Above-ground biomass and productivity in the Montado: From herbaceous to shrub dominated communities

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ABSTRACT

Our study was focused on the effect of abandonment on above-ground biomass and net primary productivity (ANPP) in a Montado in Southern Portugal. The Montado has a long history of human management and control of invasion by shrubs is achieved by clearing, ploughing and grazing. When these cease, it is invaded by Mediterranean matorral species. We hypothesized that the change in life form dominance would affect both biomass and productivity, but while the total biomass was expected to increase, the effects on ANPP were less clear. We tested our hypothesis by determining above-ground biomass and ANPP along a gradient of decreasing land use intensity, ranging from extensive grazing to 20 years of abandonment.

Above-ground biomass increased with abandonment, which was related with the increase in shrub cover. In addition, we found a decrease in herbaceous ANPP that was more than compensated by an increase in shrub ANPP in plots abandoned for longer time, resulting in a significant increase in total ANPP. This increase was strongly related with the increase in the cover of *Cistus ladanifer*, a pioneer species that colonises degraded areas and forms one of the first stages of succession of woody communities.

1. Introduction

The agro-pastoral systems of South Portugal, as most Mediterranean rangelands, have originated from natural forests following the removal of trees by human activities such as clearing, burning and grazing (Pulido et al., 2001). When agricultural practices decrease or stop, succession generally leads to the invasion by woody plants. In the studied system abandonment lead to a change in vegetation structure and composition that resulted in the replacement of herbaceous dominated communities with shrub-dominated communities, often with one or few dominant species. Shrub encroachment has been reported in many grassland and savanna ecosystems in North and South America, in Africa and Australia (e.g. Van Auken, 2000; Bowman, 2002; Hughes et al., 2006), often as a result of overgrazing of herbaceous species or changes in fire regime (Van Auken, 2000; Asner et al., 2004). It has also been reported in Greek rangelands as a consequence of decreasing land use intensity (Karakosta and Papanastasis, 2007; Zarovalli et al., 2007). Woody encroachment is likely to cause substantial alterations in the sequestration and cycling of carbon

and nitrogen (Briggs et al., 2005; Hughes et al., 2006) because grasslands are generally expected to have high biomass turnover, productivity and nutrient cycle, and only moderate capacity for carbon sequestration in biomass when compared to woody communities (Díaz and Cabido, 1997; Gill and Burke, 1999). Increases in above-ground carbon storage with shifts to woody vegetation have been reported by some authors (e.g. Jackson et al., 2002; Asner et al., 2003; Hughes et al., 2006). Several specific aspects of ecosystem function, among which above-ground net primary productivity (ANPP) was directly affected by the relative abundance of the grass and shrub functional types in a study in the Patagonian steppe (Aguiar et al., 1996). Above-ground primary productivity decreased as shrubs increased because shrubs did not fully compensate for the decrease in grass production (Aguiar et al., 1996). Zarovalli et al. (2007), and Karakosta and Papanastasis (2007) noted a decrease in herbaceous biomass and production as woody species cover increased. Considering the productivity of herbaceous and woody components together, Huenneke et al. (2002) reported a small but significant decrease in overall productivity of desertified shrub systems of New Mexico in comparison to grasslands. However, there is still a degree of uncertainty regarding how biomass and productivity of herbaceous and woody components interact in response to shifts in plant life form composition (Hughes et al., 2006), particularly in

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Mediterranean, where such studies are scarce. Studies in Mediterranean areas (Karakosta and Papanastasis, 2007; Zarovalli et al., 2007) suggest a possible decrease in herbaceous ANPP but this may be compensated by shrub productivity, resulting in no change in ANPP, or more than compensated, resulting in an increase in ANPP (Reich et al., 2001; Huenneke et al., 2002; House et al., 2003).

