Shrub encroachment in Mediterranean silvopastoral systems: *Retama sphaerocarpa* and *Cistus ladanifer* induce contrasting effects on pasture and *Quercus ilex* production

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Abstract

Silvopastoral systems are threatened worldwide by progressive loss of either tree cover or herbaceous cover due to lack of tree regeneration and shrub encroachment, respectively. Grazed Mediterranean open woodlands, as Iberian dehesa, are an outstanding example of silvopastoral system where shrub encroachment has been proposed as an effective means to facilitate tree seedling recruitment and ensure the system persistence. Shrubs also may interact with pasture understorey and tree overstorey, thereby affecting the overall system productivity. We tested the effects of shrub encroachment on pasture yield, tree growth and acorn production in years of contrasting rainfall in *Quercus ilex* L. dehesas of central-western Spain. We compared the effects of two prominent Mediterranean shrub species that differ in their ecological strategies: a N_2-fixing and sparse deep-rooting shrub (*Retama sphaerocarpa* (L.) Boiss), and a dense shallow-rooting shrub (*Cistus ladanifer* L). In intermediate and dry years, pasture yield beneath tree canopy was lower by 21 to 35 % than in open grassland. Pasture yield beneath tree canopy was not significantly affected during the wet year. *Cistus ladanifer* encroachment significantly reduced pasture yield by 68 to 98 %, tree growth by 17 to 29 %, and acorn yield by 6 to 44 %. In contrast, *Retama sphaerocarpa* significantly increased pasture yield by 11 to 157 % and tree growth by 6 to 13 %, but had a neutral effect on acorn yield. Our results suggest that pasture is more sensitive to shrub encroachment and annual rainfall variation than is *Q. ilex.* The importance of *C. ladanifer* competition and *R. sphaerocarpa* facilitation on pasture yield increased in the driest year. We conclude that the sign and intensity of shrub encroachment effects on pasture and tree production in Mediterranean dehesas are species-specific and depend on temporal variation as a function of climate.

Keywords: Acorn, Agroforestry, Competition, Dehesa, Facilitation, Overstorey-understorey interactions

1. Introduction

Intensive agricultural systems have been criticised for their negative environmental impacts, such as soil erosion, non-point-source pollution, loss of biodiversity, and fossil fuel use (Tilman et al. 2002). Multispecies cropping systems such as agroforestry systems, however, may offer a range of potential advantages in terms of increased productivity, optimisation of inputs, stability of outputs, resilience to disruption, and ecological sustainability (Malézieux et al. 2009). Extensive silvopastoral systems, such as the 'dehesas' of the Iberian peninsula, fulfill these requirements. Dehesas (from the Castilian word for 'wooded pastureland'; 'montados' in Portuguese) are traditional, open woodlands that are used by cattle, sheep, goats, pigs and horses, and are limited in their agricultural potential, owing to climatic conditions and low soil fertility (Gómez-Gutierrez and Pérez-Fernández 1996). They are also important sources of non-timber forest products, such as acorns, mushrooms and truffles, cork, and firewood. Dehesas are among the most important and widespread agroforestry land-use systems in Europe (Eichhorn et al. 2006), and they cover about 3 million hectares in Spain (MMARM 2009). Iberian dehesas play a crucial role in rural economy and have been recognised as an example of integrating traditional land-use with biodiversity conservation (Plieninger and Wilbrand 2001). These agroecosystems consist of scattered oaks, chiefly holm oak (*Quercus ilex* L. ssp. *ballota*), with an understorey that is composed of a mosaic of grasslands, croplands and shrublands, where livestock is extensively raised. Livestock is undoubtedly the most important output of the dehesas, and the diets of livestock depend largely on grass and legume forage, acorns, and tree browse production.

