WATER USE EFFICIENCY AND NET PRODUCTION OF TWO SEMI ARID GRASSLANDS IN DIFFERENT SUCCESSIONAL STAGES

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Abstract. The productivity of Mediterranean grasslands, which depends on successional stage, climatic factors and human interventions, cannot fulfil forage demands of ruminants during the dry summer period. The current paper investigates whether the successional stage of vegetation could alter the water use efficiency during the semiarid period of summer and whether the productivity of low elevation Greek grasslands may be approached by the traditional concept of succession. Seasonal trends in physiological parameters, such as net photosynthetic rate and transpiration rate as well as net productivity was recorded in the most dominant species of two grasslands at an early and late successional stage (ESS and LSS respectively). The results reveal significant differences in net photosynthetic rate, transpiration rate, and water use efficiency of the most dominant species between the two grasslands throughout the season. Net production was significantly higher in the LSS grassland especially during the drier parts of the season (middle summer). The higher water use efficiency and higher net production in late successional stages of the lowland Mediterranean grasslands that we have examined in the current study suggests a rather substantial divergence from the traditional view of the succession theory regarding productivity.
Keywords: *net photosynthetic rate, transpiration rate, leaf area index, leaf water potential, production*

Introduction

Grasslands are important terrestrial resource for Greece and other Mediterranean countries (Cosentino et al., 2014). However, today their productivity does not fulfill the forage demand of ruminants, especially during the dry period of summer, widely oscillating in space and time according to plant species composition, herbivore pressure, human activities, successional stages as well as climatic conditions (Gatti et al., 2005; Migo, 2006; Ali-Shtayeh and Salahat, 2010). The abiotic profile of an area (i.e soil, climate, landscape) as well as external factors, such as fire and grazing may affect the productivity of an ecosystem (Gurevitch et al., 2006; Fernandez et al., 2009; Salis, 2010; Long et al., 2015). In addition, the productivity of grasslands is strongly associated with the successional stage of vegetation (Würtz and Annila, 2010). There are several theories that have been put forward to explain those changes induced in composition and production of plant species at different successional stages. For example, Odum (1983) proposes that total biomass of an ecosystem increases with succession from the initial to advanced stages, while the net production is reduced. Plants at the stage of climax are the best indicator of the potential of productivity of an area (Foin, 1986; Meiners et al., 2015). However, Odum (1985) demonstrated that in stressed ecosystems the expected trends include changes in energetic, nutrient cycling, and community structure and function. In arid and semiarid regions, annual changes in productivity due to changes in precipitation

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are often much larger than those due to small changes in the composition of vegetation as a result of the improvement or_deterioration of the ecosystem (Laycock, 1989; Nippert et al., 2006; Han et al., 2015).

The stage of climax, in terms of productivity, is often not desirable because both net production and the nutritional value are low. In such cases, it would be desirable to maintain the grassland in a successional stage where the optimum composition of vegetation for grazing animals, coexists with high productivity while ensuring the balance of the ecosystem (Sharma, 2009; Han et al., 2015). In the Mediterranean basin, the productivity of grasslands depends directly on water availability and species richness, productivity and plant cover are expected to decrease with increasing aridity (Bartha et al., 2011; Meiners et al., 2015). The water is considered the more important factor for the establishment, survival and growth of plants in semiarid Mediterranean regions. Under drought conditions, natural selection favors plants with physiological adaptations that ensure the survival and growth based on the efficient use of available water (Heschel and Riginos, 2005). The low annual precipitation in the Mediterranean region combined with natural hazards of environmental degradation make an essential need to detect plants or successional stages which discourage the degradation and ensure environmental stability and high productivity (Bolle, 1995; Alcamo et al., 2007; Fernandez et al., 2009). According to Souza and coworkers (2005) there is a flexibility in plant capacity to respond to environmental changes taking into account positive or negative relationships between physiological parameters and environmental conditions.

Water use efficiency (WUE) provides a useful index for understanding the metabolism of terrestrial ecosystems as well as for evaluating the degradation of grasslands (Han et al, 2013). WUE relating two physiological parameters the photosynthetic rate (P_N) and the transpiration rate (E) is a very important index to define how efficiently individual plants use water to produce biomass (Wang et al., 2007; Bacon, 2009). Earlier models suggest that the total production of grassland increases but the net production decreases while moving from initial to advanced stages of succession (Odum, 1983; Odum, 1985). However, later experimental studies have proven that, under the influence of intense grazing, the progress of succession is correlated with an increase in net production (Casado et al., 1985; Noitsakis et al., 1992) and, therefore, alternative models should be developed to explain these deviations from Odum's theory (McNaughton and Wolt, 1973; Smith, 1988).