Our question is focused on the effect of abandonment and, more specifically, the shift from herbaceous to shrub dominated communities, on the community above-ground biomass and ANPP. We hypothesized that the change in life form dominance would affect both biomass and productivity but while the total biomass was expected to increase, because shrubs have larger biomass than herbaceous species, the effects on ANPP were less clear.

2. Methods

2.1. Study site

The study site (Monte do Vento, Mértola), with an area of 198.44 ha, is located in the Southeast of Portugal, at about 37°48′21.72″N and 7°40′44.96″W. The study site used to be under a traditional scheme of rotation of crops/fallow/pasture. The rotation scheme generally consists of cereal fields, fallow land, pastures and ploughed fields, where the farm is divided into parcels and each parcel is under different phases of the rotation cycle, creating a mosaic of fallow, pasture and cultivated fields. For two years a parcel is under cereal cultivation (wheat, oat and barley), after which land is left fallow for a period of 2–3 years. Afterwards, the parcel is ploughed to re-initiate the rotation cycle (Marta et al., 2007). In the last decades large areas have been abandoned and at the present the study site is composed of different land uses that range from grazed areas to areas abandoned for more than 20 years. We selected three land use categories which represent a decrease in land use intensity. The first category, 'grazing', is used for extensive grazing by sheep (0.99 CU/ha). These are grasslands, composed mostly of annual herbaceous species (88% of plant cover) and of some disperse cork and holm trees (less than 2% cover). The two other categories, 'intermediate succession' and 'advanced succession', represent areas that were abandoned, 10–15 years, and 20 or more years ago, respectively. The first is composed of a mixture of herbaceous species, mostly annuals (28%), and small (41%) and tall shrub (24%) species, while the second is mostly composed of tall shrubs (78%) where *Cistus ladanifer* is the dominant species representing about 52% of plant cover. We selected a total of nine parcels, three parcels under each land use category and in each parcel a permanent plot was set. Plot size was adapted to the type of vegetation, resulting in plots with 900 m^2 in grazing and 2500 m^2 in intermediate and advanced succession. Distance between plots ranges from about 50 m to more than 500 m, and two of the parcels where advanced succession plot were set are separated by parcels of intermediate succession.

The area is hilly, with poor soils and steep slopes. The dominant soils are shallow schist soils with high stoniness. Soils of the three land uses were not significantly different in soil nitrogen ($F = 0.355$, $p = 0.715$) and carbon ($F = 2.006$, $p = 0.216$) content but phosphorous significantly decreased with time of abandonment ($F = 7.008$, $p < 0.05$).

2.2. Sampling

2.2.1. Herbaceous above-ground biomass and ANPP

The methods chosen to measure above-ground biomass and ANPP, in each land use category, were determined by the dominant life form in the site. Therefore, different estimation methods were used for shrub and herbaceous vegetation.

For herbaceous vegetation, the sampling of plant above-ground biomass and ANPP followed "Method 1" of Scurlock et al. (1999). This method estimates above-ground biomass and ANPP based on a single harvest at the peak of live biomass. It assumes that any standing dead matter or litter was carried over from previous years, and death in current year is negligible. This method was considered adequate for the studied communities, which are mostly composed of annual species.

One harvest of above-ground biomass was conducted in April–May 2004 to assess maximum standing biomass (Scurlock et al., 2002). Eight quadrates of 0.25 × 0.50 m were sampled in each of the three permanent plots in 'grazing' and 'intermediate succession' land use categories, resulting in an area of approx. 1 m^2 sampled per plot. Each plot was considered a replicate, resulting in three replicates per land use category (Garnier et al., 2007). For each quadrate, all above-ground material (live and dead) was collected by clipping at ground level. Live material was separated from the dead and the two fractions were oven-dried to constant mass at 60 °C and weighed (Garnier et al., 2007). Live material was used to determine above-ground live biomass and ANPP.

