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Gerónimo A Cardozo, Florence Volaire, Pascal Chapon, Charlène Barotin, Karim Barkaoui. Can we identify tipping points of resilience loss in Mediterranean rangelands under increased summer drought?. *Ecology*, 2024, 108 (9), pp.e4383. 10.1002/ecy.4383 . hal-04675506

HAL Id: hal-04675506

<https://hal.science/hal-04675506v1>

Submitted on 22 Aug 2024

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ARTICLE

Can we identify tipping points of resilience loss in Mediterranean rangelands under increased summer drought?

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Funding information

National Agency for Research and Innovation (ANII-Uruguay), Grant/Award Number: POS_EXT_2019_1_161050; OSU OREME (University of Montpellier)

Handling Editor: G. Darrel Jenerette

Abstract

Mediterranean ecosystems are predicted to undergo longer and more intense summer droughts. The mechanisms underlying the response of herbaceous communities to such drier environments should be investigated to identify the resilience thresholds of Mediterranean rangelands. A 5-year experiment was conducted in deep and shallow soil rangelands of southern France. A rainout shelter for 75 days in summer imposed drier and warmer conditions. Total soil water content was measured monthly to model available daily soil water. Aboveground net primary production (ANPP), forage quality, and the proportion of graminoids in ANPP were measured in spring and autumn. Plant senescence and plant cover were assessed in summer and spring, respectively. The experimental years were among the driest ever recorded at the site. Therefore, manipulated summer droughts were drier than long-term ambient conditions. Interactions between treatment, community type, and experimental year were found for most variables. In shallow soil communities, spring plant cover decreased markedly with time. This legacy effect, driven by summer plant mortality and the loss of perennial graminoids, led to an abrupt loss of resilience when the extreme water stress index exceeded $37 \text{ mm } 10 \text{ day}^{-1}$, characterized by a reduction of spring plant cover below 50% and a decreased ANPP in rainy years. Conversely, the ANPP of deep soil communities remained unaffected by increased summer drought, although the presence of graminoids increased and forage nutritive value decreased. This study highlights the role of the soil water reserve of Mediterranean plant communities in modulating ecosystem responses to chronically intensified summer drought. Communities on deep soils were resilient, but communities on shallow soils showed a progressive, rapid, and intense degradation associated with a loss of resilience capacity. Notably, indexes of extreme stress were a better indicator of tipping points than indexes of integrated annual stress. Considering the role

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of soil water availability in other herbaceous ecosystems should improve the ability to predict the resilience of plant communities under climate change.

KEYWORDS

aridity, biomass production, foliage senescence, plant functional types, recovery, soil water availability, water balance model, water stress

INTRODUCTION

More frequent and intense droughts associated with higher temperatures are expected in many regions under climate change (IPCC, 2021), notably in the Mediterranean areas (Tramblay et al., 2020), where rainfall reduction during spring and summer will result in longer and more intense summer drought (Giannakopoulos et al., 2009). Native herbaceous ecosystems, including rangelands, cover around 26% of terrestrial land in the Mediterranean basin (Martin-Ortega et al., 2017). They have been exposed to severe summer droughts for millennia (Markonis et al., 2018). However, increased summer drought could affect them beyond their current adaptation range and resilience capacity (Smith, 2011). Mediterranean rangelands provide many valuable services, including feed supply for extensive pastoral systems (El Aich et al., 2021). They also protect soils against erosion, regulate the water cycle, and contribute to biodiversity conservation. In this context, there is a pressing need to understand better the mechanisms underlying rangeland functioning, dynamics, and resilience to drought (Jaurena et al., 2021), which have been less studied than intensively managed grasslands (Bengtsson et al., 2019) and remain poorly understood (Tramblay et al., 2020).

Resilience defines the capacity of an ecosystem to resist and recover from stress (Ingrisch & Bahn, 2018). Under the Mediterranean climate, resisting the dry season, that is, maintaining plant community functioning during drought, is generally impeded by the intensity and duration of summer drought, which does not allow plants to grow. In plant communities dominated by herbaceous perennial species, drought resilience rests more critically on the capacity of plants to survive during the dry season and recover to reach their initial functioning state after the dry season (Volaire et al., 2014; Volaire, 2018). However, depending on drought severity, the full recovery of some ecosystem functions can be delayed or never be attained due to drought legacy effects that continue to affect plant communities after drought (Müller & Bahn, 2022; Vilonen et al., 2022), potentially initiating a downward cycle in case of repeated extreme droughts. The alternative state theory suggests that communities

reach *tipping points* at a given level of cumulated stress when forces that push them away from their original state become stronger than feedback resilience forces (Briske et al., 2006). These processes are typically associated with drastic changes in ecosystem structure and function (Suding & Hobbs, 2009).

In drylands, ecosystem degradation under increasing aridity is characterized by abrupt structural and functional changes following three successive phases, that is, an initial phase of vegetation decline, a soil disruption phase, and a final systemic breakdown of the ecosystem (Berdugo et al., 2020, 2022). Associated with the first vegetation decline phase, three intertwined hierarchical mechanisms occur: (1) An initial decrease of above-ground biomass and density due to reduced plant growth and seedling establishment, (2) changes in species demography and cover favoring those most adapted to drought, and (3) a species turnover, resulting from the loss of species with the least adapted strategies and the colonization of more adapted species (Alon & Sternberg, 2019; Barkaoui et al., 2017; Cantarel et al., 2013; Hoover et al., 2014; Reichmann & Sala, 2014; Smith, 2011). While a reduced plant cover was linked to an early degradation process in many ecosystems (Maestre & Escudero, 2010; Turnbull et al., 2012), including the degradation of soil properties (Dlamini et al., 2014), it has been suggested that the loss of plant cover would occur at the end of the degradation process in drylands (Berdugo et al., 2020, 2022). However, relatively few studies have been conducted on these processes in the Mediterranean rangelands under climate change.

Predicting the resilience of ecosystems to drought remains challenging because these mechanisms presented above potentially co-occur and contribute to slowing down the decrease in soil water availability, reducing plant water demand and hence buffering vegetation water stress (Turnbull et al., 2012). For instance, the decrease in biomass and the changes in species composition were both associated with a significant reduction of water use, which buffered water stress and drought mortality within native Mediterranean plant communities along a soil water reserve gradient (Barkaoui et al., 2017). It raises the question about the elasticity and

limits of these buffering processes under increasing drought, especially when drought severity and frequency exceed their long-term values. In grasslands, the declines in aboveground net primary production (ANPP) (Durand et al., 2010) and long-term degradation due to drought (Ciais et al., 2005; Gang et al., 2014) have been associated with plant mortality (Griffin & Hoffmann, 2012; Hodgkinson & Müller, 2005; Poirier et al., 2012). Additionally, by modifying plant development and species composition, drought may also affect forage quality (Dumont et al., 2015; Habermann et al., 2019), including plant protein concentration (He & Dijkstra, 2014; Luo et al., 2022). However, the impact of drought on the forage quality of Mediterranean rangelands remains unclear (Dumont et al., 2015; Hidalgo-Galvez et al., 2022).

In this study, over five successive years, we analyzed the cumulative effects of increased summer droughts on the resilience of a Mediterranean herbaceous ecosystem with contrasting soil depth (shallow and deep) in southern France. We monitored the responses of plant communities and the dynamics of soil water availability with a water balance modeling approach to identify water stress indices. We addressed two main questions: (1) Do increased summer droughts modify the soil water availability and water stress of plant communities adapted to contrasting soil depths? And (2) are there tipping points in community structure (plant cover, botanical composition) and ecosystem functions (ANPP, forage quality, water use efficiency) that would trigger drastic, potentially irreversible changes in the trajectories of these rangelands under climate change?

MATERIALS AND METHODS

Site description

The study was conducted in a native grass-shrub rangeland located on the Larzac limestone plateau at the INRAE La Fage station, southern France (43°55' N, 3°05' E, 790 m above sea level). The Larzac plateau (ca. 1000 km²) is part of the Grands Causses region, where the climate is subhumid with a strong Mediterranean influence (Csb, Köppen classification), alternating cold, wet winters (mean daily temperatures: 3°C) and hot, dry summers (mean daily temperatures: 18°C). The long-term mean annual precipitation is 1028 mm (1989–2015), with a mean climatic water deficit of –224 mm during summer (June–August). Soils are made of dry dolomitic rendzinas distributed as a mosaic of different depths, textures, and fertility across topographic zones. Uphills have shallow sandy unfertile soils (18 ± 5 cm depth, hereafter “shallow”), while dolines

have deeper clay and more fertile soils (85 ± 17 cm depth, hereafter “deep”). Plant communities are dominated by native perennial graminoids (*Bromopsis erecta*, *Festuca christiani-bernardii*, *Carex humilis*), forbs (*Potentilla verna*, *Pilosella officinarum*), small shrubs (*Thymus dolomiticus*, *Helianthemum canum*), and scattered shrubs (*Buxus sempervirens*). The site has a very long history of sheep grazing. However, sheep grazing was excluded during the 5-year experiment by fencing plots.