In Mediterranean ecosystems, the natural vegetation has been modified by the interactions of climate and human intervention and has developed coping mechanisms to further changes inhibiting a possible new environmental degradation (Fernandez et al., 2009; Păcurar et al., 2014; Zimmermann et al., 2014). Ecologists have developed many theories and models to describe those changes that succession induce (Clements, 1916; Odum, 1969; Connell and Slayer, 1977; Pickett et al., 1987; Meiners et al., 2015). However, studies in several Mediterranean ecosystems have demonstrated that out of the three models proposed (facilitation, inhibition, tolerance) by Connell and Slatyer (1977), the model of "facilitation" cannot explain the function of these ecosystems under the influence of drought and respective future climate change (Valladares and Gianoli, 2007). Apparently, traditional range successional models cannot account for the productivity of the Mediterranean grasslands and there is need for the development of new alternative models

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(Bartolome, 1989; George et al., 1992). Relationships between productivity and diversity differ not only among scales and between artificial and natural gradients, but also within scales and gradient types. A better understanding of the relationships between productivity and diversity requires a thorough study of the mechanisms the establish the relationship, and whether differing mechanisms explain the variation in patterns (Rajaniemi, 2003).

These contradictory views on the relation of vegetation dynamics, successional stage and production of an ecosystem are challenging to research. The aim of this paper was to investigate whether the successional stage of vegetation could alter the water use efficiency during the semiarid period of summer and whether the productivity of low elevation grasslands may be approached by the traditional concept of succession.

Materials and methods

Study area

The study was conducted at a low elevation grasslands in Northern Greece, which was located close to Melissohori (lat. 40° 58N, log. 28° 01E), 25 km north-east of Thessaloniki, at an altitude of 170m a.s.l., constitute mainly of forage species and few patches of shrubs such as *Pyrus amygdaliformis* Vilm *and Jasminum fruticans* L. The climate of the area is classified as Mediterranean semiarid with average monthly temperatures ranging from 4.9 to 25.6 ^{o}C. The mean annual air temperature ranged from 4.4 ^{o}C (January) to 24.7 ^{o}C (August) and the average annual precipitation to approximately 409 mm. During the experimental period the annual average precipitation was 476.5 mm, while the vapour pressure deficit (VPD) ranged from 1.4 kPa (April) to 4.17 kPa (end of June).

Materials

Data were collected from two fenced (10 by 20 m) neighboring areas with the same orientation (north-east) and slope 10-12%. The two experimental areas had been excluded from grazing four years before the beginning of the study. Before fencing both experimental areas were grazed by sheep and goats without any control. At the onset of the experiment the first area had just been abandoned from cereal cultivation (early stage of succession, ESS) and the dominant species were annual grass, legumes and annual forbs (old field successsion). The second one was grassland at late stage of succession (LSS) that had been grazed for at least 20 years before fencing. The dominant species, annual and perennial grasses, with stable frequency of appearance and higher percentage of cover in the ESS grassland were: *Medicago minima* (L.) Bartal (10.43%), *Onobrychis aequidentata* (Sibth and Sm) D'Urv (10.6%), *Avena fatua* L. (10.68) and *Cynodon dactylon* L. (10.37%), while in the LSS grassland: *Lotus aegaeus* L. (1.65), *Dactylis glomerata* L. (9.24%), *Dichanthium ischaemum* (L.) Roberty (9.19%), *Chrysopogon gryllus* (L.) Trin (9.13%) and *Dasypyrum villosum* (L.) P. Candargy (23.25%). Detailed description of the two grasslands are given in Karatassiou and Koukoura (2009).