2.2.2. Shrubs above-ground biomass and ANPP

Shrub measurement techniques (e.g. Vora, 1988; Fernández et al., 1991; Armand et al., 1993; Jobbágy and Sala, 2000; Sternberg and Shoshany, 2001; Navarro and Oyonarte, 2006) used in other semi-arid areas of the world were examined with the objective of adapting a suitable, non-destructive, and relatively simple and accurate method to the shrub species in the study area. Although a large number of variables could be used to predict biomass and ANPP, variables that express the size of the crown appeared to be the most useful (Murray and Jacobson, 1982).

The collection of data for the estimation of shrub above-ground biomass and ANPP consisted of two steps.

First, in order to establish regression equations for the estimation of above-ground biomass and ANPP, we measured and harvested 6–12 individuals of the shrub species *C. ladanifer*, *Genista hirsuta*, *Helichrysum stoechas*, *Lavandula stoechas* and *Lavandula viridis*, which were the dominant shrub species in the studied plots (other shrub species present had negligible cover), at the end of the growing season. For each individual we measured: (1) Total height, defined as the maximum vertical distance from the ground level to the highest point of the plant; (2) Crown diameter, as the mean of two perpendicular diameters. From these measurements we determined crown area and volume. Crown volume was determined, for each species, using the formula of the solid that appeared to give the best fit of the natural shape of the crown. The geometric shape that best fitted the sampled species was the inverted cone. Assuming a cone shape, plant volume (V) was calculated as $V = \pi/3 r^2 h$, where r is the crown radius and h is total height.

In the laboratory, the harvested individuals were separated into green leaves and current year shoots, woody parts, and dead material. The different fractions were oven-dried to constant mass at 60 °C and weighed. Green leaves and current year shots were considered as current year production (Fernández et al., 1991; Alldredge et al., 2001) and used as an estimate of ANPP. Current year shoots are easily identifiable in all species and species sampled are either summer deciduous or semi-deciduous and therefore all (*G. hirsuta* and *H. stoechas*) or at least a large percentage of green leaves (*C. ladanifer*, *L. stoechas* and *L. viridis*) are current year production. The measured variables were regressed against dry weight (see description below).

Second, three quadrates of 6 m^2 per plot were sampled in 'intermediate' and 'advanced succession' land use categories. In each of these quadrates, we counted and measured (as above) all

the individuals of each shrub species present. Plant biomass within these quadrates was estimated by applying the developed regression equations (see description below). Total above-ground biomass values for each species in a quadrate were summed to obtain biomass per square meter. The three quadrates in each plot were averaged to yield a single value per plot.

Above-ground net primary productivity was calculated as a proportion of the total plant biomass based on the mean values obtained from the individuals collected (0.25% in *C. ladanifer*, 0.14% in *G. hirsuta*, 0.58% in *H. stoechas*, 0.40% in *L. stoechas* and 0.27% in *L. viridis*).

For 'intermediate succession' plots the above-ground biomass and ANPP of the herbaceous layer were measured as for the 'grazing' plots while for the shrub layer we proceeded as for 'advanced succession' plots. The total above-ground biomass and ANPP per plot were obtained as the sum of the herbaceous and shrub layers.

2.3. Statistics

2.3.1. Regression equations

Curve estimation regression models were used to determine the type of regression that best described the relationship, in each species, between measured variables (height, volume and area) and dry weight. The variable that best predicted dry weight was volume (V) in *C. ladanifer*, *G. hirsuta*, and *H. stoechas*, and area (A) in *L. stoechas* and *L. viridis*. The curves that best described these relationships were linear and power. The best equation for each species was selected based on the coefficient of determination. The equations selected, linear for *C. ladanifer* and *H. stoechas*, and power for *G. hirsuta*, *L. stoechas* and *L. viridis* are presented in Table 1. The coefficients of determination for the selected equations ranged from 0.889 to 0.987 (Table 1).

