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RAIN USE EFFICIENCY, PRIMARY PRODUCTION AND RAINFALL RELATIONSHIPS IN DESERT RANGELANDS OF TUNISIA

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ABSTRACT

Desert rangelands are characterised by low and highly variable rainfall regime, low forage production and high heterogeneity in the distribution of natural resources. This study was carried out in the desert rangelands of Tunisia to evaluate the response of different rangelands to annual rainfall in terms of aboveground net primary production (ANPP) and rain use efficiency over a 10-year period (2003–2012). In general, ANPP values were relatively low (123 kg DM ha^{-1} y^{-1}) but would tend to increase with increasing annual rainfall for all rangeland types. The highest value of ANPP was observed from *Stipagrostis pungens* and *Hammada shmittiana* communities (sandy-soil) during the wet year 2011. In contrast, rain use efficiency tends to decline with the highest annual rainfall and varies among rangeland types and with an average of 1·9 kg DM ha^{-1} mm^{-1} y^{-1}. Rain use efficiency tended to be higher during dry years and lower during wet years and tended to be higher on *S. pungens* and *H. shmittiana* (sandy-soils) and lower on *Helianthemum kahiricum* (loamy soils). Therefore, understanding how rainfall affects productivity in rangelands is critical for predicting the impact of land degradation on the functioning of these ecosystems. It can be used to explain production decline associated with desertification as well as to assess rangeland conditions.

KEY WORDS: plant communities; ANPP; degradation; RUE; rangelands; Tunisia

INTRODUCTION

Deserts worldwide are being affected by land degradation owing to mismanagement. Rangeland degradation frequently occurs in arid environments throughout the world. Terrestrial ecologists generally define physical rangeland degradation in terms of parameters related to vegetation and soil. Irrigation (Fallahzade & Hajabbasi, 2012), changes in vegetation recovery (Busso *et al.,* 2012), grazing (Bai *et al.,* 2013) and wind erosion (Lal, 2001; Bai *et al.,* 2013; Wang *et al.,* 2013; Wang & Jia, 2013; Houyou *et al.,* 2014) are some of the triggering processes. Although productivity in desert rangelands is one to three orders of magnitude lower than in forest ecosystems (Ludwig, 1987), desert rangelands cannot be viewed as either simple or unproductive systems. Rangeland productivity is likely to be more affected by rainfall; however, nutrients and their availability may strongly regulate both primary and secondary production (Noy-Meir, 1993). Generally, agreed indicators of desertification include accelerated soil erosion processes, loss of biodiversity and a lower productivity. In this area, aboveground net primary production (ANPP) can vary threefold to fivefold, both between years at the same location and within the same year at different locations (Huenneke *et al.,* 2001, 2002).

Drylands development requires much more input, caution and prudence, and they need higher investment and risk more irreversible land degradation (Mainguet & Da Silva, 1998; Safriel, 2009). It has long been recognised that the key factor to fight desertification/land degradation is by increasing or at least maintaining vegetation cover (Millennium Ecosystem Assessment, 2005). Otherwise, vegetation is the key factor in soil erosion processes. On the vegetated soils, erosion is negligible and directly related to land degradation (Cerdà, 1998). This in turn induces high runoff rates as a consequence of a prolonged drought and grazing pressure (Cerdà *et al.,* 1998). In some region, for example, natural reforestation may control the fate of the sediments and that extensive reforestation appeared to be the reductions in discharged sediment (Keesstra *et al.,* 2009a, 2009b). In this regard, sedimentation rates have decreased significantly because of the natural reforestation (Keesstra, 2007).

The reappropriation of such ancient techniques, such as protection, has been successful in combating erosion and land degradation. The nature of the vegetation also changed under protection (Ouled Belgacem *et al.,* 2011). In addition to this, some species can be used for combating land degradation, restoring and rehabilitating degraded land (Gui *et al.,* 2011; Li *et al.,* 2011; Wu *et al.,* 2012; Chigani *et al.,* 2012; Zucca *et al.,* 2014).

Desertification problems have become linked with climatic trends and fluctuations (Wang *et al.,* 2005). Clearly, climatic variability can have unanticipated effects (Peters *et al.,* 2013) and is inherent in dryland areas (Le Houérou,

