 588, DF = 10, p < 2 × 10⁻¹⁶; one-way ANOVA): all biomes were significantly different from one another in their EVIₜ₋₁ (supplementary figure S2(b) for results from Tukey’s HSD test for multiple comparisons) and showed even more inter-biome contrast than with VSI, with the drier biomes (Succulent Karoo, Desert, Fynbos and Nama Karoo) having greater EVIₜ₋₁ values, thus showing a higher role of lagged effects on EVI anomalies and a lower response to the climate conditions of the concurrent month than wetter biomes (e.g. Indian Ocean Coastal Belt, Forests and Albany Thicket biomes). Water availability is the key climate driver of the VSI patterns in most of our study area, except in parts of the Grassland biome (including the Lesotho Highlands), which show temperature and cloudiness as key explanatory variables (figure 2(c)). The drier portions of the Savanna, Succulent Karoo, Fynbos, Nama Karoo and Desert biomes (with enough vegetation cover to produce VSI values—see supplementary material) show a mixed signal, with no overall dominant climate variable driving VSI (figure 2(c)).

3.2. Vegetation sensitivity vs root depth

Results from the generalised least squares model indicate that in the best model (table 1) root depth, in combination with biome and growth form, significantly explain vegetation sensitivity across southern Africa (R² = 0.607, p < 0.001). This model shows a negative linear relationship between VSI and root depth (i.e. deeper roots are found in areas with lower climate sensitivity) (VSI range 9.43–43.85). Models using other variable combinations show higher Akaike information criterion (AIC) than the model shown in table 1 (see model comparisons in supplementary table S5). Results also indicate a positive linear relationship between root depth and temporal autocorrelation in EVI (EVIₜ₋₁) (i.e. deeper roots are associated with areas with higher past EVI and less associated with month-to-month climate variability) (R² = 0.665, p < 0.001) (table 1 and see model comparisons supplementary table S6) (EVIₜ₋₁ range 8.96–97.02). Additional models run with the criterion of excluding rooting depth outliers that are greater than modelled depth to groundwater have negligible differences and thus indicate robust-ness of original models that include extreme rooting depths (see supplementary material table S3). Graphical representation of linear relationships between VSI and EVIₜ₋₁ and root depth individually for biomes and growth forms reflect the relationships identified by this model and are presented in supplementary figures S3 and S4.

3.3. Depth to groundwater and root zone plant-available water holding capacity

Results indicate that as the depth to groundwater increases, root depth increases (figures 3(a) and S5(a)) and vegetation sensitivity to climate variability declines (figure S6(a)). Further, as the water holding capacity of the rooting zone for plants increases, root depth declines (figures 3(b) and S5(b)) and vegetation sensitivity to climate variability increases (figure S6(b)). These results are mostly driven by the very consistent relationships found in the savanna.

3.4. Root depth in savanna

In the Savanna biome of southern Africa, tree root depth alone can significantly explain VSI (and EVIₜ₋₁) (R² = 0.418, p < 0.001; table 2). Cross-evaluation of our model indicates consistent correlation statistics (table S7). Further, the data used for
Figure 3. (a) Log root depth vs estimated groundwater depth (metres below ground) across all biomes. At deeper groundwater depths, roots tend to be deeper. This is consistent with findings from other literature (Fan et al 2017). Groundwater classes: VS = 0–7 m, S = 7–25 m, SM = 25–50 m, M = 50–100 m. (b) Log root depth vs root zone plant-available water holding capacity across all biomes. At lower root zone plant-available water holding capacity, rooting depth tends to be higher. See supplementary figures S6(a) and (b) for individual biomes. Significance level denoted by \(*\) \(p < 0.05\), \(*\*) \(p < 0.001\); (ns) is not significant.

Data source: British Geological Survey (BGS) groundwater depth (based upon mapping provided by British Geological Survey © NERC 2012. All rights reserved) and RZWHC from ISRIC Africa Soils Database.