2.3.2. Data analysis

Differences in mean above-ground live biomass, ANPP and total above-ground dead biomass between land use categories were tested, on untransformed data, with the ANOVA or Student's *t*-test, according to the number of land use categories that were under analysis. The Pearson's correlation coefficient was used to test for correlations between above-ground live biomass and shrub cover, and ANPP and shrub cover. All statistical analyses were performed with SPSS 14.0 for windows (SPSS, Inc. Chicago, IL).

2.4. Methodological considerations

In this study, annual herbaceous ANPP was estimated by the peak of green biomass. Studies in other system indicate that if the purpose is to estimate annual primary production, peak of green biomass is one of the methodological options with the smallest error (Jobbágy and Sala, 2000). Furthermore, annual herbaceous communities fulfil the assumption that live biomass was not carried over from previous years (Scurlock et al., 2002). In the case
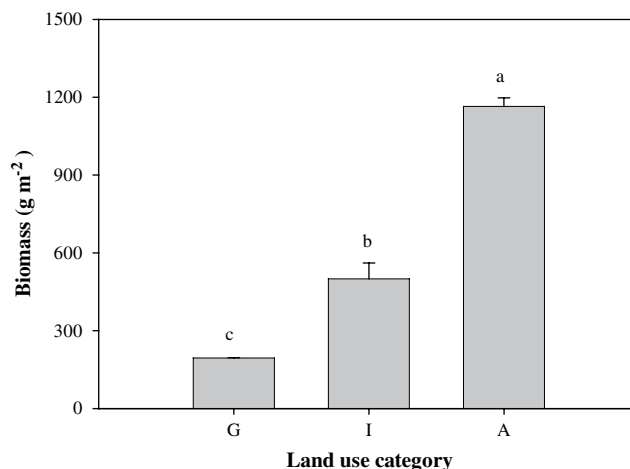
of shrubs, we assumed that current year leaf and twig biomass accounted for annual ANPP. A slight underestimation of shrub ANPP may be expected since we did not account for stem diameter changes in older branches. The use of current year biomass accumulation at the end of the growing season as an estimate of ANPP has been successful in other studies where shrub ANPP was estimated (Jobbágy and Sala, 2000). In our study, *G. hirsuta* is summer deciduous and *H. stoechas* dries out to ground level which means that all leaves are current year production. *Lavandula* sp. and *C. ladanifer*, are summer semi-deciduous implying that a certain degree of error in the estimation of the ANPP of these species may arise from the fact that some green leaves may remain from previous year, resulting in overestimation. This study did not account for litter fall, which could result in an underestimation of ANPP. However, for the sampled species leaf shed occurs mostly in the summer (e.g. 65% of leaves of *C. ladanifer* are shed from late June to October; Correia et al., 1992), after our sampling had occurred, which should decrease the error resulting from not accounting for litter fall. Additionally, we calculated ANPP of each individual species as a proportion of the biomass of that species. We compared the proportions obtained for each of the sampled species were compared with those obtained in other studies when these were available for the same species. Values found in other studies ranged from 0.21 to 0.27 in *C. ladanifer* (Simões, 2002; Navarro and Oyonarte, 2006), and from 0.21 to 0.35 in *L. stoechas* (Armand et al., 1993; Navarro and Oyonarte, 2006), were about 0.15 in *Gennista* sp. (Navarro and Oyonarte, 2006). Values found in the present study were generally within the range of those reported for the same species, except in the case of *L. stoechas* which showed higher values. Even though one should be aware of the possible errors resulting from the methodology used, we consider that it was adequate for the purpose of this study.

3. Results

Above-ground biomass differed significantly between all land use categories, from a minimum of 194.71 $\mathrm{g\,m^{-2}}$ in 'grazing' to a maximum of 1164.89 $\mathrm{g\,m^{-2}}$ in 'advanced succession' (Fig. 1).

The increase in above-ground biomass after abandonment was strongly related to the increase in shrub cover (Table 2), particularly *C. ladanifer*.