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1996; Darkoh, 1998; Harris, 2010; Reynolds, 2013). Many authors have attempted to link the changes in rangeland production to rainfall (Diarra & Breman, 1975; Floret & Pontanier, 1978; Strugnell & Pigott, 1978; Cornet, 1981; Deshmukii, 1984; Hiernaux, 1984; Le Houérou, 1984; Schönbach *et al.,* 2012; Polley *et al.,* 2013; Martin *et al.,* 2014; Guido *et al.,* 2014). Le Houérou *et al.* (1988) reviewed pasture production studies from numerous semi-arid ecosystems to estimate the efficiency with which rainfall is converted into plant production. The conclusion was that each millimetre of rainfall produces on average of 4 kg DM ha^{-1}. The relationship between average annual rainfall and plant productivity across arid regions has substantial predictive ability (Le Houérou, 1984). However, for a given site, the relationship between annual rainfall and yearly plant productivity has limited explanatory power (Lauenroth & Sala, 1992). Recent studies, on soil water availability and plant water use, have emphasised that the relative availability of different sources of water may play an important role in structuring communities and seasonal productivity (Ehleringer & Dawson, 1992; Snyder & Williams, 2000; Schwinning & Ehleringer, 2001; Ferrante *et al.,* 2014; Bansal *et al.,* 2014; De Boever *et al.,* 2014). In turn, spatial patterns of vegetation, together with morphological and physiological attributes of plants, greatly affect water fluxes and availability (Cerdà, 1997; Zucca *et al.,*2014).

In southern Tunisia, rainfall is extremely variable in both time and space (Le Houérou, 2009), with the result that the desert rangelands have frequent droughty periods that have a marked effect on the vegetation (Gamoun *et al.,* 2011). However, drought alone cannot be responsible for desertification but can add to the problem.

In fact, rainfall amount and grazing can be considered as two principal determinants of desert rangeland functioning (Gamoun *et al.,* 2011, 2012). Therefore, climatic variations, particularly droughts, control major trends in plant species composition, diversity (Noy-Meir, 1973; Weltzin *et al.,* 2003; Köchy *et al.,* 2008) and the pattern of primary production (Gamoun *et al.,* 2010; Gamoun, 2013a). In deserts, the low and highly variable precipitation levels, high temperatures and high evapotranspiration ratios limit both plant abundance and productivity to very low levels (Noy-Meir, 1973, 1985; Polis, 1991).

We take primary productivity as the focal rangeland process. We suggest that water limits plant growth in drylands. Rain use efficiency (RUE), the ratio of ANPP to mean rainfall, could be a critical indicator for evaluating the response of primary productivity to variability of rainfall in arid and semi-arid ecosystems (Le Houérou, 1984; Le Houérou *et al.,* 1988; Sala *et al.,* 1988, Le Houérou, 2000). Essentially, with increasing aridity and evapotranspiration, RUE becomes more neglected over time (Le Houérou, 1984). However, this widely accepted view recently has been challenged by several studies (Paruelo *et al.,* 1999; Huxman *et al.,* 2004; Vermeire *et al.,* 2009). Therefore, changes in RUE have been suggested as an integral measure for evaluating ecosystem state, land degradation and desertification (Prince *et al.,* 1998; Ruppert *et al.,* 2012). It has been proposed that ecosystem degradation results in a reduction in RUE; thus, RUEs can be interpreted as an index of ecosystem or range condition (Le Houérou, 1984).

This research was carried out in the desert rangelands of Tunisia, and we ask what is the relationship between ANPP and annual rainfall?

MATERIALS AND METHODS

This study was conducted in desert steppes of plain Elouara at an elevation of approximately 170 m a.s.l. in the south-eastern part of Tunisia. Elouara test area belongs to the Remada region in the governorate of Tataouine. The mean annual temperature is 22°C, with the highest monthly mean temperature of 40°C and the lowest mean temperature of 11°C (Gamoun, 2014). Based on the nearest long-term weather station at Remada region, the mean annual rainfall was 66 mm (2003–2012), with large inter-annual fluctuations, usually occurring in an approximately 10 rain days between October and March.

The area considered for this study, which is one of the most extreme examples of desert rangelands, is situated about 20 km northest of Remada delegation (32°24′8″N, 10°35′26″E to 32°27′52″N, 10°45′34″E). In spite of inappropriate rainfall and soil conditions, biodiversity is considered important in terms of species richness and can exceed 60 species under the ungrazed condition (Gamoun, 2013b, 2014). Four characteristic plant communities of the desert rangelands were selected. These natural resources were consistently and widely used for grazing livestock, especially sheep, goat and camels. Figure 1 presents a map of the study sites, their characteristics are summarised in Figure 2. The characteristics of different rangelands are established and distributed as follows.