Two fundamental concerns were recently highlighted regarding the conservation of extensive silvopastoral systems worldwide: the progressive loss of tree cover resulting from the lack of natural tree regeneration (Gibbons et al. 2008) and excessive encroachment of woody plant species, defined as the establishment, development and spread of indigenous shrubby plants

(Roques et al. 2001; Price and Morgan 2008; Van Auken 2009). Similar issues have been observed in Iberian dehesas (Pinto Correira and vos 2004; Pulido et al. 2010). Lack of oak recruitment in Iberian dehesas has been mainly attributed to the intensification of grazing and associated management practices such as shrub clearing and rotational ploughing, which are implemented to control shrub invasion, to promote pasture production, and to prevent fire (Pulido et al. 2001). Yet recent studies have shown that shrub encroachment in Mediterranean open woodlands may have positive effects on early recruitment of oak species (Gómez-Aparicio et al. 2004; Pulido et al. 2010) and on soil rehabilitation (Simões et al. 2009).

Shrubs can dramatically affect the spatial distribution and cycling of nutrients by altering soil structure, microbial biomass, soil moisture, and microclimate, and by concentrating organic matter beneath their canopies (Van Auken 2009). These processes, in turn, can exert an important influence on the tree or herbaceous understorey. Some studies have reported positive effects of shrub encroachment on pasture yield relative to open grassland in arid environments (e.g., with the desert shrub *Ambrosia dumosa*; Holzapfel and Mahall (1999)), whereas other studies came to the opposite conclusion in temperate grassland environments (e.g., with the clonal shrub *Cornus drummondii*; Lett and Knapp (2005)). Studies regarding the effects of trees on pasture production have also produced contradictory results (Moreno and Pulido 2009). In fact, plant-to-plant interactions are strongly edaphoclimatic context-dependent and species-specific. Accordingly, increasing the scale of a study (e.g., time, species, spatial extent) results in frequent reversals in the sign of an interaction (Sthultz et al. 2006). For example, Gea Izquierdo et al. (2009) showed that the positive effects of trees on pasture yield in Iberian dehesas occur only in years where there is no water limitation during spring growth.

Another concern in any shrub-encroached woodland, which has received less attention, is the effect of a shrub layer on the tree overstorey. This information is essential if we have to assess the

overall productivity of shrub-encroached dehesas and other grazed open woodlands, which depends on the sum of yields for both pasture and tree components. Previous studies in dehesas have shown that shrub encroachment may significantly reduce soil water (Cubera and Moreno 2007a) and N supply (Moreno and Obrador 2007), thereby decreasing tree growth and acorn production (Moreno et al. 2007). However, these studies did not permit the authors to discern shrub species effects. Our study examined the effects of two shrub species, *Retama sphaerocarpa* (L.) Boiss. (Fabaceae) and *Cistus ladanifer* L. (Cistaceae), which are widely distributed throughout the Mediterranean zone. These shrub species have contrasting ecological strategies for successful establishment in dehesas. We focused on *Q. ilex* since it is the most prominent tree species in Iberian dehesas and other Mediterranean silvopastoral systems.

Retama sphaerocarpa (hereafter referred to as *Retama*) is a leguminous shrub with N_2-fixing capabilities that generally grows in scattered patches (Gómez Sal et al. 1999). This shrub species develops a dimorphic root system with long surface lateral roots and very deep roots that allow the plant to tap deep water sources (Haase et al. 1996). *Retama* can exert strong facilitative effects on the biomass of the herbaceous understorey (e.g., Pugnaire et al. 1996). The rock rose *Cistus Ladanifer* (referred to as *Cistus*), by contrast, forms extensive and mostly aggregated populations, and develops shallow, dense root systems that retain water in the upper soil layers (Talavera et al. 1993; Silva et al. 2002). *Cistus* also produces phytotoxic compounds (likely allelopatic) that may have inhibitory effects on the herbaceous understorey (Herranz et al. 2006). *Q. ilex* can be considered as a foundation tree species in the dehesa. A foundation species can drive by himself much of the structure of many dependent community members by creating locally stable conditions for other species, and by modulating fundamental ecosystem process (Ellison et al. 2005). For example, the vast horizontal and vertical surface of soil that is explored by *Q. ilex* roots, together with their deep spatial segregation with respect to grass roots, may help limit tree-

grass competition and allow trees to meet their water needs during the dry Mediterranean summers in deeper soil layers (Moreno et al. 2005). Consequently, *Q. ilex* is expected to be less affected than pasture species by changes in water and nutrient supply in the uppermost soil layer (Moreno et al. 2007).