Above-ground net primary productivity ranged from 194.71 $\mathrm{g\,m^{-2}}$ in 'grazing' to 271.15 $\mathrm{g\,m^{-2}}$ in 'advanced succession'

Table 1
Regression equations (W_t = estimated weight in g, V = canopy volume in cm^3, A = canopy area in cm^2), coefficients of determination (r^2), significance (p), and number of samples (n).

	Equations	r^2	p	n
Cistus ladanifer	$W_\mathrm{t} = 90.819 + 0.002 \times V$	0.953	<0.001	12
Genista hirsuta	$W_\mathrm{t} = 0.003 \times V^{1.027}$	0.973	<0.001	6
Helichrysum stoechas	$W_\mathrm{t} = 7.009 + 0.003 \times V$	0.987	<0.001	6
Lavandula stoechas	$W_\mathrm{t} = 0.213 \times A^{0.872}$	0.960	<0.001	6
Lavandula viridis	$W_\mathrm{t} = 0.009 \times A^{1.366}$	0.889	<0.001	6

Fig. 1. Above-ground biomass in grazing (G) and intermediate (I) and advanced (A) succession land use categories ($F = 115.07$, $p < 0.0001$, $n = 9$). Values in intermediate succession represent the sum of plant biomass in the herbaceous and shrubs layers.

Table 2
Relationships (Pearson's correlation coefficients) between above-ground biomass, ANPP and shrub cover.

|	Shrub cover	Cover of C. ladanifer
Above-ground biomass	0.887**	0.985**
ANPP$_{Total}$	0.70*	0.885**
ANPP$_{shrubs}$	0.858*	0.972**

Significance levels: *$p < 0.05$, **$p < 0.01$.

(Fig. 2). When the herbaceous and shrub layers were separately analysed (Figs. 3 and 4), intermediate succession had a significantly lower herbaceous ANPP when compared to 'grazing' (Fig. 3; $t = 4.14$, $p < 0.05$), and significantly lower shrub ANPP when compared to 'advanced succession' (Fig. 4; $t = 5.38$, $p < 0.05$).

Additionally, data for the total above-ground dead biomass of the herbaceous layer were analysed. This analysis showed a significantly higher (Fig. 3; $t = 3.58$, $p < 0.05$) amount of dead material in 'intermediate succession' when compared to grazing. The increase in ANPP of the shrub layer was strongly related with the increase in the cover of C. ladanifer (Table 2). As shown in Fig. 4, shrub ANPP and Cistus ANPP significantly increased from 'intermediate' to 'advanced' succession while the sum of ANPP of the other shrubs did not change significantly.

4. Discussion

Above-ground biomass of shrub communities showed lower values than those reported for Mediterranean shrub communities (2190–4600 g m^{-2}, Ehleringer and Mooney, 1983) and than those found by Simões (2002) for the above-ground biomass of C. ladanifer in a study in South Portugal (1605–1936 g m^{-2}). Above-ground net primary productivity of shrub communities showed higher values than those reported for Mediterranean shrub communities (110–130 g m^{-2}, Ehleringer and Mooney, 1983) but lower than reported by Simões (2002) for the sum of green leaves and current year shoots of C. ladanifer in a study in South Portugal (420.6–538.8 g m^{-2}).