Summer drought treatment

We selected eight plots of around 20 m² in shallow soils ($n = 4$) and deep soils ($n = 4$) following the design from previous studies at the site (Barkaoui et al., 2017; Bernard-Verdier et al., 2012; Pérez-Ramos et al., 2012). In June 2016, we divided each plot into two adjacent subplots. We used one subplot to apply an increased drought treatment during summer using rainout shelters (hereafter “drought”) and the other as an experimental control of the non-manipulated summer drought (hereafter “ambient”). Rainout shelters consisted of open “hoop houses” (6 m²) made of an aluminum structure covered by clear polycarbonate plastic (Figure 1) that were set up for around 75 days from mid-June (e.g., 15 June) to the end of August (e.g., 28 August). They excluded 100% precipitation and created a warmer and drier microclimate during the summer period for the five experimental years (Table 1; Appendix S1: Figure S1).

Climate and microclimate conditions

The local meteorological station of the INRAE La Fage station provided data on daily mean temperature (T), relative air humidity (RH), precipitation (PP), and Penman–Monteith evapotranspiration (ET₀). Mean temperature and relative air humidity were also recorded (Campbell Scientific Ltd.) locally below and outside the hoop houses in two subplots in shallow and deep soils to assess microclimate variations between treatments and topographic zones.

The climate varied considerably during the five years of experiments (2016–2021). Precipitation was close to the long-term mean (1989–2015) in 2016 (–19 mm), higher in 2017 (+359 mm) and 2019 (+220 mm), and lower in 2018 (–129 mm) and 2020 (–89 mm), creating an alternation between humid and dry conditions from one year to another (Table 1; Figure 2). During summers, precipitation ranged from 25 to 140 mm, averaging 25 mm below the long-term

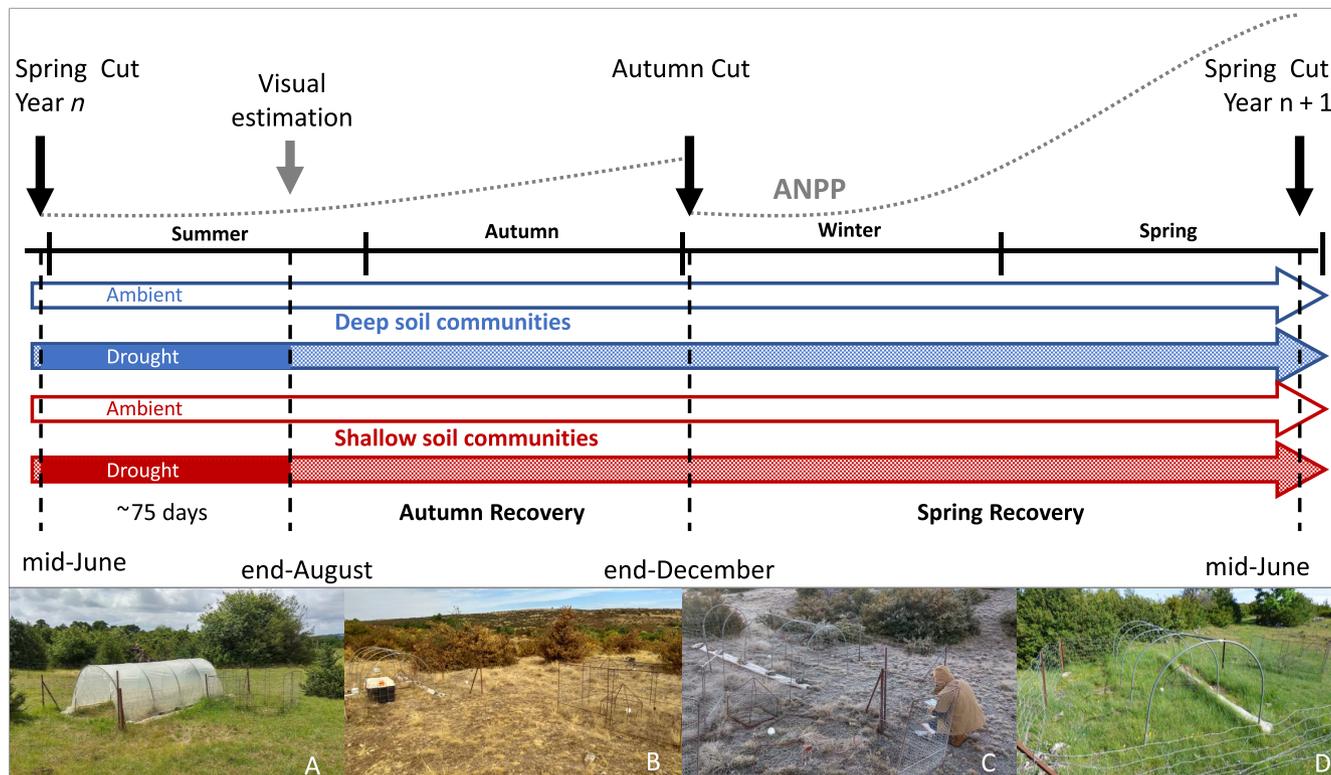


FIGURE 1 Annual experimental procedure for five years. During the increased summer drought-imposed treatment (“Drought”), no rain and higher temperatures were imposed under rainout shelters (solid red and blue areas in horizontal arrows). Cuts of aboveground biomass (black vertical arrow), visual assessments of the vegetation when the rainout shelters have been removed (gray arrows). Photo (A) installation of the rainout shelter at the end of spring, (B) end of a dry summer, (C) winter, and (D) rainy spring. Photos A, B, and D were taken by Pascal Chapon, and photo C by Gerónimo Agustín Cardozo. ANPP, aboveground net primary production.

TABLE 1 Characterization of the rainfall manipulation period: Annual (June–June) and spring (March–June) for each year.

Year	Climate manipulation period							Annual			Spring		
	Date start	Date end	No. days	PP (mm)	PP-Et0	RH (%)	T (°C)	PP (mm)	PP-Et0	T (°C)	PP (mm)	PP-Et0	T (°C)
2016 (1)	21-Jun	13-Sep	84	140	−229	67	18.9	1009	293	10.2	163	−143	12.3
2017 (2)	01-Jun	17-Aug	77	148	−184	73	18.4	1387	567	10.0	477	199	10.9
2018 (3)	15-Jun	28-Aug	74	96	−308	66	20.4	899	−75	10.7	216	−97	10.0
2019 (4)	19-Jun	28-Aug	70	82	−328	63	20.5	1248	286	10.5	298	−28	11.6
2020 (5)	19-Jun	27-Aug	69	25	−367	61	20.9	939	−5	10.9	205	−120	10.6
Experimental mean	15-Jun	29-Aug	75	98	−283	66	19.8	1096	213	10.5	272	−38	11.1
Long-term mean ^a	75	123	−224	70	18.2	1028	231	9.8	278	−4	10.5

Note: Experimental (during five years for the ambient treatment) and historical means for average manipulation rainfall period, of cumulative rainfall (precipitation—PP), difference between (PP) and cumulate evapotranspiration (ET0) by Penman–Monteith, average daily relative humidity (RH%) and average daily temperature (T , in degrees Celsius) are reported.