Table 2. Generalised linear model parameter estimates, standard error, confidence interval, test statistic (\(t\)-value), \(p\)-value (bold values indicate significance at \(p<0.05\)) and \(R^2\) for VSI model for the Savanna biome.

| Parameters     | Parameter estimates | Std. error | CI          | Test statistic | \(p\)  |
|----------------|---------------------|------------|-------------|----------------|--------|
| \(\alpha\) (intercept) | 48.43               | 2.41       | 43.71 – 53.15 | 20.11          | <0.001 |
| \(\beta\) log(root depth)  | –2.60               | 0.39       | –3.37 – –1.83 | –6.61          | <0.001 |
| Observations   | 63                  |            |             |                |        |
| \(R^2\)        |                     |            | 0.418       |                |        |

4. Discussion

4.1. Vegetation sensitivity and temporal autocorrelation in EVI varies across biomes

Biomes in the study region show significantly different vegetation sensitivity to climate variability (VSI) and temporal autocorrelation in EVI (EVI\(_{t-1}\)) from one another, reflecting the varying ability of species, plant functional types and ecosystems to respond to climate variability in drylands. In the four driest biomes in the study region—Desert, Succulent Karoo, Nama Karoo and Fynbos (10–80, 20–290, 100–520 and 200–800 mm total annual precipitation respectively, supplementary table S1), we observe the highest influence of lagged effects (EVI\(_{t-1}\)) and thus a weaker relation of EVI anomalies to month-to-month climate variability. In the wetter, more forested biomes, we observe the lowest influence of the temporal autocorrelation in EVI and the highest influence of month-to-month climate variability. The best explanation for the lack of association between EVI anomalies and month-to-month climate variability is that vegetation in the driest biomes tends to have traits that allow for buffering short-term (monthly) climate variability (e.g. drought and high evaporative demands), through facilitating access to groundwater reserves.

4.2. Vegetation sensitivity can be explained by root depth

Our model results provide evidence in favour of the hypothesis that the observed variation in remotely-sensed aboveground sensitivity to climate variability can, to a significant extent, be explained by root depth (hypothesis i) in water-limited environments. Within
the limited empirical root depth data available, this hypothesis is shown to be consistent across the studied biomes and growth forms of southern Africa. This finding suggests that plants with deeper roots might be able to tap into deeper water resources, reducing sensitivity to month-to-month climate variability. This is also supported by the association between higher temporal autocorrelation in EVI (EVI$_{t-1}$) and deeper roots where deep rooted plants are likely more dependent on groundwater and less responsive to daily variability in surface water availability (hypothesis ii). Our findings are very much in line with those from a study in the Kgalagadi Transfrontier Park in Botswana where it was observed that *Vachellia erioloba* and *Vachellia haematoxylon* (previously *Acacia*, known to root very deeply), did not show significant canopy dieback in times of drought even though they are facultatively deciduous species (Shadwell and February 2017). The authors suggested this is because these species could continue to obtain water for photosynthesis by tapping deeper water resources. The regions known for these deep-rooted *Vachellia* species coincide with the areas in our study with lower vegetation sensitivity and the deepest roots in our dataset (e.g. *V. erioloba* and *Senegalia flecki* in the Botswanan Kalahari; Obakeng 2007). This link is worth exploring, especially considering research demonstrated by Stevens *et al* (2016) in semi-arid South African Savannas, where deciduousness has water cues as opposed to the globally more common temperature and light cues.

Relationships between vegetation sensitivity and root depth display the same trends across the biomes with sufficient data (i.e. Savanna, Fynbos and Succulent Karoo, figures S3(a) and (b)), but the range of sensitivity values vary. This suggests that while similar plant rooting strategies exist, biome and growth form may also play an important role in the way this is then manifested in terms of response, in agreement with our hypothesis iii. The best model for this relationship indicates that growth form does not statistically contribute to the relationship, however the overall model does improve with its inclusion. This variable is therefore an ecologically informed inclusion in the model. It should also be noted that herbaceous and graminoid growth forms require further study as our results for these growth forms individually were inconclusive due to limited data.