The herbaceous species that generally dominate early secondary successional sites return most of their biomass to the soil each year. As perennial species, particularly shrubs, increase in abundance, biomass increases more rapidly because woody species retain
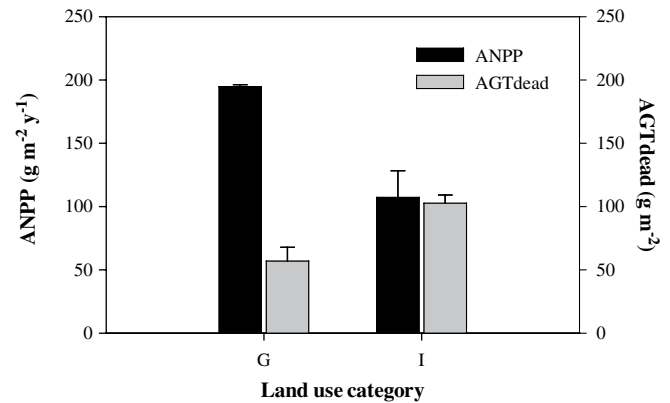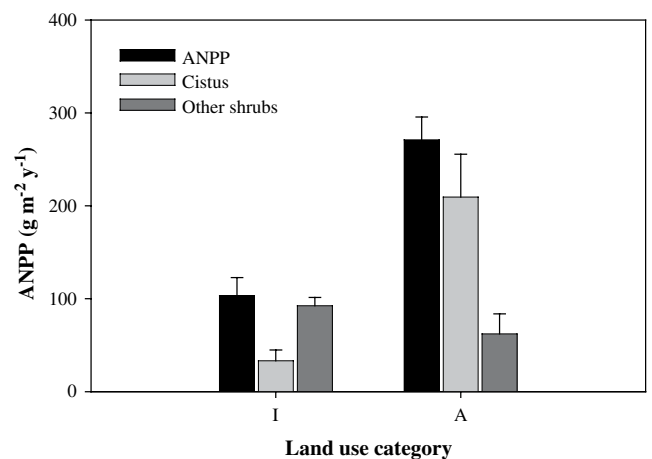

Fig. 3. Above-ground net primary productivity (ANPP) and above-ground dead plant material (AGTdead) of the herbaceous layer in grazing (G) and intermediate succession (I) land use categories. Both variables are significantly different among areas (ANPP: $t = 4.14$, $p < 0.05$, $n = 6$; AGTdead: $t = 3.58$, $p < 0.05$, $n = 6$).

a larger proportion of their biomass than do herbaceous species (Chapin et al., 2002). Our results showed an increase in total above-ground biomass with abandonment time and are therefore consistent with what would be expected following the replacement of herbaceous with woody species. The increase in above-ground biomass through succession in our study was strongly related to the increase in shrub cover. Differences in biomass thus reflect the changes in the dominant life form.

When only herbaceous species were taken into account, the above-ground biomass and ANPP decreased from 'grazing' to 'intermediate succession' in our study. Herbaceous biomass and production were also significantly reduced as shrub cover increased in Greek rangelands (Karakosta and Papanastasis, 2007; Zarovalli et al., 2007). The accumulation of dead material has important implications for productivity and community composition by intercepting light, and shading seeds and seedlings (Facelli and Pickett, 1991; Grime, 2001). In herbaceous communities, most of the aerial biomass is allocated to short lived organs resulting in a rapid accumulation of litter in early stages of succession (Facelli and Pickett, 1991). The higher mass of herbaceous above-ground dead material in 'intermediate succession' is likely to be a consequence of the absence of grazing, which together with the increase
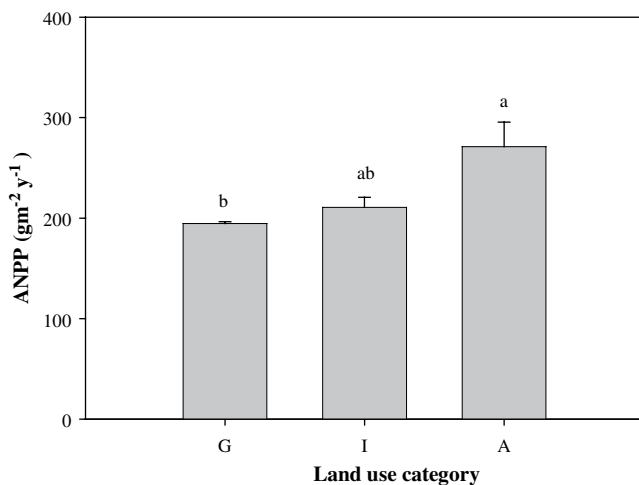
Fig. 2. Above-ground net primary productivity (ANPP) in grazing (G), intermediate (I), and advanced (A) succession land use categories ($F = 6.95$, $p < 0.05$, $n = 9$). Values in intermediate succession represent the sum of plant biomass in the herbaceous and shrub layers.