^a27 years (1989–2015).

mean. The climatic water deficit ranged from −184 to −367 mm, and was, on average, 59 mm more severe than the long-term mean. Mean temperatures remained stable over the past 32 years, although summers were,

on average, 2.4°C warmer in 2018, 2019, and 2020 than the long-term mean. The rainout shelters intercepted 25–105 mm of summer precipitation according to the year, increased the average temperature by 0.7–1.5°C,

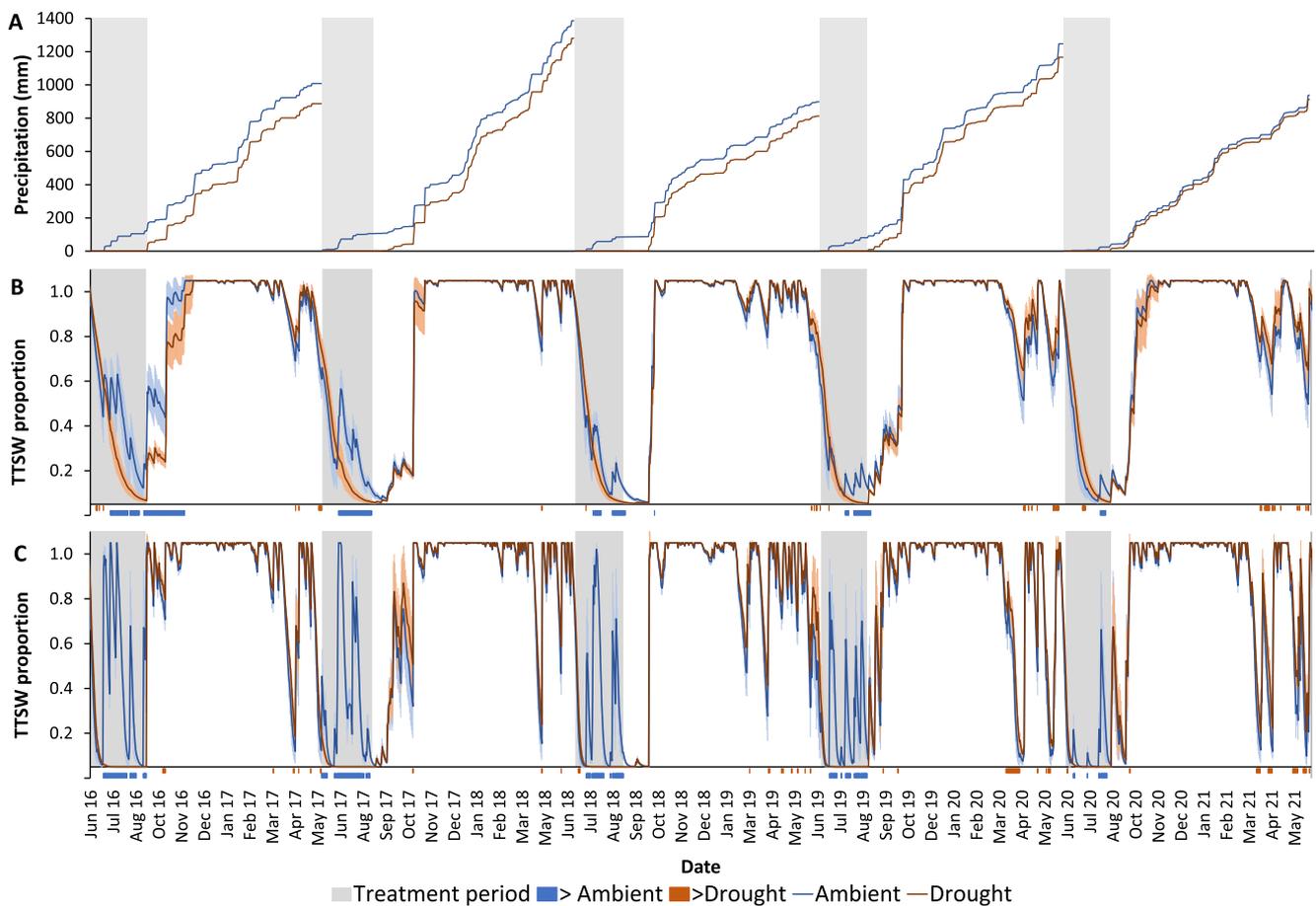


FIGURE 2 Cumulative precipitation (in millimeters) for each year and for five experimental years (A). Proportion of “Total transpirable soil water” (TTSW) over time for deep soils (B) and for shallow soils (C). The gray vertical bar represents an experimental summer rain shelter. The “Ambient” (blue line) and “Drought” treatments (orange line) are represented with SD for (B) and (C). Blue and orange bars down 0 represent a statistical difference greater than 5% (*t*-test, *p* < 0.01) between both situations for each day. When blue, the “Ambient” TTSW proportion is higher than the summer of the “Drought” treatments (>Ambient), and when orange, the “Drought” TTSW proportion is higher than for the “Ambient” (>Drought) treatments.

and reduced the average relative humidity by 0.8%–2.3%. As a result, they created climatic conditions close to the driest summer of the last 32 years (Table 1; Appendix S1: Figure S2).

Soil water monitoring and water balance modeling

We monitored the soil water content (SWC, in millimeters) monthly in all 16 subplots using capacitance moisture probes (DIVINER 2000, Sentek Pty Ltd, Stepney, Australia). Probes measured SWC at each 10-cm soil layer throughout the soil profile (max. 1 m depth). We used soil analyses and calibration curves from previous studies to account for soil texture variations at the site (Barkaoui et al., 2017). We assessed the local soil water properties based on the SWC measurements. We estimated the field capacity (FC, in millimeters) and the wilting point (WP, in millimeters) of each soil profile as the mean of the 10%

highest and the 10% lowest SWC values measured during winter and summer, respectively. We calculated the total transpirable soil water (TTSW, in millimeters) as the difference between FC and WP to estimate the available plant soil water reserve. On a given day, we determined the available soil water (ASW, in percentage) as the level of filling of the TTSW reserve.

We used a bucket-type water balance modeling approach to interpolate the observed values of SWC at a daily time step and assess the daily dynamics of ASW as follows:

$$ASW_{i,t} = 100 \times (SWC_{i,t} - WP_i) / TTSW_i, \tag{1}$$

$$SWC_{i,t} = SWC_{i,t-1} + PP_t - D_{i,t} - ETa_{i,t}, \tag{2}$$

$$ETa_{i,t} = \begin{cases} ET0_t \times k_i, & ASW_{i,t} > 30 \\ \left(\frac{ASW_{i,t}}{30}\right) \times ET0_t \times k_i, & ASW_{i,t} \leq 30, \end{cases} \tag{3}$$

where $ASW_{i,t}$, $SWC_{i,t}$, $ETa_{i,t}$, and $D_{i,t}$ are the available soil water, soil water content, actual evapotranspiration and drainage for plant community i at day t (or $t-1$), PP_t and $ET0_t$ are the precipitation and reference Penman–Monteith evapotranspiration of day t . Drainage has been estimated as the difference between PP and $(FC - SWC)$: if $PP < (FC - SWC)$, water fills the soil reserve (until reaching FC). If $PP > (FC - SWC)$ at day t , the excess of water is assumed to percolate (= drainage). The runoff has been neglected in this approach. The k_i is a parameter reflecting the maximum evapotranspiration capacity of plant community i under non-limiting conditions determined by the “crop coefficient” method (Allen et al., 1998). We assumed that plant communities used soil water at their maximum rate ($ET0_t \times k_i$) as long as ASW exceeded 30% of $TTSW$, the most used threshold (Allen et al., 1998; Barkaoui et al., 2017). Below this threshold, we assumed that evapotranspiration was affected by water stress and decreased until ASW fell to 0%. We estimated the parameter k_i for each of the 16 subplots (plant community) using a reverse modeling approach based on pseudorandom search optimization with the ordinary least square method (Price, 1977). Finally, we evaluated the accuracy of the model using a bootstrap resampling procedure over five years of SWC measurements. After 1000 iterations, we obtained robust values of the slope, bias, r^2 , and root mean square error (RMSE) of the relationship between modeled and measured SWC ($r^2 = 0.97$; $p < 0.001$; Appendix S1: Figure S4). The bootstrap procedure confirmed the accuracy of the model (98.7%) and no biases. The adjustment was better in deep soils than shallow soils ($r^2 = 0.93$ vs. 0.59; $p < 0.001$) with high precision for both (96.3% and 79.7%).