The first objective of this study was to determine the effect of shrub encroachment, either by *Retama* or by *Cistus,* on pasture yield, *Q. ilex* growth, and acorn production. We hypothesised that *Retama* encroachment would induce positive effects on pasture because of its N_2-fixing ability and negative effects on *Q. ilex* production because of tree-shrub competition for soil water during summer drought (i.e., they have similar sparse deep-rooting systems). We also hypothesised that the shallow-rooted shrub species, *Cistus,* would induce negative effects on pasture and neutral effects on *Q. ilex* production because of tree-shrub complementary use of soil resources (i.e., spatially segregated root systems). Lastly, we posited that pasture would be more responsive to shrub encroachment than mature *Q. Ilex* because of low dependence of *Q. ilex* and high dependence of pasture on resources in the uppermost soil layer. The second objective was to determine the effects of trees on pasture yield. Since the Mediterranean climate is characterised by wide variation in inter-annual precipitation, the third objective was to examine whether the sign and magnitude of plant-to-plant interactions (i.e., tree-pasture, shrub-pasture, shrub-tree) vary over the course of four years. We hypothesised that increasing drought pressure would increase the intensity of plant-to-plant interactions according to the recently reformulated stress-gradient hypothesis (Maestre et al. 2009), which states that the sign of an interaction depends on the interacting species, and predicts that facilitation increases with increases in abiotic stress, when the beneficiary (e.g., herbaceous plants) and benefactor (e.g., *Retama*) species are competitive and stress tolerant, respectively. In contrast, this refined stress-gradient hypothesis predicts that the

effect of neighbours can be negative with increases abiotic stress when both interacting group of species (e.g., herbaceous plants and *Cistus*) have similar 'competitive' life histories. Our findings will be useful to better understand and manage shrub-encroached Mediterranean silvopastoral systems.

2. Material and methods

2.1. Study sites and experimental design

The study was conducted in different dehesa farms (referred to as sites) located in the north of the Extremadura region of central western Spain (39º27'-40º12'N, 05º90'-06º30'W), in flat or gently sloping (3-5 %) terrain, located at an average 400-500 m asl. The oligotrophic and acidic soils (pH (1:2.5 water) ca. 5.0) are classified as Chromic Luvisols and Dystric Cambisols (IUSS Working Group WRB 2006). The climate is Mediterranean, with dry and hot summers, and cool and rainy winters. Mean annual temperature is 15.7 ºC, and mean annual precipitation is 568 mm (Aldehuela del Jerte station, 40º00' N, 6º13' W, 2000-2010 records). Over the four years (2007, 2008, 2009 and 2010) of the study, the rainfall accumulated in each hydrological year (October-September period) represented 94, 80, 62, and 128 % of the 10-y average, respectively (Fig. 1). This means that 2007 can be considered as intermediate, 2008 as dry, 2009 as very dry, and 2010 as a wet year. Monthly average temperature was similar among these four years (Fig. 1).

Twenty nine study sites were randomly selected, all of them included a *Q. ilex* overstorey (see Table 1 for relevant characteristics) and a pasture understorey dominated by annual native Mediterranean herbaceous species only, especially the grasses *Avena sterilis*, *Bromus hordeceaus* and *Gaudinia fragilis*, the legumes *Ornithopus compressus*, *Trifolium resupinatum* and *Trifolium angustifolium*, and the forbs *Stellaria media, Helianthemum guttatum and Raphanus*

raphanistrum. Prior and during the study, the sites were grazed by cattle, sheep and horses. In each

site, two adjacent plots (0.5-1 ha) differing in vegetation structure were selected: scattered *Q. ilex*

with (referred to as encroached) or without (referred to as control) a shrub understorey. A shrub

understorey (see Table 1 for relevant characteristics) had developed in the encroached plots

because of a recent (last 10-15 years) reduction in grazing pressure, led to promote early tree

recruitment. Fifteen experimental sites included a *Retama*-encroached plot and its respective

control plot, while 14 included a *Cistus*-encroached plot and its respective control plot (totalling