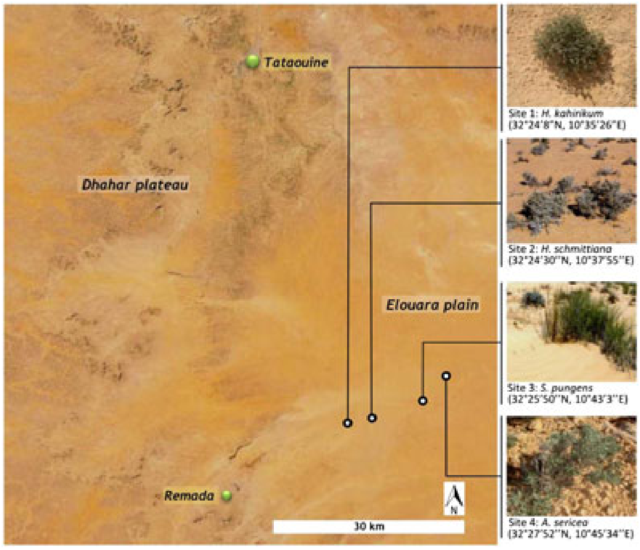

Figure 1. Location of the four research sites on Landsat map of plain Elouara in the governorate of Tataouine. This figure is available in colour online at wileyonlinelibrary.com/journal/ldr.

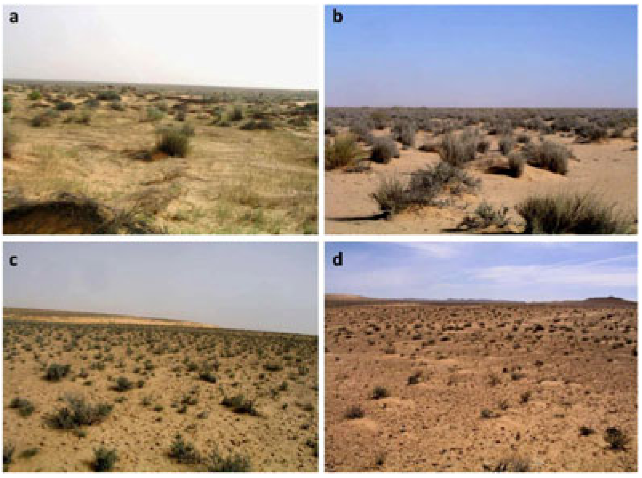

Figure 2. Photographs showing different rangelands types: (a) psammophytes of *Stipagrostis pungens* on sand accumulation being grazed by camels from the typical desert vegetation site where vegetation promotes infiltration and minimises runoff; (b) example of an almost flat, sandy area in the Elouara plain unit with a vegetation dominated by *Hammada schmittiana*; (c) good stand of *Anthyllis sericea* community type in stony terrain showing the spacing of the shrubs; and (d) stand of the *Helianthemum kahiricum* community type in the desert rangelands. This figure is available in colour online at wileyonlinelibrary.com/journal/ldr.

- Site 1 (32°24′8″N, 10°35′26″E). *Helianthemum kahiricum* [(Desf.)] community on loamy-textured soil and with crusted surfaces, good water retention capacity (13%), low organic matter content (0·5–1%) and basic pH (Floret & Pontanier, 1982). It follows that in areas characterised by light infrequent rains, as in most arid zones, the amount of soil water available on an annual basis is much lower on loamy soils (Le Houérou, 2009).
- Site 2 (32°24′30″N, 10°37′55″E). *Hammada schmittiana* [(Pomel) Ilji] community on deep sandy-soil, it is classified as sierozem. It is characterised by more complete water infiltration and lower water retention (6–10%). The pH is greater than 7, the organic matter content decreases progressively with depth (1% and below) (Floret & Pontanier, 1982). Sand grains vary from coarse to medium size and are rarely fine (Le Houérou, 2009).
- Site 3 (32°25′50″N, 10°43′3″E). *Stipagrostis pungens* [(Desf.) de Winter] community on sand accumulation coarse textured with high infiltration rates. This soil is isohumic (subdesertic called sierozems) with a very low water retention capacity (range from 6% to 9%), little organic matter (0·5–0·7%) and a pH of about 8 (Floret & Pontanier, 1982). This habitat is characterised by high storing rain of water. Psammophytes (sand-loving plants) constitute the bulk of the sand dune vegetation (Zahran, 2010).
- Site 4 (32°27′52″N, 10°45′34″E). *Anthyllis sericea* [Lag. subsp. *Henoniana* (Coss.) Maire] community on limestone soil, more or less flat, covered by large flagstones of limestone. Also called regosol with high stone content and low water retention capacity (range from 8% to 11%). The soils are characterised by medium to fine texture (Zahran, 2010). Often, the latter covers the slight slope, thereby reducing infiltration and percolation, increasing runoff and encouraging erosion (Floret & Pontanier, 1982). From a chemical viewpoint, the soils are usually alkaline with a pH from 7·5 to 9 and low organic for the most part (0·7%).

Aboveground net primary production was estimated during the growing season of 2003 to 2012 in the peak season of primary production and when development of the annual vegetation was at its prime. In each of the four rangelands, ten subsamples were taken from 2 m × 2 m quadrats to determine aboveground plant community productivity while minimising loss of plant productivity that was largely responsible. The selection of the plot for sampling was random, but measurements were carried out in sites not grazed during the current growing season. Aboveground biomass production measurements were made during spring of every year and determined by cutting the herbaceous plant. It is the portion or amount of forage vegetation available for animal consumption. Usually, it is the fresh mass that was determined in the field for the whole leaves and twigs (current season's growth). The collected samples were air dried and weighed for estimation of dry matter production on $\mathrm{kg\,ha^{-1}}$.