Water stress indices

Water stress can be quantified at various timescales. At day t , we determined the instantaneous (daily) water stress intensity as the absolute difference between the actual ($ETa_{i,t}$) and the maximum ($ET0_t \times k_i$) evapotranspiration for each plant community. To assess water stress over the years, we calculated the “Dynamic Water Stress” index (DWS) defined by Porporato et al. (2001):

$$DWS = \begin{cases} \left(\frac{\overline{\Delta ET_s} \times \overline{D_s}}{r_i \times D_g} \right)^{1/\sqrt{\overline{F_s}}}, & \overline{\Delta ET_s} \times \overline{D_s} < r_i \times D_g, \\ 1, & \text{otherwise} \end{cases} \quad (4)$$

where $\overline{\Delta ET_s}$ (in millimeters per day) is the mean intensity of daily water stress (s) during the year, $\overline{D_s}$ (in days) is the mean duration of water stress phases (i.e., when

$\overline{\Delta ET_s} > 0$), $\overline{F_s}$ is the mean frequency of water stress phases, and D_g (in days) is the effective plant growth (g) duration considering all days above 2.5°C at the site. The parameter r_i (in millimeters per day) reflects the water stress resistance of a plant community (i). However, r_i was unknown for the studied plant communities and was fixed at 0.5 mm day^{-1} , as suggested by Laio et al. (2001). We determined $\overline{\Delta ET_s}$, $\overline{D_s}$ and $\overline{F_s}$ from the modeled SWC dynamics. The DWS range between 0 and 1 in case of no stress and maximal stress conditions, respectively. In addition, considering that plants respond to extremes more than mean stress intensities (Knapp et al., 2002), we calculated the “Extreme Water Stress” index (EWS) by analogy with the “uppermost transpiration stress index” suggested by Bartholomeus et al. (2012). EWS is the annual mean of the most intense water stress conditions (upper quartile) calculated during a “mobile window” of 10 days over the year:

$$EWS = \left(\frac{\sum_{Q_3}^{\max} \left(\sum_{10\text{day}} (\Delta ET_s) \right) \right) / n_{>Q_3}, \quad (5)$$

where Q_3 is the value of the third quartile of the distribution curve of all mobile windows over the year, ΔET_s (in millimeters per day) is the intensity of daily water stress, and $n_{>Q_3}$ is the number of observations higher than the Q_3 level. In the study of Bartholomeus et al. (2012), the EWS ranged between 7 and $35 \text{ mm } 10 \text{ day}^{-1}$.

Measurements on vegetation

We visually estimated the total plant cover (0%–100%) in each quadrat at the end of spring (June, before cutting plants) and the percentage (0%–100%) of dry or dead foliage in the aerial biomass (hereafter “senescence”) in each quadrat at the end of spring (June, before cutting plants) and at the end of summer (August).

In addition, botanical surveys were conducted in 2012 and 2021 to assess species abundance before (baseline reference) and after the drought experiment. The species were classified according to growth forms (graminoids, including grasses and cyperaceous), legume forbs, non-legume forbs, and dwarf shrubs and life cycle (annuals and perennials).

We also measured ANPP (in kilograms of DM [dry matter] per square hectare) each year for autumn (December) and for spring (June) by cutting all living plants at 2 cm height from the ground in three 0.25-m^2 quadrats within each treatment subplot ($n = 48$ quadrats). We calculated the ecosystem water use efficiency (WUE) at the subplot level following Huang et al. (2016) as the ratio

between ANPP (annual and seasonal), as a proxy of gross primary production, and ET derived from the water balance model. Furthermore, we determined the forage quality using the spring biomass samples. First, harvested plants were sorted into two groups, graminoids (grasses and cyperaceous) and the rest (forbs and dwarf shrubs), oven-dried at 60°C for 48 h, and weighed in order to assess the proportion of graminoids in spring biomass. We then measured the neutral detergent fiber content (NDF) as defined by Van Soest (1967) using a fiber analyzer (ANKOM Technology Corporation, Fairpoint, NY, United States), the crude protein content (NCP) following the DUMAS method with an elemental analyzer (Flash2000; Thermo Fisher Scientific), and the biomass digestibility as cellulase digestibility (Aufrere, 1982; adapted in a Daisy incubator of ANKOM Technology) that were analyzed by INRAE-Lusignan laboratory.

Statistical analysis

We performed all statistical analyses in R version 4.2.3 (R Core Team, 2023). We compared TTSW, SWC, ASW, and ETa between soil types, treatments, and seasons by ANOVA. Linear regression allowed the relationship between soil depth and TTSW to be tested, and the parameter k was tested by t -test. We tested the effect of increased summer drought on the water stress indices (DWS and EWS) across years using repeated measures mixed models, using the *lme4* package (Bates et al., 2015). In mixed models, we included the drought treatment, soil type, year (as a factor), and their interactions as fixed effects and plot as a random effect. We also used the same type of mixed models but with quadrat nested within subplot as random effects to determine whether increased summer drought affected plant senescence, plant cover, annual and seasonal (autumn and spring) ANPP and WUE, the proportion of graminoid biomass, and forage quality. We selected the best models between many candidate models that combined different fixed effects and their interactions, based on the Akaike information criterion corrected for small samples ($\Delta AIC_c > 2$). To know the total variance explained by the final model, we calculated marginal and conditional R^2 with the *MuMIN* package (Nakagawa & Schielzeth, 2013). We tested for significant differences between groups using post hoc Tukey honestly significant difference tests, with the *emmeans* package (Russell et al., 2024). A resilience index (RES) was calculated for most of the variables as the ratio between plant response under drought versus ambient treatment according to Ingrisich and Bahn (2018). Significant differences to 1 (full recovery) were tested by t -test.

We then tested the relationship between plant cover, plant senescence, and water stress indices using simple linear regressions. We used segmented regression models with breakpoints to identify tipping points and significant slope changes in the relationship between spring plant cover (and all response variables) and EWS, with the *segmented* package (Muggeo, 2008). Finally, we compared the composition in plant growth forms and life cycles between soil types, treatments, and the two botanical survey dates (before and after the drought experiment) using ANOVA. To meet normality assumptions, plant cover, summer senescence, and spring graminoid biomass proportion data were arcsine transformed, while ANPP and WUE data were log transformed.

RESULTS

Soil water content dynamics

Shallow soils had lower FC and higher WP, resulting in 82% lower TTSW than deeper soils ($p < 0.001$). Independently from soil texture, soil depth explained most variations among the different plots in both TTSW ($r^2 = 0.92$, $p < 0.001$; Appendix S1: Figure S3) and maximum evapotranspiration capacity (estimated by parameter k ; $r^2 = 0.72$, $p < 0.001$; Appendix S1: Figure S3).

The SWC varied according to seasons (i.e., summer < autumn < spring < winter, $p < 0.001$) and was, on average, lower in shallow soils (24.9 ± 12.5 mm) than in deep soils (196 ± 67.8 mm). The minimum SWC, measured each year at the end of summer, was on average lower in shallow than in deep soils (7.5 ± 0.6 vs. 92.9 ± 6.0 mm, $p < 0.001$) but did not differ between ambient and drought treatments ($p = 0.084$; Figure 3). No difference was detected in SWC of the top 20 cm at the end of summer between soils and treatments ($p = 0.117$), but deep soils had an important water reserve in deeper layers (Appendix S1: Figure S4).

The mean annual ASW was slightly lower in shallow soils (69%) than in deep soils (72%, $p = 0.016$), with seasonal and interannual variations following precipitation. Like SWC, ASW was the lowest during summer for both shallow and deep soils, but minimum values were achieved on average 57 days earlier in shallow soils. The drought treatment decreased ASW more in shallow soils (-5.0%) than in deep soils (-2.2%). In autumn, once rain-out shelters were removed, ASW remained lower under the drought treatment from 0 to 57 days, depending on the occurrence of autumn precipitations (Figure 2). Mean daily evapotranspiration (ETa) ranged between 0.0 and 7.6 mm and was, on average, 50% lower on shallow soils than on deep soils ($p < 0.001$). It was also lower under