29 paired plots in the whole study). In each site, paired encroached and control plots were located

close to one another (i.e., less than 100 m apart), to select plots of similar soil type and slope. All

paired plots had not been cropped, fertilised, or tree-pruned during this period. Hence, plots were

arranged in a randomised complete block (i.e., site) design to determine the effect of shrub

encroachment on pasture yield ($n = 3$ for *Retama*; $n = 3$ for *Cistus*; see Table 1), annual branch

elongation of trees ($n = 15$ for *Retama*; $n = 14$ for *Cistus*), and acorn yield ($n = 10$ for *Retama*; $n = 10$ for *Cistus*).

Additionally, the effect of *Q. ilex* on pasture yield was tested in six sites (same sites used to

test the effect shrub encroachment on pasture yield), but only in their respective control plots to

avoid the confounding effects of shrub encroachment. Samples were located at three different

positions with respect to tree trunks (east side): beneath the tree canopy (ca. 2 m), in the tree

canopy periphery (ca. 5 m), and beyond the tree canopy (ca. 20 m), the latter of which was

considered to be beyond the influence of the trees (Gea-Izquierdo 2009).

2.2. Pasture yield

The herbaceous understory (referred to as pasture) was manually harvested (cut at ground level) in

early June (i.e., at the peak of green biomass) in 2007, 2008, 2009, and 2010 to determine the

effect of shrub encroachment and *Q. ilex* on pasture yield. This method permits precise estimates of annual above-ground net primary productivity and assumes that any standing dead matter or litter accumulation from previous years and in the current year is negligible (Scurlock et al. 1999). Herbaceous vegetation samples were collected in 0.5 x 0.5 m quadrats that were protected from livestock grazing by exclusion cages (1 x 1 m at the base x 0.5 m in height). Samples were dried at 65 °C for 48 h.

To test the effect of shrub encroachment on pasture yield, encroached and their respective control plots were sampled, beyond the tree canopy (ca. 20 m) to avoid confounding effects of trees. In each site, we sampled six (*Cistus* sites) or eight (*Retama* sites) quadrats per plot. In encroached plots, each protected quadrat was located in the subcanopy area of a randomly selected shrub so that the centre of the exclusion cage was approximately at 1 m from the shrub trunk. During cage installation and further pasture harvesting, shrubs remained undisturbed. To test the effect of trees on pasture yield, in each site, each position was sampled around six (in three sites) to eight (in three sites) mature and scattered trees.

2.3. Annual branch elongation of trees

Current-year tree shoot (annual branch elongation) samples were collected in early August (i.e., when shoot elongation had been completed) of 2007, 2008, and 2009 to determine the effect of shrub encroachment with *Retama* or *Cistus* on tree shoot elongation. We sampled 12 trees per site, i.e., six in each encroached plot and six in its paired control plot. In each plot, shoots were sampled from the same trees in each year. Forty shoots (10 per cardinal direction, i.e., N, S, E, W) were collected from the mid-crown of each sampled tree. Shoots were transported to the laboratory and

length of each shoot was measured with a ruler (to 1 mm). Unit shoot elongation per tree was determined using the mean of forty shoots.

2.4. Acorn yield

Acorn and lignified cupule samples were collected from mid-November to mid-December of the same three years to assess the effect of shrub encroachment with *Retama* (*n* = 10 sites) or *Cistus* (*n* = 10 sites) on mean acorn dry mass, number of acorns, and acorn yield. In each site, 20 trees were sampled, ten in the encroached plot and ten in its paired control. Beneath the crown of each sampled tree, fallen acorns and lignified cupules were collected in four randomly-positioned 0.5 x 0.5 m quadrats (each of which was located along each of the cardinal directions), and bulked into one composite sample per tree. Acorn dry mass (excluding cupules) was determined after drying sound samples at 65 °C for 48 h. Lignified cupules were counted to estimate the number of acorns per m^2 of canopy, as these are not consumed by wildlife (Cierjacks and Hensen 2004). Acorn yield (g m^{-2}) was calculated using mean acorn dry mass and number of acorns per m^2 of canopy.