Rain use efficiency for each sampling site is determined as the amount of ANPP in a given area per AR: RUE = ANPP/AR, where RUE is rain use efficiency ($\mathrm{kg\,ha^{-1}\,mm^{-1}}$), ANPP is aboveground net primary production ($\mathrm{kg\,ha^{-1}}$) and AR is annual precipitation (mm). It is worth noting that water is lost through evaporation, surface runoff; erosion factors and deep drainage were not taken into consideration, likely leading to an RUE underestimation. Then, pattern of RUE and ANPP was examined in all sites among rainfall gradients. Then further, we explored the relationships between ANPP and annual rainfall and between RUE and annual rainfall for all sites.

Statistical Analysis

Differences in ANPP and RUE among the different rangeland types were analysed. All analyses were performed using SPSS software (SPSS for Windows, Version 11.5, Chicago, IL, USA). Statistical differences were tested using analysis of variance, and means were separated using least significant difference ($p \leq 0{\cdot}05$).

RESULTS

Aboveground Net Primary Production Dynamic

Differences in ANPP were assessed using the linear model and analysis of variance. ANPP averaged 123 $\mathrm{kg\,DM\,ha^{-1}\,y^{-1}}$ among years and vegetation types. The ANPPs reported during the study period were significantly different among year ($F = 321$; $p < 0{\cdot}0001$) although it was significantly different among the four rangelands ($F = 394$; $p < 0{\cdot}0001$). Decreasing rainfall significantly reduced ANPP of all four rangelands. *H. kahiricum* communities were most affected by decreasing rainfall amounts, whereas *S. pungens* communities were less affected (Figure 3). In this fact, the highest value of ANPP was found on *S. pungens* communities (157·8 kg DM ha^{-1} y^{-1} in 2011). The lowest value of ANPP was found on *H. kahiricum* communities (75·3 kg DM ha^{-1} y^{-1} in 2009). There was, however, no significant interaction between years and vegetation types ($F = 0{\cdot}16$; $p = 1$).

As expected, rainfall was a significant determinant of ANPP. Taken as a whole, ANPP increased with increased rainfall for any vegetation type. The results of the analyses of ANPP—annual rainfall relationships—demonstrated that the correlation was highly significant at a level of <0·05. All plant communities showed similar trends in ANPP related to annual rainfall ($r^2 = 0{\cdot}99$; $p < 0{\cdot}0001$) (Figure 4).

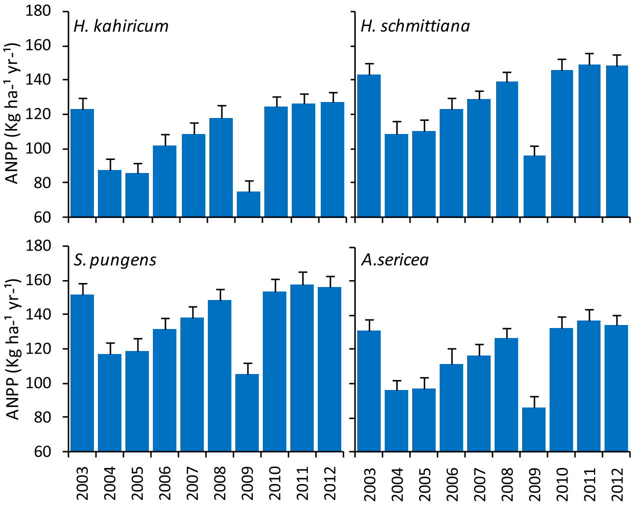

Figure 3. Aboveground net primary production (ANPP) of four types of rangelands during 10 years between 2003 and 2012. This figure is available in colour online at wileyonlinelibrary.com/journal/ldr.

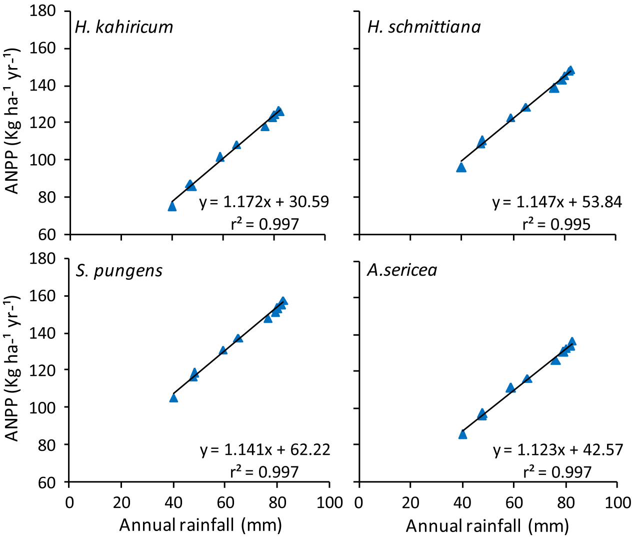

Figure 4. Relationships between annual rainfall and aboveground net primary production (ANPP) of four types of rangelands. This figure is available in colour online at wileyonlinelibrary.com/journal/ldr.