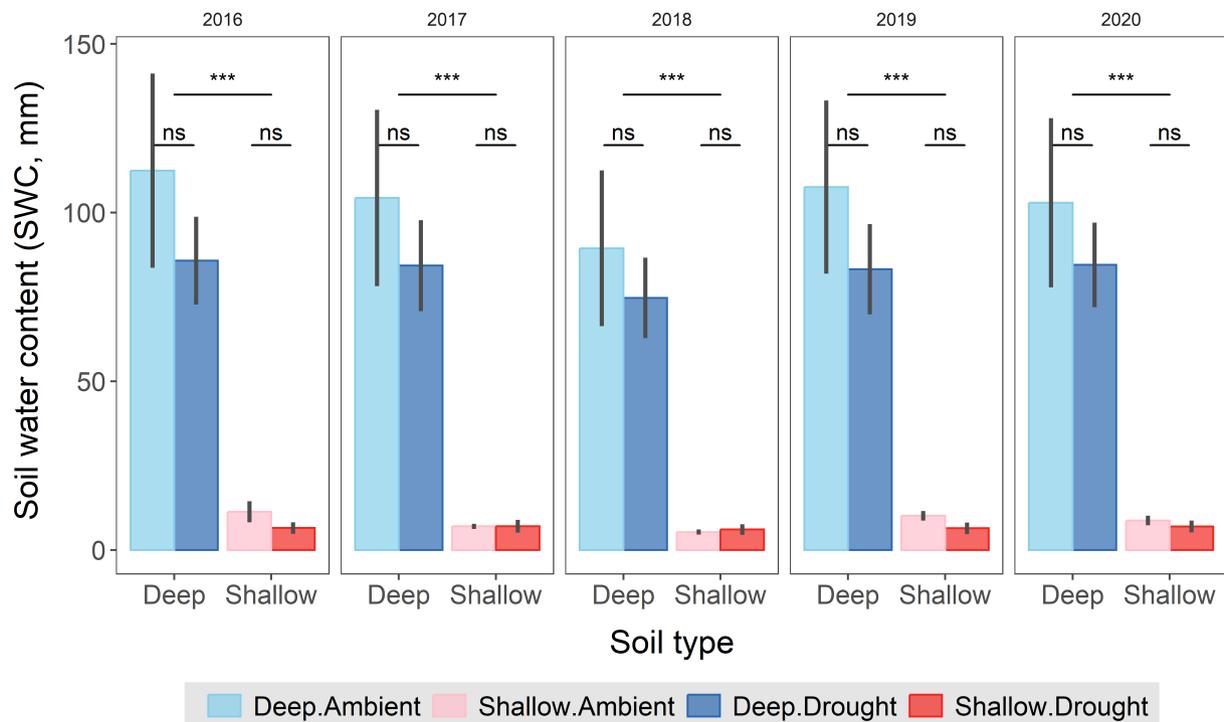


FIGURE 3 Minimum total soil water content (SWC, in millimeters) at the end of summer for five experimental years, across soil types and treatments. Significance levels (ns $p > 0.05$, $***p < 0.001$) are shown between treatments for each soil type and between soil types.

the drought treatment, with a more significant reduction on shallow soils (-36%) than on deep soils (-18%).

Water stress

The DWS and EWS indices were related to each other ($r = 0.62$, $p < 0.001$), both increased with decreasing TTSW ($r^2 = 0.89$ and 0.66 , respectively $p < 0.001$), and were the highest for the communities on shallow soils (Figure 4A,B). Higher DWS was explained by higher drought frequency (number of periods below 30% ASW), not by drought duration or ET reduction (Appendix S1: Figure S6). DWS did not differ between treatments and years. In contrast, EWS was on average 20% higher under the drought treatment (Figure 4A,B) and was significantly affected by year (Appendix S1: Table S1), making EWS a more responsive index to drought than DWS.

Tipping points in plant cover and senescence

Spring plant cover and summer senescence were negatively correlated with each other. Spring plant cover was lower on shallow soils (64%) than on deep soils (96%), and declined more on shallow soils (-46%) than on deep soils (-5.0%) over the years. Summer plant senescence

was consistently higher on shallow soils (74%) than on deep soils (58%) but increased more on deep soils (60%) than on shallow soils (34%) over the years (Table 2, Figure 5). In addition, increases in summer senescence were associated with reductions in plant cover the following spring ($r^2 = 0.25$, $p < 0.001$), especially in communities on shallow soils ($r^2 = 0.35$; $p < 0.001$; Figure 6A).

The effect of the drought treatment on plant cover depended on the community and year (interaction $p < 0.01$; Table 2), so that the RES showed the responses of the plant communities over the years for both soil types. Plant cover did not respond to the drought treatment on deep soils, whereas it decreased by 29% during the last three years on shallow soils ($p = 0.018$; Figure 5). Conversely, the drought treatment increased plant summer senescence more on deep soils ($+48\%$) than on shallow soils ($+26\%$). Furthermore, the effect of the drought treatment on plant summer senescence decreased over the years (Table 2), with a trend in RES between year 1 and year 5 (Table 2, Figure 5).

More generally, plant senescence increased with DWS ($r^2 = 0.14$, $p < 0.001$) and even more with EWS ($r^2 = 0.50$, $p < 0.001$), while spring plant cover decreased with increasing levels of water stress during the former years: DWS ($r^2 = 0.25$, $p < 0.001$) and EWS ($r^2 = 0.54$, $p < 0.001$). A steep decrease in spring plant cover was detected whenever EWS of the former year exceeded 36.7 ± 1.5 mm 10 day $^{-1}$ (CI = 33.6–39.8, $p < 0.001$) of cumulated water deficit

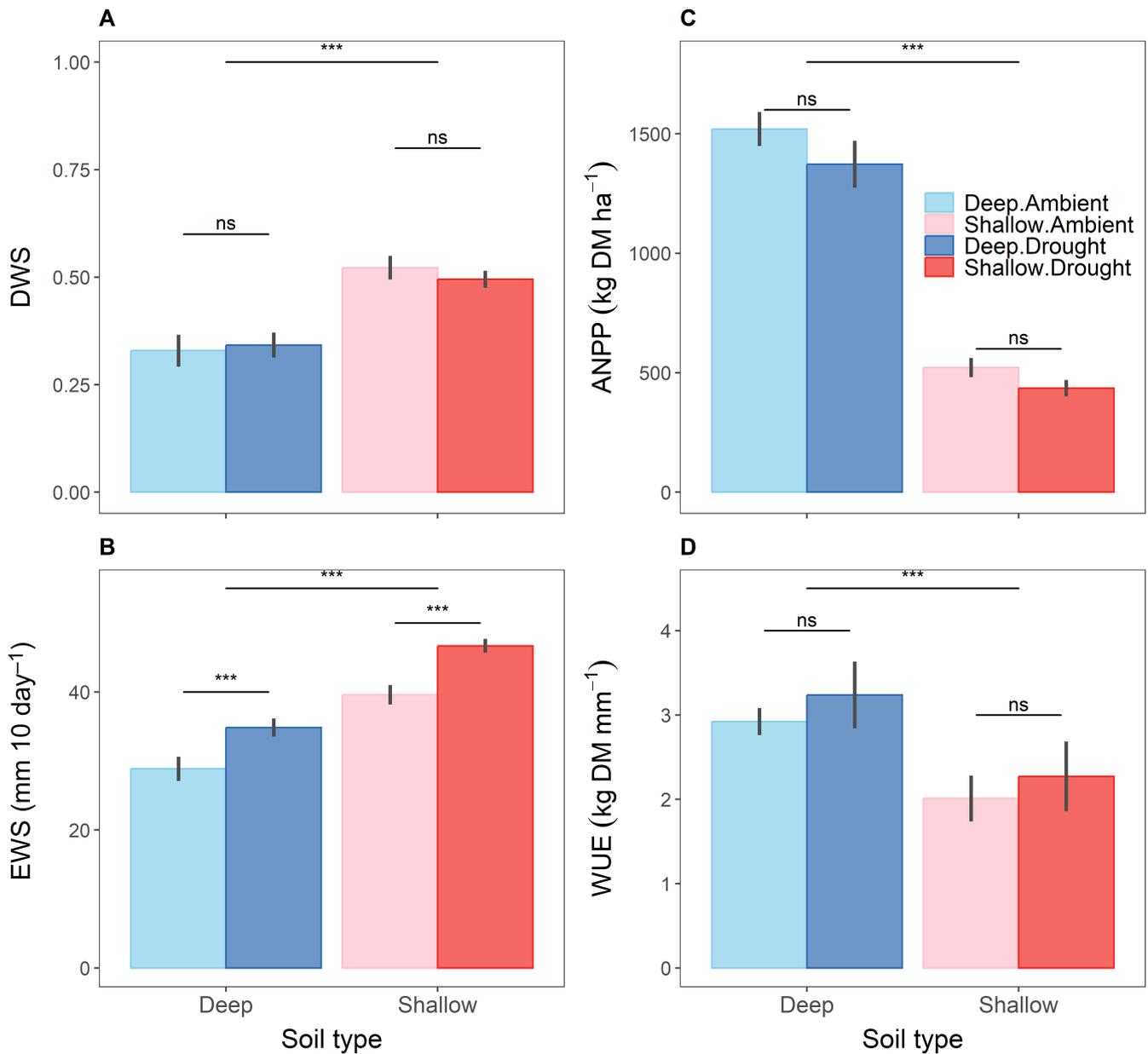


FIGURE 4 Average (over the five experimental years) dynamic water stress (DWS) (A), average extreme water stress (EWS) (B), average annual aboveground net primary production (ANPP) (C) and average annual water use efficiency (WUE) (D) for soil type and treatment. Deep (blue) and shallow (red) soil plant communities. “Ambient” and “Drought” treatments are light and dark colors, respectively.

($r^2 = 0.68$, $p < 0.001$), which occurred mainly on shallow soils (Figure 6B). Such a tipping point, when calculated for other response variables (Figure 7), gave critical EWS values in a similar range (between 33 and 47 mm 10 day⁻¹), but with less goodness-of-fit ($r^2 < 0.40$).