2.5. Data analyses

We analysed the effect of trees on pasture yield using repeated-measures ANOVA, with two between-subject factors (site and position) and one within-subject factor (year). To meet assumptions of normality and homoscedasticity, the data were rank-transformed prior to analysis. Although rank transformation provides weak estimates of interaction terms (Conover and Iman 1981), this choice was considered more powerful than nonparametric tests for main effects within each year. The effect of shrub encroachment on pasture yield, tree shoot elongation, mean acorn

dry mass, number of acorns, and acorn yield was analysed using repeated-measures ANOVA, with two between-subject factors (site and shrub understorey presence) and one within-subject factor (year). Data were log-transformed prior to analysis to comply with ANOVA assumptions. In all post hoc analyses, we used Tukey's HSD test to separate treatment means when ANOVA showed significant effects ($p < 0.05$). All statistical analyses were performed using Statistica 7.0 (StatSoft, Inc., Tulsa, OK, USA).

Shrub encroachment effects on pasture yield and *Q. ilex* performance (shoot elongation and acorn yield) in 2007, 2008 and 2009, were expressed relative to those in the control treatments (i.e., relative yield *sensu* Fowler 1982) that were set as the reference (normalised to 1). We then plotted the results in a diagram that simplifies interpretation of treatment response magnitude, facilitates multiple year and treatment comparisons, and identifies possible mechanisms (i.e., shrub encroachment facilitation or competition) associated with observed pasture or tree responses.

3. Results

Pasture yield decreased in the vicinity of the trees (on average, 192, 169, 145 g m^{-2}, beyond, within the limits of, and beneath the tree canopy, respectively), but the pattern varied among years. In 2007 and 2008, pasture yield in the peripheral area and beyond the tree canopy was significantly higher by 25 to 79 % than that beneath the tree canopy (Fig. 2). A similar pattern was observed in 2009, but position was not statistically significant as was the case in 2010. In all years, pasture yield was significantly higher in the *Retama*-encroached plots than in their respective control plots (244 g m^{-2} vs. 166 g m^{-2}, respectively; Fig. 3a). In contrast, with one exception (i.e., in 2010), pasture yield was significantly lower in the *Cistus*-encroached plots than in their respective control plots (174 g m^{-2} vs. 212 g m^{-2}, respectively; Fig. 3b). Pasture yield was significantly lower in the

very dry year (2009) compared to the other three years, irrespective of the presence of *Q. ilex* or *Retama*, while the presence of *Cistus* mitigated among-year differences.

Quercus ilex shoot elongation in all years was significantly higher in the *Retama*-encroached plots than in their respective control plots (7.5 cm y^{-1} vs. 6.9 cm y^{-1}, respectively; Fig. 4a). Opposite results were found in the *Cistus*-encroached plots, which exhibited significant lower values with respect to their respective control plots (5.4 cm y^{-1} vs. 7.0 cm y^{-1}, respectively; Fig. 4b). Shoots grew significantly more in 2008 than in 2007 and 2009, regardless of the presence of *Retama*, while the presence of *Cistus* mitigated among-year differences.

In the three study years, mean acorn dry mass was significantly lower in *Retama*-encroached plots than in control plots (1.4 vs. 1.7 g $acorn^{-1}$, respectively; Fig. 5a). Both numbers of acorns and acorn yield were not significantly different among treatments (on average, 50 acorn m^{-2} and 71 g m^{-2}, respectively; Fig. 5c, 5e). Mean acorn dry mass, number of acorns (with one exception in 2008), and acorn yield were significantly lower on *Cistus*-encroached plots than on control plots (1.4 vs. 1.7 g $acorn^{-1}$; 62 vs. 73 acorn m^{-2}; 77 vs. 119 g m^{-2}, respectively; Fig. 5b, 5d, 5f). Mean acorn dry mass and acorn yield in 2008 were significantly lower than in 2007 and 2009, and differences among years were mostly independent of encroachment.