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Physiological parameters

Net photosynthetic rate (P_N), and transpiration rate (E) were measured in the dominant species of each grassland with the portable infrared gas analyzer system LI-6200 (LI-COR Lincoln, NE). Seasonal measurements were obtained on clear sunny days at around solar noon (12.00h -14.00h) and approximately 15 days intervals. All measurements were conducted on mature and intact fully expanded upper leaves. The water use efficiency (WUE) was calculated as the ratio between carbon gain (P_N) to water loss (E) (Guo et al., 2006; Bacon, 2009). For each parameter, the values given are averages of the four replications of the five dominant species of LSS grassland and of four dominant species of the ESS grassland.

The above ground, dry biomass (net production) was estimated by randomly taken samples of cut vegetation at ground level every twenty days during the growing season. Each sample, for each grassland consisted of ten sampling units of 50 cm x50 cm quadrats. Following removal of the previous year, production was separated into leaves and stems. Leaf area was measured using the leaf area measurement system (Area measurement system, Delta-T-Devices). To determine the dry weight, leaves and stems of sampled species were placed in an oven for 48 hours at 70 °C. The Leaf Area Index (LAI) was also estimated following Gurevich and coworkers (2006).

Statistical analysis

To determine differences in the ecophysiological response of the species of the two grasslands during the growing season we performed a two-way analysis of variance (ANOVA) on all parameters studied (Steel and Torrie, 1980). Following a significant interaction between grassland and time one way ANOVA on effects of the five sampling times in each grasland was performed. Means of the two grasslands at each sampling date were compared using the t-test for independent samples ($\alpha = 0.05$). All statistical analyses were performed using the SPSS statistical package v. 21.0 (SPSS Inc., Chicago, IL, USA).

Results and discussion

The two-way analysis of variance reveals significant differences ($p \leq 0.01$) between the two grasslands for most of the parameters recorded (i.e. P_N, E, WUE, production). Also, time (season) significantly affected ($p \leq 0.0001$) all these parameters (P_N, E, Ψ, WUE, production). The interaction between time (during the growing season) and grassland was significant for parameters ($p \leq 0.0001$) but water potential, indicating differential physiological response of the species of the two grasslands throughout the season.

Leaf water potential (Ψ) showed a declining trend during the growing season in species of both grasslands (*Figure 1*, $F_{4, 75} = 6.2$ and $F_{4, 95} = 14.1$, $p \leq 0.001$ for ESS and LSS respetively) but no significant differences ($p>0.05$) was found between the two areas at each sampling time ($t< 0.99$, df=34, $p>0.05$). The species of each grassland presented significant higher values of water potential at the beginning of the growing season (middle April) and the significantly lower values in the last days of June (LSD-test among different dates within each grassland, $p<0.05$). It is well appreciated that water deficit (intensity, and/or duration) causes a number of significant modifying

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functions in photosynthesis and other physiological processes, which may be species specific (Mojayad and Planchon, 1994; Wang et al., 2003; Zlatev et al., 2012).

Our results demonstrate that overall (including all dominant species) during the growing season the two grasslands expressed differential sensitivity to water deficit conditions (*Figures 1, 2*). The net photosynthetic rate in species of the LSS grassland was significantly higher than that of species in the ESS grassland ($t>3.48$, $df= 34$, $p\leq0.001$) for most dates during the growing season. No significant differences between the species of two grasslands were recorded only in the middle of May ($t=0.548$, $df=34$, $p =0.587$) at Ψ values ranging between -1.6 MPa and -1.86 MPa (*Figure 2a*). Apparently, the effects of micro- and macro- climatic conditions were more favorable for the perennial species compared to annual ones. In species of the ESS grassland, P_N significantly increased following a significant decrease (LSD-test among different dates, $p \leq0.001$) in Ψ up to -1.8 MPa, following a declining trend in lower values of leaf water potential. In contrast, as the growing season progressed and Ψ reduced (*Figure 1*) in species of the LSS grassland P_N peaked at higher Ψ values, decreased and a stabilized between -1.7 MPa and -2.4 MPa and finaly dropped in lower Ψ values (*Figure 2a*). The mean net photosynthetic rate of species in the LSS grassland (8.57 ± 0.46 $\mu mol.m^{-2}.s^{-1}$) was significant higher ($F_{1,170}$ =109.9 $p\leq 0.0001$) than that of species in the ESS grassland (4.30 ± 0.289 $\mu mol.m^{-2}.s^{-1}$). It seems that the perennial species, which mainly consisted the vegetation of the LSS grassland, were able to maintain a high rate of photosynthesis for longer periods of time than the annual species, prevailing in ESS, under lack of water in the leaf tissue. This is in agreement with data given in McNaughton (1991), Saint Pierre and cowerkers (2004, 2004a), Lambers et al. (2008) and Souza and coworkers (2009). However, there are some annual species, such as *Dasypyrun villosum* that, departing from the expected response, in advanced stages of succession can express similar photosynthetic capacity with perennial species, in order to survive and thrive (Karatassiou and Noitsakis, 2010).