Fig. 4. Above-ground net primary productivity of all shrubs sampled (ANPP), of Cistus ladanifer (Cistus) alone, and the sum of other shrub species (other shrubs) in intermediate (I) and advanced succession (A) land use categories (ANPP: $t = 5.38$, $p < 0.01$, $n = 6$; Cistus: $t = 3.41$, $p < 0.05$, $n = 6$; other shrubs: $t = 1.29$, $p > 0.05$, $n = 6$).

in shrub cover may explain the decrease in both biomass and ANPP of herbaceous vegetation in this area. A negative effect of larger amount of above-ground dead material on ANPP in ungrazed plots was also reported by Altesor et al. (2005) for temperate sub-humid grasslands.

Different types of vegetation can attain similar above-ground productivities because of compensating factors in the productive structure of the community. In a study which encompassed forest, scrub, and herbaceous Mediterranean communities, Ehleringer and Mooney (1983) reported a difference between these communities of 30-fold in above-ground biomass and only a 2-fold difference in above-ground productivity. A study in a temperate oak savanna, showed that an increase in ANPP with increasing woody plant cover was caused by an increase in woody ANPP large enough to more than compensate for the decrease in grass ANPP (Reich et al., 2001). In contrast, ANPP was reduced with shifts from grass to woody plant dominance in desertified systems of New Mexico (Huenneke et al., 2002). In our study, the shift from herbaceous to woody dominance resulted in an increase in woody ANPP and in a decrease in herbaceous ANPP as well as in a significant change in the community ANPP. The increase in shrub ANPP was mostly accounted by *C. ladanifer* and it was in the plots dominated by this species ('advanced succession' plots) that ANPP significantly increased. *C. ladanifer* is a pioneer species that colonises degraded areas and forms one of the first stages of succession of woody communities (Correia, 2002). Under favourable conditions, *C. ladanifer* successfully competes with other species and quickly spreads over recently disturbed areas. This species can grow fast and attain large amounts of biomass in a short amount of time (Nuñez et al., 1989). Patón et al. (1998) found a production of 170 g m^{-2}, in natural communities, in 2-year-old *C. ladanifer*, and Simões (2002), reported values ranging from 420.6 to 538.8 g m^{-2} for photosynthetical active components for this species. In the studied system, the early ruderal herbaceous communities were replaced by pioneer shrub species that have themselves high growth rates. Therefore the increase in ANPP may not be a surprising result in these systems.

5. Conclusions

Our study showed an increase in total above-ground biomass with abandonment time indicating a positive effect of the shift to woody vegetation on total above-ground biomass. Total ANPP was significantly higher in 'advanced succession' than in 'grazing' while herbaceous ANPP decreased indicating a negative effect of increase in shrub cover on herbaceous ANPP. The decrease in herbaceous ANPP was compensated by the increase in shrub ANPP, which was greatly due to the high ANPP of *C. ladanifer*. Woodiness is particularly important in enhancing carbon sequestration because woody plants tend to contain more carbon, live longer, and decompose more slowly than smaller herbaceous plants (Díaz et al., 2005). Therefore the shift from herbaceous to shrub-dominated communities may result in higher accumulation of C in these ecosystems, contributing to reduce CO$_2$ in the atmosphere. On the other hand, this shift represents an increase in the flammability (higher LDMC and canopy height) and amount of fuel (more biomass) which may increase the probability and severity of fires (Lavorel and Garnier, 2002; Pausas, 2004). Since the regeneration of *Cistus* species is generally favoured by fire (Pausas, 1999; Correia, 2002), a positive feedback between fire and the maintenance of *Cistus* dominated shrublands may occur.

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