For the individual Savanna tree model, the strong relationship between root depth and the aboveground response to both month-to-month climate variability and previous EVI (VSI and EVI$_{t-1}$) indicates that root depth is likely to play a key role in buffering sensitivity to future climate change. It is therefore important to understand which regions have deep roots that offer this enhanced resistance to climatic variability, and which ones may be more vulnerable to short-term climate anomalies. The ability to predict root depth as we have shown in the Savanna biome of southern Africa (figure 4) represents a step forward in this direction and could inform future natural resource management strategies of
groundwater reserve management and conservation strategies under changing climates. Our model predicted root depths of up to 67 m in Savanna regions that correspond to the dry limits of the study extent including the Kalahari Desert (figure 4), where there is likely very low vegetation productivity. The trees that do grow in these regions represent a priority for field validations and for the study of the mechanisms of surviving drier limits of this biome, including tree access to deep water resources via very deep roots.

The environmental correlates associated with the VSI data (figure 2(c)) predictably indicate that across most of southern Africa the primary driver of climate sensitivity is water availability. However, areas with lower sensitivity, which correspond to the driest biomes (e.g. Desert, Succulent Karoo, Fynbos andNama Karoo), do not indicate sensitivity to current water availability as defined in the VSI (Seddon et al 2016) (figure 2(c)) and show a mixed signal with no overall dominant variable driving VSI. This is likely due to underlying drought adaptations, such as deeper roots shown in this study, but may also include succulent water storage in the Desert, Succulent andNama Karoo and more efficient water use in the Fynbos (Skelton, 2014, Skelton et al 2015) through isohydry for example (West et al 2012).

The positive correlation between root depth and depth to groundwater (figures 3(a) and S5(a)) agrees with global trends (Fan et al 2017). The negative relationship between root depth and root zone water holding capacity (figures 3(b) and S5(b)) is in line with observed effective rooting depth in temperate biomes (see Speich et al (2018), who also find non-conformity of Mediterranean ecosystems which could relate to the patterns we observe in Fynbos (figure S5)) and offers another line of evidence that deeper and shallower rooted plants differ greatly in where they are accessing water from. Both confirm our hypothesis iv. These relationships, taken alongside the negative relationship between VSI and groundwater depth and the positive relationship between VSI and root zone water holding capacity (figures S6(a) and (b)), support the hypothesis that plants with deeper roots that can access deeper groundwater resources (beyond the shallower rootable depth (Leenaars et al 2018)) to cope with drier periods, are less sensitive to climate variability. Our findings align with previous work in semiarid regions of California showing that groundwater dependent vegetation is unaffected by periods of lower rainfall (Elmore et al 2003). Relatively, previous studies also suggest that precipitation reliant vegetation e.g. non-native cheat grass in the Great Basin, USA, shows higher variability than native shrubs and grasses that typically have deeper roots and depend on groundwater (Bradley and Mustard 2005).

Due to the difficulties in field collection, root depth data in this study are limited in size and spread. Furthermore, some of the available data are pre-2000 so they may not fully represent current traits, for e.g. if non-native species have invaded an area. To deal with this as far as possible, we checked the validity of these data by consulting original literature and correlating root depth against modelled groundwater depth data. These checks supported our findings and led us to conclude that the root depth data are reliable and representative of the vegetation in their associated remote sensing pixels.

4.3. Implications

The results of our study hold important implications for the understanding of vegetation resistance and eventual resilience to current and future climate change. Applications of this knowledge may prove key for dryland biodiversity conservation under future climate change by providing information about which biomes, growth forms, belowground trait strategies and indeed species may be more vulnerable in a drier future, as determined by the ability to access groundwater resources with deeper roots. This knowledge can further inform conservation management strategies under climate change, where for example, restoration of dry regions may select for species that have traits such as the ability to root deeply, to improve the future adaptability of these systems.

These applications can be extended to agricultural systems in Africa, where along with aridification, irrigation of crops is very limited. Our findings support calls for a shifted focus in drylands to crops with resilient traits (Satori et al 2021), such as enhanced root investment, which preliminary findings suggest could be favoured under future climates (Manners et al 2021). Additional benefits of this approach could exist for crops where yield is gained from belowground plant parts, which might be less affected by short-term drought than aboveground plant parts.

In those biomes that do not have species that have evolved deeper roots as an adaptation to drier periods or do not have the ability to plastically alter root depth (or other traits), plants may not be able to tolerate future drier climatic conditions. This could result in mass plant mortality during drier times or drought periods, and/or gradual shifts in species compositions where some species can tolerate drier conditions and will replace those that cannot. This will also in part depend on the rate of groundwater reduction, and whether this will exceed potential root growth (Naumburg et al 2005).