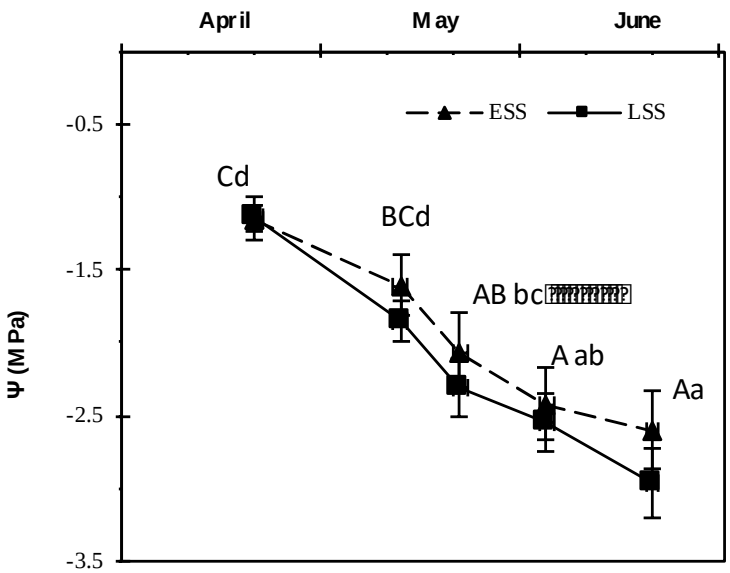

Figure 1. *Seasonal pattern of the leaf water potential (Ψ) for two grasslands early (ESS) and late (LSS) successional stages. Values present means ± SE. Small and capital letters indicate significant differences (LSD-test, p<0.05) within LSS and ESS grassland respectively.*
**Indicates significant differences (t-test,. p<0.05).*

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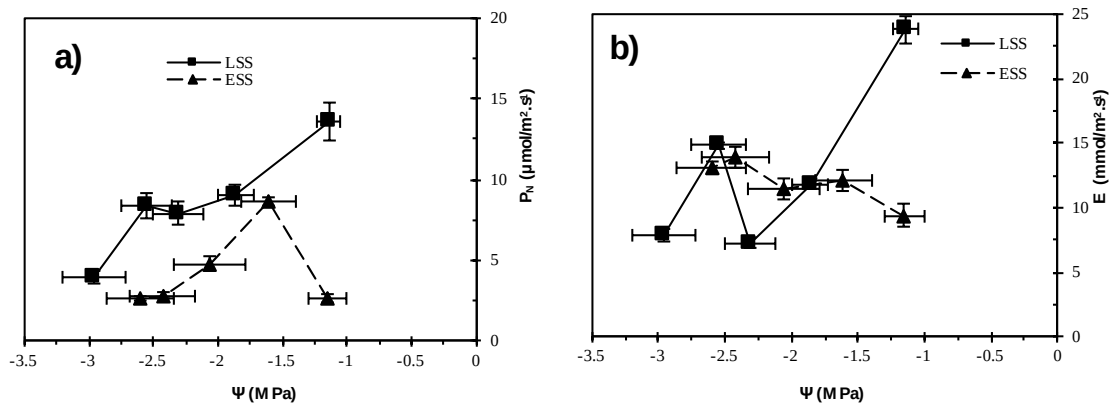

Figure 2. *The relationship between leaf water potential (Ψ) and (a) net photosynthetic rate (PN), and (b) transpiration rate (E) for two grasslands in early (ESS) and (LSS). Values present means ± SE.*