Variation in Rain Use Efficiency

Rain use efficiency per rangeland types determined across years ranged between 1·5 and 2·7 kg DM ha^{-1} mm^{-1}. Most importantly, they clearly show strikingly high RUE in dry years. Analysis of variance revealed that the difference in RUE had a significant relationship with annual rainfall ($F = 150$; $p < 0{\cdot}0001$) and plant communities' factors ($F = 373$; $p < 0{\cdot}0001$). Interaction effect between annual rainfall and rangeland types in affecting the RUE was significantly higher ($F = 3{\cdot}4$; $p < 0{\cdot}0001$).

Contrary to the trend of ANPP, RUE also increased at reduced levels of annual rainfall. RUE showed greater variability in response to rainfall and rangeland types with clear trends emerged (Figure 5). RUE that decreased with increasing rainfall may be explained by degraded desert vegetation. The year 2009 was very dry and yielded high RUEs at all plant communities. The two wettest years were 2011 and 2012, years during which the RUE values were generally low for all plant communities. Figure 6 reveals significant negative correlation between annual rainfall and RUE on all plant communities ($r^2 = -0{\cdot}99$; $p < 0{\cdot}0001$). It shows that RUE is a function of annual rainfall at all plant communities, RUE is essentially higher for lower rainfall amounts.

DISCUSSION

Variations in ANPP and RUE were associated with both annual rainfall and plant community's type or plant functional group (Table I). Similarly, Gamoun (2014), in a study assessing the effect of drought on plant communities in the desert rangelands of Tunisia, found that the natural vegetation is in accordance with annual rainfall and vegetation type. In the same experiment, a study on these same four plant communities, they showed that vegetation cover on *H. kahiricum* steppe has been more greatly affected by drought than the other steppes, while diversity has been

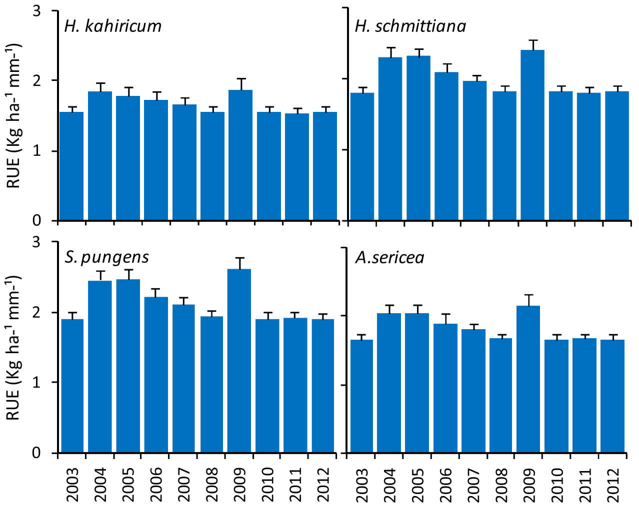

Figure 5. Rain use efficiency (RUE) of four types of rangelands during 10 years between 2003 and 2012. This figure is available in colour online at wileyonlinelibrary.com/journal/ldr.

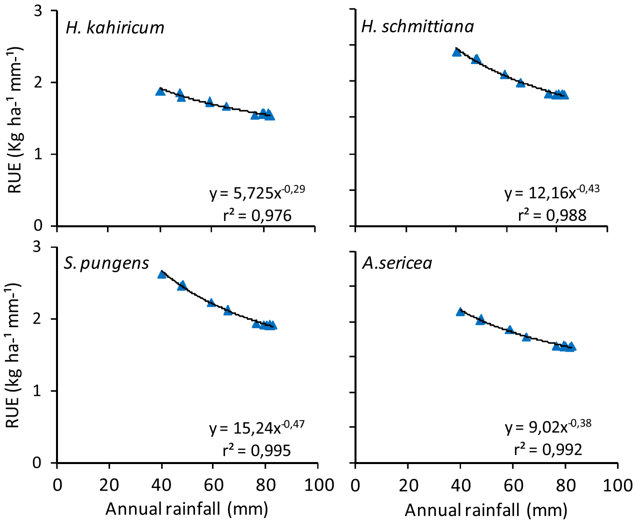

Figure 6. Relationships between rain use efficiency (RUE) and annual rainfall of four types of rangelands. This figure is available in colour online at wileyonlinelibrary.com/journal/ldr.

affected by drought on all steppes and mainly on *H. kahiricum* and *A. sericea* steppes.