Changes in plant functional type abundance

The initial plant growth form composition differed between shallow and deep soil communities with less

dwarf shrubs (66%, $p < 0.001$) in deep soil communities. After nine years, including some of the driest years ever recorded, ambient communities had fewer graminoids in both types of soils (41%, $p < 0.001$). Plant communities exposed to increased summer drought for five years had fewer graminoids in both shallow ($p < 0.001$) and deep soils ($p = 0.018$) and more non-leguminous forbs in shallow soils ($p = 0.005$). Furthermore, there were fewer perennial species compared with the initial state on shallow soils in drought treatments ($p < 0.001$) (Appendix S1: Figure S7).

TABLE 2 Best model parameters of repeated measures mixed model, for the main variables, Treat (treatment) and aboveground net primary production (ANPP).

Variables	(Intercept) ^a	Treat ^a	Soil ^a	Year ^b	Treat: soil ^a	Treat: year ^b	Soil: year ^b	Treat:soil: year ^b	R^2_m/R^2_c
Spring plant cover									0.79/0.86
χ^2	550.9	1.5	49.2	8.0	1.0	4.5	14.8	2.0	
<i>p</i>	<0.001	0.261	<0.001	0.149	0.295	0.436	0.001	0.738	
Summer senescence									0.66/0.80
χ^2	53.2	33.5	22.2	48.6	4.2	11.3	24.5	8.8	
<i>p</i>	<0.001	<0.001	<0.001	<0.001	0.039	0.023	<0.001	0.066	
ANPP									0.64/0.77
χ^2	75.8	0.1	24.4	2.4	0	1.8	3.1	2.4	
<i>p</i>	<0.001	0.513	<0.001	0.818	0.967	0.715	<0.001	0.315	
Spring water use efficiency									0.48/0.65
χ^2	26	1.3	0.1	6.1	1.2	0.8	18.4	2	
<i>p</i>	<0.001	0.381	0.474	0.335	0.281	0.84	0.06	0.743	
Spring graminoid biomass									0.37/0.61
χ^2	130.1	0.3	4.6	27	0.8	3.2	6.8	20	
<i>p</i>	<0.001	0.567	0.032	<0.001	0.357	0.526	0.146	<0.001	
Biomass digestibility									0.67/0.43
χ^2	1122.7	0.7	6.2	21.6	2.3	3.3	2.7	10.1	
<i>p</i>	<0.001	0.393	0.013	<0.001	0.132	0.513	0.616	0.038	
Biomass nitrogen content									0.62/0.72
χ^2	1070.1	1.3	41.6	23.9	0.1	9	0.8	8.6	
<i>p</i>	<0.001	0.25	<0.001	<0.001	0.718	0.06	0.935	0.072	
Biomass fiber content									0.19/0.43
χ^2	719	0.4	0.1	13.3	2.4	4.9	6.7	20.5	
<i>p</i>	<0.001	0.509	0.834	0.01	0.118	0.294	0.15	<0.001	

Note: Marginal (m) and conditional (c) R^2 are presented. Values in bold indicate significant effects ($p < 0.05$).

^adf = 1.

^bdf = 4.

Changes in biomass production and quality

Mean annual ANPP and WUE ranged from 431 to 1497 kg DM ha⁻¹ and 1.2 to 5.6 kg DM mm⁻¹ across plant communities, treatments, and years. The ANPP was, on average, 67% lower on shallow soils than on deep soils (Table 2; Figure 4C; Appendix S1: Figure S8), and overall decreased with decreasing TTSW ($p < 0.001$). Although the ANPP was not affected by the drought treatment, an interaction between soil type and year on the response to the drought treatment showed that drought effects on ANPP were statistically detected only from year 4 (2019) and only on shallow soils, where RES is lower than 1 (Figure 5; Appendix S1: Figure S8).

Contrary to ANPP, the drought treatment did not impact WUE, and the RES showed a high variability between years and soil types (Figures 4D and 5; Appendix S1: Figure S9). Seasonal differences in ANPP were, on average, four times ($F_{1,480} = 386.0$; $p < 0.001$) higher in spring than in autumn. The drought treatment reduced the ANPP in autumn by 34.2% over the five years ($p < 0.001$), but not in spring ($p = 0.457$; Appendix S1: Figure S8). Similar to ANPP, WUE was 3.4 times ($F_{1,160} = 167.8$; $p < 0.001$) higher in spring than in autumn, but seasonal WUE remained unaffected by drought treatment (Appendix S1: Figure S9).

The proportion of graminoids in spring biomass varied between years and soils (Figure 5; Appendix S1:

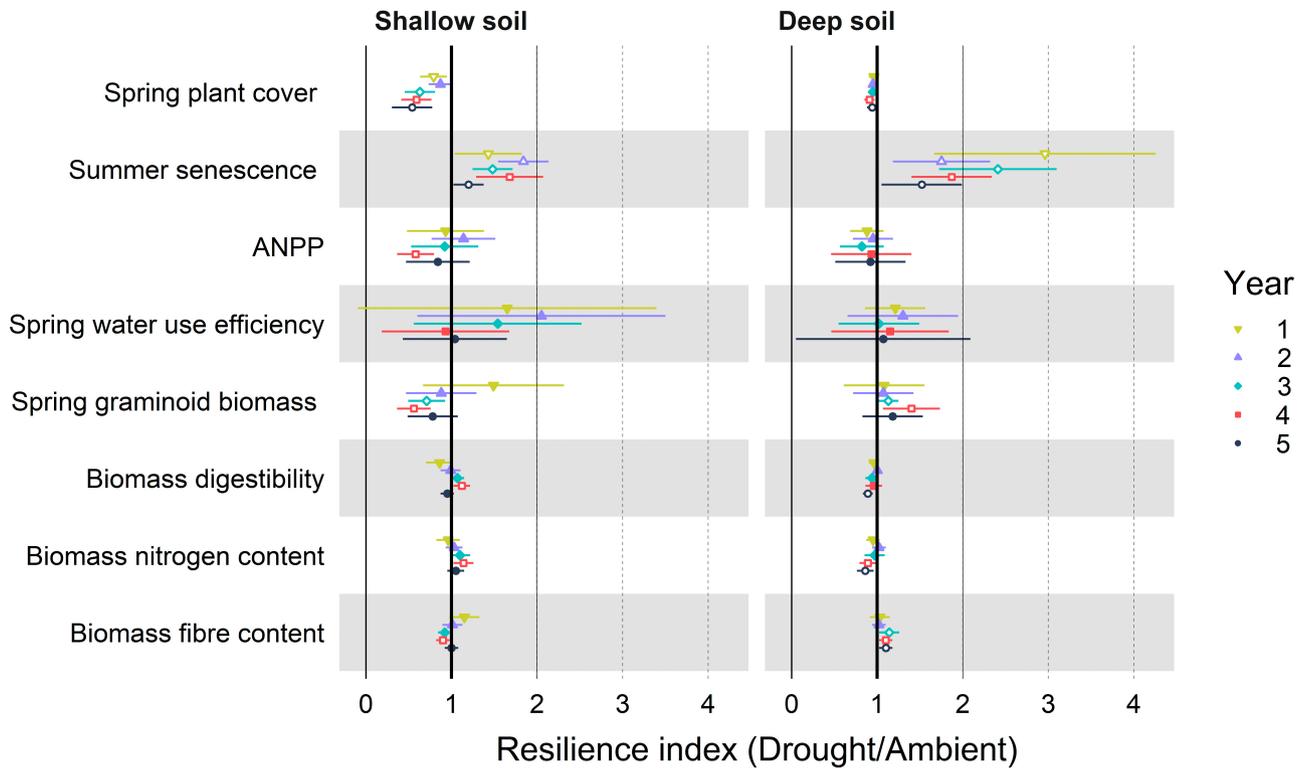


FIGURE 5 Forest plot of the resilience index between the Drought and Ambient treatments, for the main variables, for shallow and deep soil communities, and for each year (1–5). Null effect = 1. The open symbols indicate significant differences to 1 ($p < 0.05$). ANPP, aboveground net primary production.