Patterns of E in relation to Ψ were different for the species of the two grasslands. Significant differences were found among sampling dates in E values within each grassland (*Figure 2b*, $F_{4,75}$= 5.1 and $F_{4,95}$= 117.9, p≤ 0.001 for ESS and LSS respetively). In species of the ESS grassland E values increased until middle of June (Ψ= -1.61MPa) and then stabilized, while those in the species of the LSS grassland following a dramatic initial decrease fluctuated in lower Ψ values. As far as transpiration rate is concerned, the species of the two grasslands expressed different response in higher values of Ψ around -1.15 MPa and and relatively similar in lower values of water potential (*Figure 2b*). As the growing season progressed to the drier summer the water potential decreased (*Figure 1*, Ψ>2.6 MPa), and those species at advanced stages of succession (LSS) showed lower rates of transpiration compared with species at earlier stages of succession (ESS), because the sensitivity of the stomatal apparatus to drought is increased in late successional species in response to the decrease in leaf water potential and increase in VPD (Karatassiou and Noitsakis, 2010). Houssard and coworkers (1992), Bazzaz (1996) and Chapin II and coworkers (2011) have demonstrated that plants at early stages of succession expressed higher transpiration rates compared to plants that are in advanced stages of succession.

The above differences in net photosynthetic and transpiration rates between plants in ESS and LSS (*Figure 2a,b*) suggest that water use efficiency would vary between the species of the two grasslands. Indeed, WUE was significantly higher (t-test, df=34, p≤0.05) throughout the growing season (except early May) in LSS plants compared to ESS ones (*Figure 3*). Only in the first days of May the species of the two grasslands expressed similar water use efficiency (t=0.842, df=34, p>0.05). Moreover, significant differences during the growing season presented in each grassland (p≤0.001).

However, the changes of WUE become more interesting when are plotted against water potential (*Figure 4*). The rate of WUE of the species of the both grasslands during the growing period showed no substantial differences up to a value of -1.8 MPa water potential. In lower leaf water potential values, species at LSS and ESS departed a great deal in WUE values (*Figure 4*). For the same relatively low value of Ψ (approximately -2.45 MPa) the WUE of plants in LSS grassland was almost three times higher than in the ESS.

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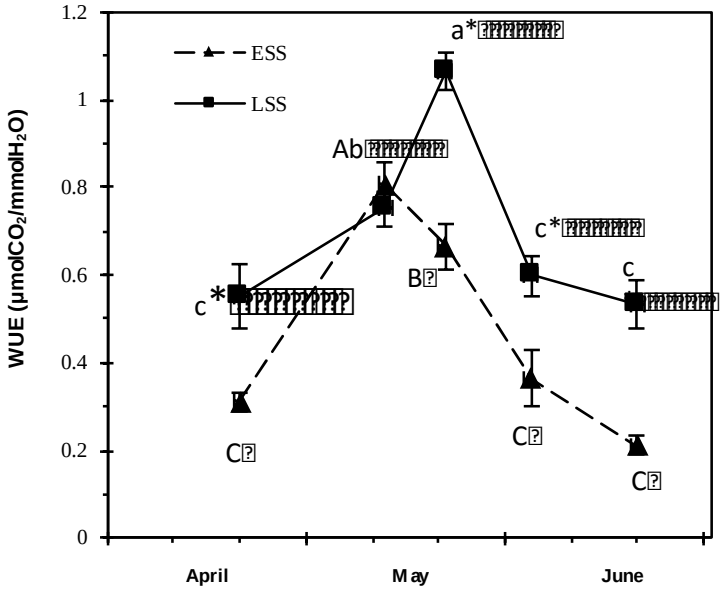

Figure 3. *Seasonal patterns of water use efficiency of two grasslands in early (ESS) and late (LSS) successional stages. Values present means ± SE. Small and capital letters indicate significant differences (LSD-test, p<0.05) within LSS and ESS grassland respectively. *Indicates significant differences (t-test, p<0.05).*