The results of these experiments showed that, with increased annual rainfall, the ANPP was increased on all four plant communities, suggesting that rangeland productivity was mainly driven by climatic factors. Broadly speaking, ANPP was also positively correlated with increasing annual rainfall. This finding is generally consistent with previous studies in other rangelands around the word (Noy-Meir, 1973; Le Houérou & Hoste, 1977; Le Houérou *et al.,* 1988; Sala *et al.,* 1988; Burke *et al.,* 1997; Hooper & Johnson, 1999; Paruelo *et al.,* 1999; Lauenroth *et al.,* 2000; Huxman *et al.,* 2004; Bai *et al.,* 2008; Yang *et al.,* 2008; George *et al.,* 2010; Gamoun *et al.,* 2011; Golodets *et al.,* 2013; Gamoun, 2014; Eisfelder *et al.,* 2014).

In addition to the effect of annual rainfall, vegetation may react otherwise. However, there were clear differences depending on rangeland types. This study showed that ANPP changes in response to vegetation type. ANPP measured on the *S. pungens* communities is the highest followed by *H. schmittiana*, *A. sericea* and *H. kahiricum* communities. The different plant communities' types seem to indicate different soil types. Thus, there were clear differences depending on soil types. Because each type of vegetation was represented by soil type (Floret & Pontanier, 1982; Gamoun *et al.,* 2011; Gamoun, 2013a, 2013c), however, ANPP should be affected by soil texture and soil fertility (Ehleringer, 2001). Noteworthy, each soil type can be expected to respond differently to annual rainfall effect. In loamy soils with high water capacity, most desert rains do not penetrate beyond 30 cm, thus favouring plants with shallow roots and rapid growth pulses, particularly ephemerals. In sandy-soils, where capacity is lower, less water will be stored in this zone and much will percolate deeper, shifting the advantage to deep-rooted perennials (Noy-Meir, 1973). Beside water deficit, the soil environment is harsh due to serious soil erosion, causing considerable losses of N, P and other soil nutrients (Xu *et al.,* 2013).

The greatest effect of rainfall on ANPP was observed on sand accumulation (*S. pungens*), followed by sandy-soil (*H. schmittiana*), limestone soil (*A. sericea*) and loamy soil (*H. kahiricum*). Thus, soil depth, in such coarse sands, appears as key factor in capacity to store water (1 mm of rain moistens 1 cm of soil depth, and the amount of available water is 0·75 mm cm^{-1}) (Le Houérou, 2009). In this context, Noy-Meir (1973) emphasises that, in arid and semi-arid regions, coarse, sandy substrates are usually favourable for plant growth because water percolates through the surface layers quite rapidly. These dry out quickly, but the moisture is held in subsurface layers where it is protected from evaporation, thus remaining available to plants for long periods of time. This has been referred to as the main cause of the 'inverse texture effect'. The root system of *Aristida pungens* is strictly adventitious, roots appear at the base of the new modules. Thus, the module (runner) rooted can make use of light rain (Bendali *et al.,* 1989). Therefore, another possible explanation could be that the extensive root system for *S. pungens* increases the ability of the shrubs to exploit soil water and nutrients and decreases soil evaporation as the tuft provides more shade for the soil surface. Furthermore, the

Table I. Differences between plants communities and years in RUE (kg DM ha^{-1} mm^{-1}) and ANPP (kg DM ha^{-1} y^{-1}) from 2003 to 2012

		Plant communities							
		Helianthemum kahiricum		*Anthyllis sericea*		*Hammada schmittiana*		*Stipagrostis pungens*	
Year	*p* (mm)	ANPP	RUE	ANPP	RUE	ANPP	RUE	ANPP	RUE
2003	79·27	123·30	1·56	130·70	1·65	143·20	1·81	151·30	1·91
2004	47·51	87·90	1·85	96·10	2·02	109·20	2·30	116·90	2·46
2005	48	86·20	1·80	97·40	2·03	110·80	2·31	118·70	2·47
2006	59	101·70	1·72	111·30	1·89	123·30	2·09	131·10	2·22
2007	65·27	108·80	1·67	116·70	1·79	128·90	1·97	137·80	2·11
2008	76·34	118·20	1·55	126·50	1·66	138·90	1·82	148·00	1·94
2009	40·08	75·30	1·88	86·00	2·15	96·30	2·40	105·30	2·63
2010	80·3	124·80	1·55	132·90	1·66	145·90	1·82	153·30	1·91
2011	82·5	126·20	1·53	136·70	1·66	149·10	1·81	157·80	1·91
2012	81·7	127·20	1·56	134·00	1·64	148·30	1·82	155·40	1·90

RUE, rain use efficiency; ANPP, aboveground net primary production.

depth of root penetration into the sand may be much higher than into the other soil types.