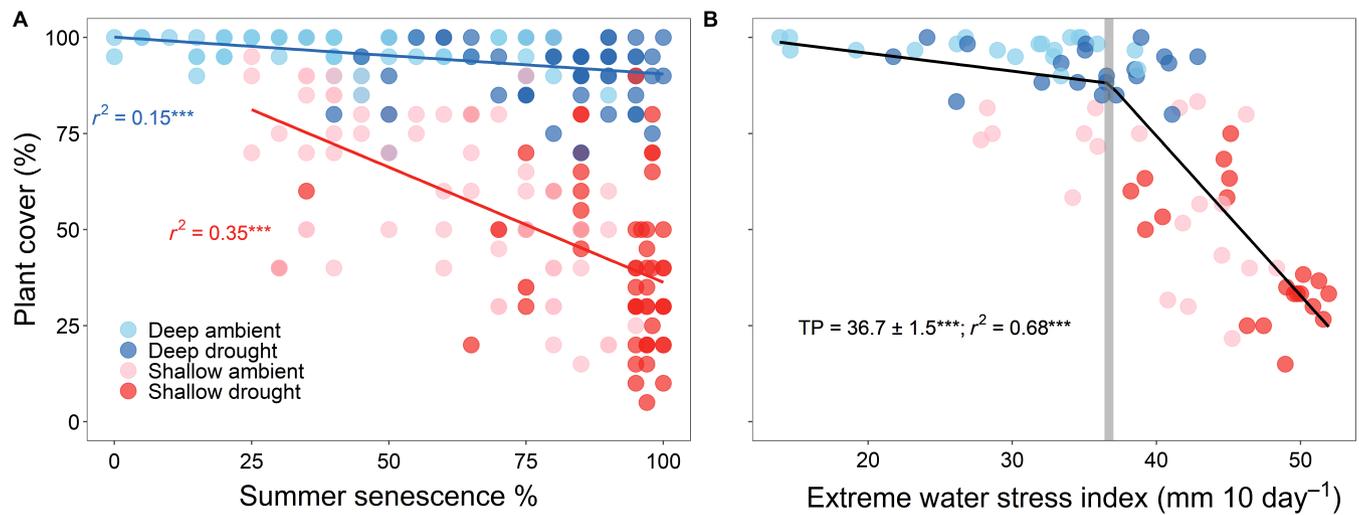


FIGURE 6 Relationship between spring plant cover and (A) summer senescence of the previous year ($n = 240$), the blue and red lines represent general regression for deep and shallow soils, respectively; and (B) annual index of “Extreme Water Stress” (EWS) (in millimeters per 10 days) of the year before ($n = 80$). The vertical gray line in (B) represents the modeled tipping point (TP) for degradation and the solid black line is a general segmented regression. r^2 and the significance level (***) $p < 0.001$ are shown for all regressions.

Figure S10). However, in the driest year (year 3) and the wettest year (year 4), the proportion of graminoids was lower in shallow soil communities and higher in deep soil communities under drought versus ambient treatments.

Forage quality differed among plant communities, treatments, and years. Shallow soils had lower nitrogen content (26%) and digestibility (11%) than deep soils, while the fiber content was similar. Furthermore, drought treatment had an increasing effect on fiber

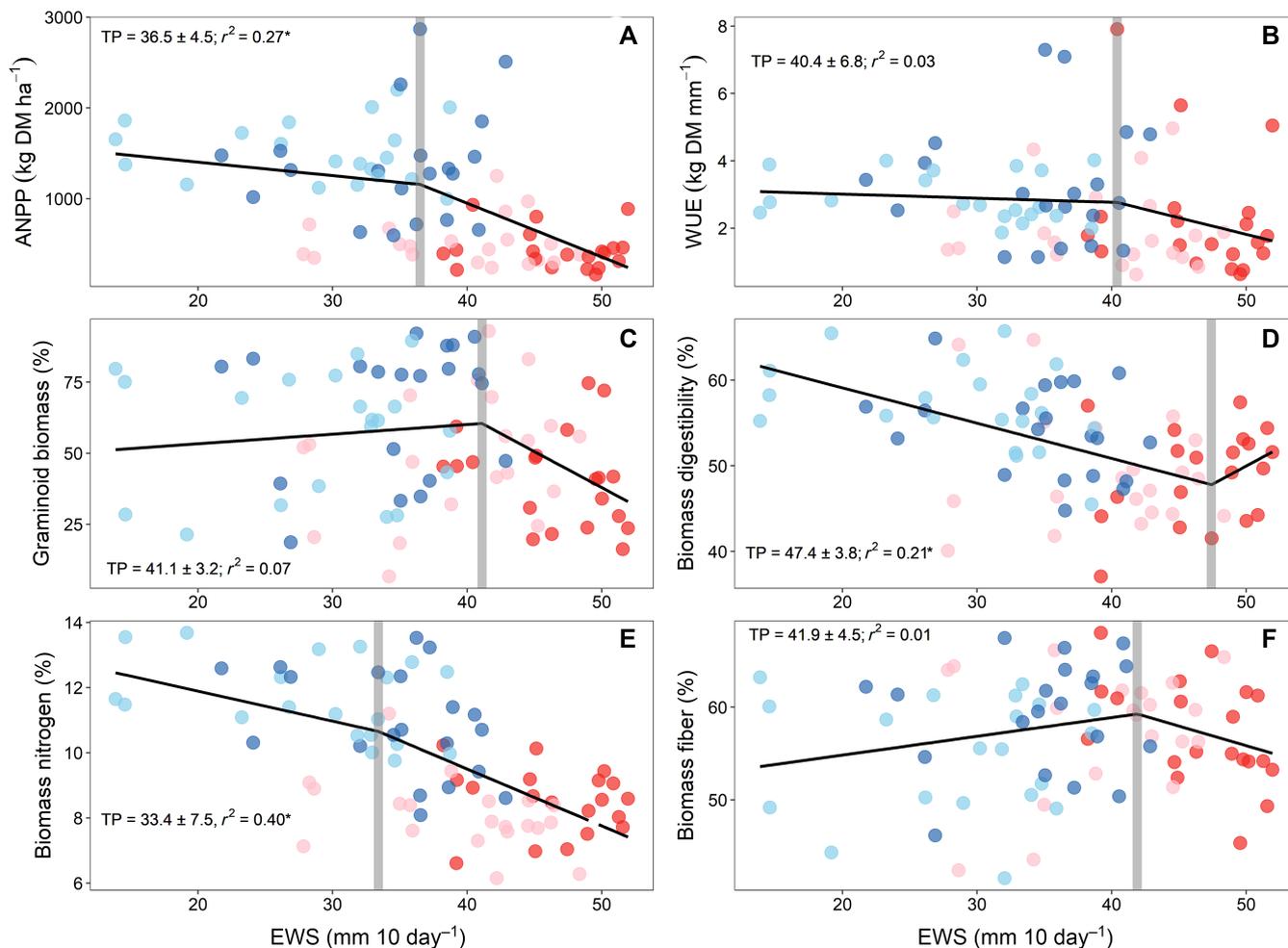


FIGURE 7 Relationship between (A) aboveground net primary production (ANPP), (B) water use efficiency (WUE), (C) graminoid biomass, (D) biomass digestibility, (E) biomass nitrogen, (F) biomass fiber and annual index of extreme water stress (EWS). The vertical gray lines represent the modeled tipping point (TP). The solid black line is a regression for all data with a breaking point. Deep (blue) and shallow (red) soil plant communities; ambient (light) and the increased summer drought (dark symbols) treatments r^2 and the significance level ($*p < 0.05$) are indicated for all regressions.

content and biomass digestibility over the years, but with differences between plant communities that is revealed with the variations over years of RES (Table 2; Figure 5; Appendix S1: Figure S11). On shallow soils, the fiber content strongly increased (8.2%), while digestibility (7.6%) decreased from year 1 (June 2017). In contrast, the fiber content decreased (5.8%), while digestibility (5.2%) slightly increased on shallow soils in year 4 (June 2020). On deep soils, the RES of plant communities was affected at the end of the experimental period with a reduction in forage quality under the drought treatment with lower digestibility (5.8%, $p = 0.023$) in the last year and with a reduction in nitrogen content (1.6%, $p = 0.004$) in the last two years. In addition, the fiber content was higher for communities under increased droughts in the last three years (4.3%, $p = 0.028$) (Figure 5; Appendix S1: Figure S11). Fiber content was positively related to the

proportion of graminoid biomass across all communities, treatments, and years ($r^2 = 0.24$, $p < 0.001$). Conversely, the nitrogen content in the biomass in the last year was positively related to the proportion of leguminous forbs ($r^2 = 0.08$, $p = 0.032$). Biomass digestibility was negatively correlated with the fiber content ($r^2 = 0.57$, $p < 0.001$) and positively with the nitrogen content ($r^2 = 0.58$, $p < 0.001$), without any significant correlation with plant functional groups.

DISCUSSION

By excluding rainfalls from June until August over five consecutive years, we experimentally increased summer water deficits by 25–150 mm, which typically range from 200 to 300 mm, exposing the Mediterranean rangelands

to consistently drier and somewhat warmer summers. This sought to match climate change scenarios predicted for Mediterranean areas (Giannakopoulos et al., 2009; Trambly et al., 2020).