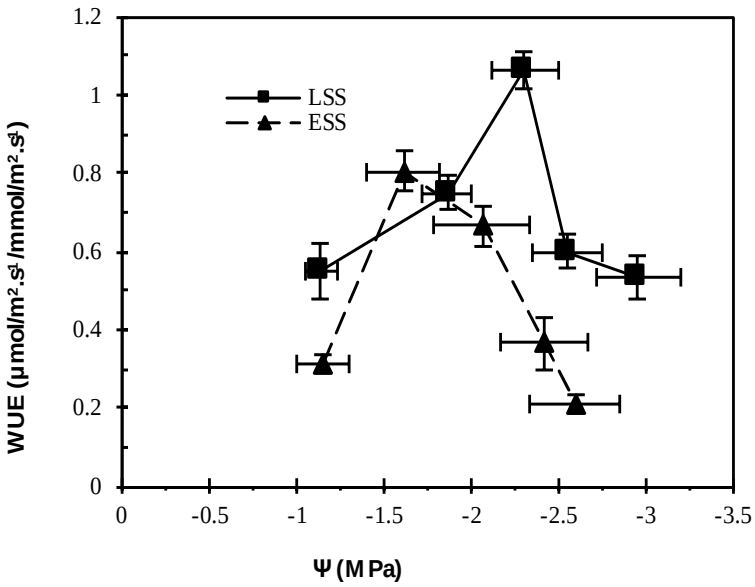

Figure 4. *Relationship between leaf water potential (Ψ) and water use efficiency (WUE) for two grasslands in early (ESS) and late (LSS) successional stages. Values present means ± SE.*

The early and late successional species differ in photosynthetic characteristics and these differences expected to increase when the plant grow in similar environmental conditions (Souza et al., 2005). The more efficient use of water under conditions of water deficit in species of grasslands at an advanced stage of succession (LSS) suggests

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that the forage species at this successional stage follow the k-selected strategy (Gurevich et al., 2006; Meiners et al., 2015). Most species at LSS are perennial species that invest in higher biomass production, because they have higher efficiency per unit of water used and survive under drought conditions (Heschel and Riginos, 2005) .

The differential behavior of the two grasslands ($WUE_{ESS}<WUE_{LSS}$) means that the species of LSS grassland transpire smaller quantities of water per unit of CO_2 (weight) diffuse in mesophyll. Therefore, species of the LSS grassland need to consume smaller amounts of water per unit of photosynthetic products relative to species of the ESS grassland. Consequently, species of the LSS grassland present more efficient ecophysiological adaptations under drought conditions, and achieve a favorable water balance (Han et al., 2015). Higher water use efficiency at late successional stages is directly connected with higher net production.

From the above results, we expect that the changes in net production during the growing period of both grasslands (*Figure 5*) followed a similar trend with the change of water use efficiency (*Figure 4*). However, the net production of each grassland presented significant differences throughout the growing season ($F_{3,36}$ =117.3 and $F_{3,36}$ = 58.1, $p \leq 0.001$ for ESS and LSS respetively).

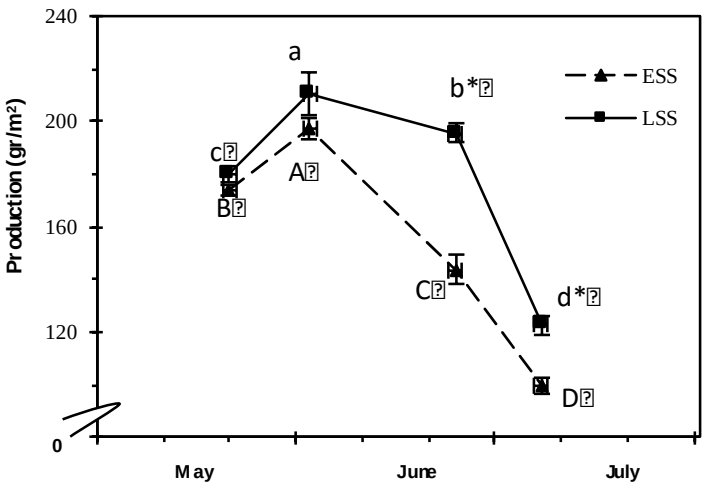

Figure 5. *Seasonal changes of net production of the two grasslands (ESS and LSS) during the semi-arid growing period. Values present means ± SE (n =10). Small and capital letters indicate significant differences (LSD-test, p<0.05) within LSS and ESS grassland respectively. *Indicates significant differences (t-test, p<0.05).*

Net production of the LSS grassland during the dry season, especially after mid-May, was significantly higher (t>4.9, df=18, $p \leq 0.0001$) than that of the ESS grassland that was protected from grazing for five years before these measures were taken. The production of the ESS and LSS grasslands ranged from 99 g/m^2 to 198 g/m^2 and 122 g/m^2 to 216 g/m^2 respectively. Both grasslands showed significantly higher production than that reported for low elevation grassland in Greece in other studies (Platis et al., 2004). In addition, the lower production of the ESS grassland was primarily due to the large participation of broadleaf grasses and annual legumes (Karatassiou and Koukoura, 2009) in the composition of the vegetation, which significantly limits their production under low rainfall (Rajaniemi, 2003; Nippert et al., 2006; McCain 2010).