Gamoun (2014) shows that *H. kahiricum* and *A. sericea* steppes are most affected by drought, this may be attributed to soil sealing, which plays a key role in crusts formation. Therefore, the reducing growing vegetation is said to crust, which is a physical barrier to plant germination, mainly annual species. In degraded desert areas, wind erosion is the limiting factor for vegetation on sand dunes. Yet, in spite of accumulations of windblown sand in the shelter of the small shrubs on limestone and loamy soil, rains may evaporate too quickly from the soil surface and sand can easily dry out. On thin layers of loose sand, however, evaporation loss is relatively high, and the negative effects of sand accumulation on shrubs may dominate over the potentially positive effects. Otherwise, all soil moisture is evaporated, and layers beyond that depth are permanently dry.

In degraded rangelands, ANPP varied markedly among habitats (Li *et al.,* 2009). Breckle *et al.* (2008) suggest that, from an ecological point of view, sand deserts have more ecological conditions favourable for plant cover and species diversity and that desert perennials species develop extensive root systems to be able to exploit soil water from deeper horizons (Groom, 2004). Likewise, Le Houérou (2009) suggests that the amount of soil water available on an annual basis is much higher in coarse sandy-soils than in skeletal and loamy soils. Moreover, Floret & Pontanier (1982) showed that soil water remains available 2 months longer in deep sandy-soil than in limestone and loamy soils.

All these edaphic characteristics, and relating those to likely hydrological impacts, accentuate that sandy-soil is more productive than limestone and loamy soils. These results corroborate therefore those found in previous studies (Le Houérou, 2009; Gamoun *et al.,* 2012; Gamoun, 2014) that have emphasised the higher productivity of sandy-soil than limestone and loamy soils. Hence, one can say that ANPP can be governed by a number of factors, including climatic factors, vegetation type and soil type. The importance of these factors is more significant in wet years than in dry years.

Generally, RUE remained at a low level compared with humid ecosystems but was as well significantly affected by vegetation type and annual rainfall. The sandy-soil is marked by the highest RUE, whereas the lowest RUE was recorded on loamy soil, because in sandy-soils, water is more available for biotic activity. Results confirm earlier studies, suggesting that RUE tended to be higher on sandy-soils and lower on loamy soils (Le Houérou & Hoste, 1977; Floret & Pontanier, 1984; Le Houérou *et al.,* 1988; Le Houérou, 1982, 1999).

Otherwise, the low frequency of large rainfall events along with flat topography suggests that runoff is not important in this ecosystem and, therefore, water runoff from the rare rainfall is probably not an important agent of soil moisture. Similarly, if there exists rainfall, this runoff water cannot subsequently accumulate in depression, where it can evaporate more easily.

In this study, from 2003 to 2012, RUE significantly decreased with increased annual rainfall and varied from 1·5 to 2·7 kg DM ha^{-1} mm^{-1} and overall mean of 1·9 kg DM ha^{-1} mm^{-1}. These findings show that these results are in accordance with the previous study in arid ecosystem when RUE averages to 2 kg DM ha^{-1} mm^{-1} (Le Houérou & Hoste, 1977; Ludwig, 1986; Holm, 2000; Squires *et al.,* 2010). Contrary to the arid ecosystem, in a semi-arid ecosystem, RUE varied between 2·4 and 3·9 kg DM ha^{-1} mm^{-1} (Guevara *et al.,* 2000; Jobbagy & Sala, 2000; Snyman, 2001; O'connor *et al.,* 2001). Increases of unproductive water loss by runoff and high bare soil evaporation on grazed sites have been viewed as the most important reasons for low RUE (Le Houérou, 1984; Snyman, 2005; Bai *et al.,* 2008). Le Houérou (1984) reviewed the fact that the magnitude of evaporation from soil surface in arid and semi-arid rangelands varies from 20% to 70% of the infiltrated rain.

Rain use efficiency tended to be higher during dry years and lower during wet years. Regarding the year's effect, RUE was highest in the dry year in 2009. The widely accepted view is that RUE should increase with annual rainfall, as the proportion of effective rain increases with decreasing aridity (Le Houérou, 1984), until other environmental factors limit ANPP. Although this relation seems reasonably satisfactory, it would mean that rangeland production would increase indefinitely as rainfall increases; however, this is not true because, as rainfall increases, other limiting factors such as soil infertility, soil texture and temperature arise. Nevertheless, RUE is also highly dependent on soil and vegetation type and environmental conditions and therefore may not necessarily respond linearly with rainfall. RUE was a better predictor of rangeland production than annual rainfall and had a curvilinear relationship by different vegetation types to rainfall.