In those biomes already using deeper roots to deal with water stress, inevitable decline in groundwater resources due to climate change and human extraction (Liu 2011, Mamuye and Kebebewu 2018, Chiloane et al 2021) may present a challenge to these plants’ survival. Previous studies have shown that in areas with groundwater extraction, groundwater dependent plants had a reduced capacity to cope with drought than those where groundwater extraction is
not present (Stromberg et al 1996, Elmore et al 2003, 2006). Groundwater pumping can thus switch a system from one buffered from drought to being sensitive to drought (Elmore et al 2003). Related to this, deeper-rooted species have been suggested to play a key role in maintaining groundwater resources themselves (e.g. facilitating surface water penetration to deeper soils or redistribution of water in soils via hydraulic lift) (le Maitre et al 1999). If these species are no longer able to survive in drier times due to groundwater decline, and are subsequently lost to these systems, groundwater reserves may be impacted and consequently affect ecosystem functioning and services through a decline in water provision. This feedback is an unwelcome possibility for drylands such as those in southern Africa, where ecosystems and human livelihoods are inextricably linked to water availability and where severe water shortages are predicted for the future (Davis and Vincent 2017).

Our work thus highlights the ecological importance of the maintenance and protection of groundwater resources, particularly across the worlds’ drylands. The recent droughts witnessed in the Western Cape of South Africa (2015–2018; (Naik and Abiodun 2019)) saw increased extraction of groundwater through existing and newly sunk household level boreholes (Ziervogel et al 2019). More frequent and severe droughts, such as this, could fundamentally change groundwater reserves which are already declining due to extraction by invasive plant species in this region (le Maitre et al 2019).

4.4. Future directions
Although great progress has been made in the field of root ecology with the collation of existing root data and the ability to use remotely-derived data to predict root depth, as we have shown for the Savanna biome, and is shown in other studies (Yang et al 2016, Fan et al 2017, Jiang et al 2020, Stocker et al 2021), we still require more efforts in field-based root data collection. We still lack comprehensive spatial, temporal, and taxonomical coverage, including the relative contributions of intraspecific variation and trait plasticity in response to environmental changes. The lack of data limits our ability to quantify plastic responses and track changes in root depth over time. Our study assumed roots in earlier periods (pre-2000) have similar root depths to the more recent past (2000–2020). However, future studies will benefit from investigating the potentially dynamic response of root traits over time as the rate of climatic changes accelerates. Field studies are key and existing data cannot be scaled up using species means linked to occurrence data (supplementary figure S8) because it is likely that intraspecific differences modulated by local climate factors cannot be ignored (e.g. topography-related water gradients; Kühn et al 2022, and Fan et al 2017). Systematically designed trait collection field campaigns (accounting for spatial spread, inclusion along topography, intraspecies variability) are required, and in the case of southern Africa, these should focus on under-sampled, highly biodiverse, and potentially vulnerable biomes (e.g. Desert, Fynbos). This would allow for the models in our study to be applied more widely, and for an explicit mechanistic understanding of the processes involved in the relationships we report in this study to be gained.

5. Conclusions
This study demonstrates the utility of explicitly linking strategically collected field trait data, albeit limited in size and spread, with spatially continuous remote sensing data to observe and predict environmental patterns and responses to climatic changes. Through this approach, we observe that belowground traits are reflected in aboveground vegetation signals. Specifically, we show that root depth is a key trait determining vegetation sensitivity to climate variability in southern Africa, with the proposed underlying mechanism being that deeper roots enhance access to deeper water resources that remain available in periods of drought or reduced surface water availability. Our findings support the hypothesis that deeper roots play (and will likely do so increasingly) an important role in the resistance of vegetation to climate change in southern Africa and potentially across drylands globally, which are set to become warmer and drier.

Data availability statement
The data that support the findings of this study are available upon reasonable request from the authors.

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Author contributions
N K and M M-F conceptualised the research and designed the approach with comments from all authors. N K and M S collected, processed, and analysed the data with assistance from M M-F and C T. N K wrote the first draft of the manuscript with significant contributions from all authors (M M-F, M S, C T and K J W).
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