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The largest production of the LSS grassland over the ESS grassland could be attributed to the different value of leaf area index (LAI) (*Figure 6*). The LAI controls light interception of plant and influences gas exchange (water, carbon) between vegetation and the atmosphere, and is a key variable to model the carbon and water exchange between vegetation and the atmosphere (Leuschner et al., 2006). Two way ANOVA reveals that both grassland ($F_{1,72}$= 6.2, p≤ 0.05), time of the season ($F_{3,72}$= 159.6, p≤0.0001) and their interaction ($F_{3,72}$ = 66.4, p≤0.0001) are significant predictors of the LAI (*Figure 6*). Seasonal patterns of LAI differ a great deal between the two grasslands.

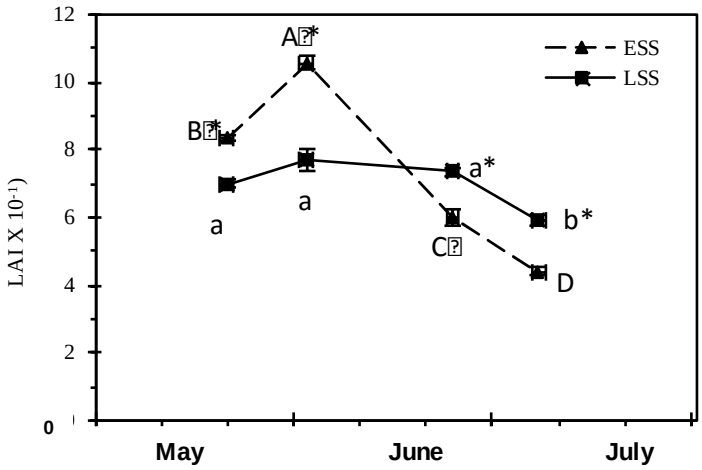

Figure 6. *Seasonal changes of leaf area index (LAI) of the two grasslands (ESS and LSS) during the semi-arid growing period. Values present means ± SE (n =10). Small and capital letters indicate significant differences (LSD-test, p <0.05) within LSS and ESS grassland respectively. * Indicates significant differences (t-test, p<0.05).*

The water deficit appears to have minimal effects on the production of the LSS grassland that exhibited low and approximately constant leaf area index (LAI) throughout the growing season (*Figure 6*), which decreased only in the end of the growing season (LSD-tests, p≤0.0001). According to Liu et al. (2015) and Meiners (2015) the high leaf area index indicates that the photosynthesis of species that compose the LSS grassland should not be limited by the intake of light or the accumulation of assimilates. In contrast, species of ESS grassland showed a decrease in leaf area index for reducing water loss, which enabled them to survive under water deficit conditions. Similar results were obtained by Bai and coworkers (2004) for grasslands at different succession stages in China under dry and hot climatic conditions. Interestingly in this study grassland at advanced successional stages expressed both higher species richness and productivity (Karatassiou, 1999; Karatassiou and Koukoura, 2009).

Although generalizations regarding response of all similar grasslands in the Mediterranean should be avoided it becomes apparent that in the low elevation Mediterranean grasslands the model proposed by Odum (1983, 1985) fails to explain net production. The species that compose the vegetation in these successional stages are mostly perennial, with mechanisms that enable them to use efficiently the water during the hot and dry season, with a favorable impact on net production of grasslands (Saint Pierre et al., 2002; Gallego and Distel, 2004; Fernandez et al., 2009)

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Conclusions

The higher water use efficiency and higher net production in late successional stages of the lowland Mediterranean grasslands that we have examined in the current study suggests a rather substantial divergence from the traditional view of the succession theory regarding productivity. Apparently, the vegetation (species) in the Mediterranean region has developed specific mechanisms of adaptation and survival to thrive and persist under the dry and hot summer conditions prevailing in the area.

Therefore, both the structure and productivity of grasslands in this region could be explained by a model in which, besides others important parameters, the water use efficiency should be taken into account as an index of productivity as well of drought adaptation in low elevation areas.

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