Further increases in annual rainfall amounts usually reduce RUE due to increasing unproductive water losses, for example, via runoff and drainage (Paruelo *et al.,* 1999; Bai *et al.,* 2008). However, soil characteristics, such as water-holding capacity, texture, permeability and depth, are major determinants of soil water availability and have important effects on the site-level RUE (Noy-Meir, 1973; Le Houérou, 1984; Sala *et al.,* 1988). However, previous studies also showed that a dry year following a wet year usually has high RUE for a given site (Le Houérou, 1984; Brueck *et al.,* 2010; Gao *et al.,* 2013). Consistent with these findings, my results showed a higher RUE in the dry year in 2009 than in 2008 at all sites. This was because ANPP decreased by 29–36% in 2009 compared with 2008, while rainfall amount was 47% less, which consequentially translates into higher RUE.

Several possible mechanisms could explain the increased RUE for water-limited years. Furthermore, previous studies have suggested that RUE may be affected by biogeochemical constraints. While water availability determines grassland productivity in semi-arid regions, nutrient availability is the main limiting factor under wet conditions (Li *et al.,* 2011). ANPP in arid and semi-arid ecosystems is usually limited or co-limited by nitrogen availability, which is tightly coupled with water availability through biogeochemical feedbacks (Lauenroth *et al.,* 1978; Chapin *et al.,* 1986; Vitousek & Howarth, 1991; Schimel *et al.,* 1997; Burke *et al.,* 1998; Hooper & Johnson, 1999; Xiao *et al.,* 2007; Gao *et al.,* 2011). Ludwig & Flavill (1979) found that primary productivity was reduced in the Chihuahuan desert (North America) as a consequence of nitrogen limitation, while Floret *et al.,* (1982) found that nitrogen limitation reduced productivity in the Tunisian part of the Sahara during wet periods. Bai *et al.* (2008) reported that the RUE could be substantially increased by chronically altering resource availability, such as N addition. However, the wet year in 2010 did not show high RUE values but rather the lowest, indicating a depletion of soil nutrients within the dry year in 2009 under unfavourable growing conditions and carryover affecting the growth in 2010. Thus, effective rainfall available for stimulating biological processes is decreased. Therefore, the lower RUE may reflect the inability of plants to effectively use precipitation in the wet years.

Likewise, RUE is strongly linked to ecosystems functioning and thus very responsive to range condition and exhaustion status. Rangelands in good condition or little degraded have RUE varying between 3 and 6 kg DM ha^{-1} mm^{-1}, even at the limit of the deserts under mean annual precipitation of 80–150 mm, particularly on sandy-soils (Floret & Pontanier, 1982; Le Houérou, 1982; Joffre *et al.,* 1988; Guevara *et al.,* 1996). These results suggest that RUE is lower compared with those in good and little degraded rangelands. About this study, we therefore suggest that the lowering of the RUE (overall mean of 1·9 kg DM ha^{-1} mm^{-1}) may indicate degradation risk due to increasing grazing pressure and drought. Le Houérou (2006) suggested that the RUE was below 1 kg DM ha^{-1} mm^{-1} in degraded rangelands. This finding has been recently reviewed by many studies showing that protection and moderate grazing may increase rangeland productivity (Gamoun *et al.,* 2012; Gamoun, 2013b, 2014; Gamoun *et al.,* 2015). While under average rainfall condition, defoliation increased RUE in long-term lightly, but not heavily, grazed treatment (Varnamkhasti *et al.,* 1995).

CONCLUSION

Rangeland productivity was positively correlated with annual rainfall and varied greatly among years for the four desert rangelands as well. A greater proportion of ANPP occurred at the *S. pungens* and *H. shimittiana* communities at the sandy-soil, whereas the lowest ANPP was recorded at the *H. kahiricum* communities at the loamy soil.

In the same way, RUE was affected by rainfall and rangeland types, but there was a strong negative correlation with rainfall. Hence, RUE declined with increasing rainfall at all plant communities, also showing a tendency to be higher in dry years and lower in wet years.

Rain use efficiency values were generally low for desert rangeland. However, their declined trends as a response to increasing of annual rainfall indicate that the rangeland is degraded and that land use may partly or totally mask effects of rainfall on ANPP and RUE.

Because the desert rangelands pose formidable problems for sustainable development, short-term action is required while maintaining a longer term perspective. These may be used for desertification assessment and rangeland degradation. Thereby, they would allow for predictions of expected future rangeland on pastoralism and livestock production that may change people's vision and behaviour, as well as their attitude toward and understanding of pastoralists. This change in attitude can increase interest in and awareness of pastoralists and can stimulate thinking about the sustainability of rangelands. Any grazing management strategy that enhances vegetative cover improves water use efficiency and conserves the soil resource. Grazing management should be the first consideration in developing nutrient and water availability.

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