Our study brings a novel perspective to the rainfall manipulation experiments, usually based on a permanent reduction in rainfall over either the entire year (e.g., Hoover et al., 2018; Knapp et al., 2017) or the growing season (e.g., Batbaatar et al., 2022; Hoover et al., 2021). Focusing on chronic summer drought, we aimed to simulate the prolonged and intensified summer conditions predicted in the Mediterranean under climate change (Giannakopoulos et al., 2009; Trambly et al., 2020). Our modeling approach of soil water balance with the calculation of water stress indices allowed a sound comparison of plant communities submitted to contrasting experimental drought treatments. This approach is even more necessary when plant communities have a range of soil depth and soil water reserve as was suggested by Vicca et al. (2012).

Our results reveal a strong interaction between drought treatment, soil type, and experimental year in the functional response of this Mediterranean subhumid rangeland.

A contrasting resilience of Mediterranean plant communities to increased summer drought according to soil depth

The resilience of the studied Mediterranean plant communities was mainly based on post-drought recovery, which was affected by the development of lasting effects of drought—a common pattern in Mediterranean biomes (Müller & Bahn, 2022; Vilonen et al., 2022). The soil water reserve determined the resilience and thus, deep and shallow soil plant communities responded differently to multiannual increases in summer drought. The variation of the RES differed for most variables between years and between soil types.

In deep soils, plant communities had access to a larger water reserve, which probably allowed plants to extract water stored deeper in the soil (Figure 3; Appendix S1: Figure S3). Consequently, the exclusion of summer rainfalls was not enough to induce a drop in summer plant senescence and to jeopardize the recovery of spring plant cover, annual ANPP and WUE (Figure 5; Appendix S1: Figures S7 and S8). A similar stability of ANPP observed over three years in a previous, shorter-term, multi-year drought experiment (Batbaatar et al., 2022) was interpreted as the resilience capacity of deep soil communities adapted to environments characterized by summer droughts. Our results show that the ANPP resilience is maintained until ESW exceeds

35–40 mm 10 day⁻¹ and that other ecosystem functions could be less resilient. Specifically, the stability of plant functional type composition was affected before ANPP, as revealed by the significant increase of graminoid biomass proportion in the last experimental years (Figure 5; Appendix S1: Figure S9). Such changes in composition have been observed in previous studies of drought manipulation (De Boeck et al., 2018; Hoover et al., 2014; Wilcox et al., 2021). This change in plant functional groups had negative consequences for forage quality: a reduced nitrogen content was associated with the increase of graminoid biomass, suggesting a possible nutritional limitation in the long term if summer drought intensifies (De Long et al., 2019; Luo et al., 2022).

In contrast, plant communities on shallow soils had access to a smaller soil water reserve (Figure 3; Appendix S1: Figure S3), making them more sensitive to the intensified summer drought, and the ESW consistently exceeded 37 mm 10 day⁻¹. This led to an apparent legacy effect on spring plant cover, resulting in a loss of resilience capacity, as evidenced by lesser ANPP in rainy years. This lower growth potential was associated with an increased proportion of annual species as a long-term response to increased summer drought. The differences between intensified summer drought and ambient plant communities increased over the years, especially from the fourth year of the experiment when the rainy conditions allowed a high ANPP in the ambient communities.

The loss of resilience has been associated with communities crossing “structural thresholds” (sensu Briske et al., 2006), for instance corresponding to a degradation below 50% of plant cover (Dlamini et al., 2014; Maestre & Escudero, 2010). Furthermore, decreases in ANPP have been considered to indicate the start of a vegetation decline phase (Berdugo et al., 2020, 2022). Our results show that plant cover can decrease even before any impact on ANPP is observed, suggesting that the “systemic breakdown” phase may begin earlier than the usual pattern reported in more arid climates (Berdugo et al., 2020, 2022). The “structural threshold” of degradation was related to a reduced proportion of graminoid biomass, which reached 57% (Appendix S1: Figure S9) after the second year of the experiment, which was in line with recent observations from multiannual drought experiments in arid regions (Luo et al., 2023).

In the Mediterranean rangelands, herbaceous species cease aerial growth under summer drought and shed most of their foliage when the water deficit is intense. However, the proportion of dead foliage (senescence) in the biomass at the end of the summer is not necessarily a sign of mortality of the perennial species. Plant survival can only be

assessed as plant recovery after complete rehydration (Barkaoui & Volaire, 2023). In this study, we used plant cover in spring (with no limiting water conditions) following the summer drought as a means to estimate plant survival and recovery. Plant senescence at the end of the summer correlated with a reduction of plant cover during the following spring in shallow soil communities suggesting that some perennial plants died during the summer and were not replaced nor compensated by annual plants. Conversely, summer senescence in deep soil communities was not associated with a reduction in the following spring plant cover, highlighting that most perennial plants could survive and showing the importance of soil water availability on plant survival and the ecosystem resilience capacity of these communities (Figure 6A).

Tippling points are associated with the magnitude of extreme water stress

Summer is already a dry season in the Mediterranean, a condition which plants have adapted to over millennia (Markonis et al., 2018). Intensified summer droughts could test the limits of such adaptation, particularly if detrimental legacy effects emerge and affect the following growing seasons.

The EWS correlated more closely than DWS with spring plant cover and summer senescence and was, therefore, the most meaningful in explaining differences in the resilience among plant communities. An EWS threshold of 37 mm 10 day⁻¹ was associated with a tipping point triggering a steep reduction in plant survival at the end of summer and then, of plant cover the following spring. However, the modeling approach has limitations. Although the global model (considering both types of soils) had a good adjustment ($r^2 = 0.97$), it was not so good when considering shallow soil communities ($r^2 = 0.59$). The tipping point identified in EWS could therefore be even lower if the water balance model overestimates the SWC in shallow soils.

Thresholds associated with limited rainfall, soil moisture reduction, and specific or cumulative water stress have been identified in previous studies (Griffin & Hoffmann, 2012; Hodgkinson & Müller, 2005; Poirier et al., 2012). Compared with other water stress indices, EWS is simpler and more robust (based on evapotranspiration reduction) as it is well correlated with the physiological limit of plant survival (Bartholomeus et al., 2012; Volaire et al., 1998). Identifying reliable indicators of early stages of degradation in plant community structure is increasingly relevant also from an applied point of view, to anticipate ecosystems at greater risk of crossing tipping points under accelerating climate change

(Maestre & Escudero, 2010; Oñatibia & Aguiar, 2022; Trambly et al., 2020).

CONCLUSION

The resilience of herbaceous communities of native Mediterranean rangelands to intensified summer drought depended primarily on the soil water reserve. A threshold of cumulated extreme stress was identified above which community structure and ecosystem function degraded rapidly. This threshold was associated with legacy effects on plant spring cover resulting from water stress effects upon end-of-summer plant survival that correlated well with the ESW index. Consequently, plant communities on the deepest soils showed higher resilience to intensified summer drought. In contrast, only a few years of intensified drought were enough to lead communities on shallow soils to exceed such a tipping point and initiate a process of community degradation that may be difficult to reverse.

AUTHOR CONTRIBUTIONS

Gerónimo A. Cardozo analyzed the data and wrote the publication. Florence Volaire and Karim Barkaoui designed the experiment, analyzed the data, and led the writing. Pascal Chapon ran the experiment and contributed to the data collection and analysis. Charlène Barotin assayed forage quality and contributed to the data collection and analysis.

ACKNOWLEDGMENTS

We thank the experimental station of La Fage (INRAE) for the facilities and the experimental platform of CEFE for technical support. Gerónimo A. Cardozo thanks National Agency for Research and Innovation (ANII-Uruguay) (Grant Numbers POS_EXT_2019_1_161050) for his PhD scholarship. Thanks to OSU OREME (University of Montpellier) for financial support. We thank Fernando A. Lattanzi for his suggestions to improve the text.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data (Voltaire et al., 2024) are available in the Observatoire de Recherche Montpelliérain de l'Environnement's OSU OREME Data Portal at <https://doi.org/10.15148/ae01ac0d-352a-45ec-b67a-6cbb97d56ee0>.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Cardozo, Gerónimo A., Florence Voltaire, Pascal Chapon, Charlene Barotin, and Karim Barkaoui. 2024. "Can we Identify Tipping Points of Resilience Loss in Mediterranean Rangelands under Increased Summer Drought?" *Ecology* e4383. <https://doi.org/10.1002/ecy.4383>