In all years, *Retama* encroachment induced significant facilitative effects on pasture yield and *Q. ilex* growth (Fig. 6). In contrast, *Cistus* encroachment induced significant competitive effects on pasture yield, *Q. ilex* growth, and acorn yield. In both *Retama* and *Cistus* encroachment treatments, the magnitude of the relative change in pasture yield was higher than that in tree shoot elongation and acorn yield for the three years. The magnitude of relative changes in pasture yield in the driest year (2009) was higher compared to that in 2007 and 2008, but no evident patterns were observed for tree shoot growth or acorn yield.

4. Discussion

4.1. Tree effect on pasture production

In near-intermediate and dry years (2007, 2008 and 2009), we found a competitive effect of trees

on pasture yield, with markedly lower production beneath the tree canopy than in the open areas,

although position differences for 2009 were not statistically significant. In the wet year (2010),

however, the sign of the tree-pasture interaction shifted, and increasing water availability resulted

in a neutral effect of trees on pasture production. Therefore, our data suggest that pasture yield

beneath the trees was likely governed by water availability in the dehesas that were studied. This

conjecture is supported by data from Cubera and Moreno (2007b), who performed a study in

similar semiarid dehesas during dry and wet periods (annual rainfall ranging from 318 to 604 mm).

They found that soil water content was reaching the wilting point beneath the tree canopy

compared to beyond the tree canopy, where some water remained unconsumed. As a result, lower

water availability beneath the tree canopy probably outweighed the commonly expected

facilitative effects of trees on pasture yield, which result due to moderate shade (Moreno 2008)

and soil nutrient enrichment (Gallardo et al. 2000).

4.2. Cistus ladanifer effect on tree and pasture production

Cistus induces significant negative effects on pasture yield, which confirms our hypothesis. This

yield reduction beneath the *Cistus* canopies was substantially more severe than that beneath the

tree canopies. These results suggest that pasture in our silvopastoral systems is more sensitive to

Cistus competition than *Q. ilex* competition. We believe that this behaviour reflects a higher

belowground competition potential of *Cistus* in the uppermost soil layer. This assumption is

supported by data from Rolo and Moreno (*unpublished results*), who performed a companion study on our sites, and showed that most of the pasture and *Cistus* fine roots were located in the superficial soil horizon, whereas the root profiles of *Q. ilex* were almost uniformly spread along the soil depth. The allelopathic action of *Cistus* also may have contributed to reduced pasture yield by inhibiting seed germination and radicle growth of annual herbaceous understorey (Chaves et al. 2001; Herranz et al. 2006).

We did not expect to find a negative effect of the shallow-rooted *Cistus* on the deeply rooted *Q. ilex*. In fact, we expected to find a neutral effect of *Cistus* on tree production because of rooting-niche separation that usually allows complementary use of soil resources among plants of different functional types, especially in arid and semi-arid environments (Scholes and Archer 1997). It is possible that *Cistus* and *Q. ilex* were actually not partitioning soil resources, despite obvious differences in their root profiles. For example, Midwood et al. (1998) showed in a semiarid savanna parkland that the shallow-rooted Neotropical shrub *Zanthoxylum fagara* (L.) Sarg. had stem water δ^2H and δ^{18}O values generally similar to those of the deeply rooted honey mesquite *Prosopis glandulosa* Torrey, indicating that these co-occurring woody plants were consistently using soil water from the same depths of the soil profile. The authors argued that the lack of evidence for distinct resource partitioning implies that competition for soil moisture may be the interaction prevailing among plants in woody mixed-systems. Alternatively, intense shrub competition effects on tree overstorey may result from the likely ability of the shallow-rooted shrub understorey to extract and immobilise moisture and nutrients which might otherwise percolate to deeper depths where tree roots are concentrated (Barnes and Archer 1999). This ability could have been strengthened by the relatively and typically high shrub cover in our *Cistus* plots (i.e., average of 77 %).

4.3. Retama sphaerocarpa effect on tree and pasture production

Retama encroachment facilitates growth of pasture. This behaviour was indicated by the significant increase in yield beneath compared to beyond the shrub canopy in open sites. Several studies in Mediterranean ecosystems have shown the potential of *Retama* to improve its own environment through positive feedback processes (e.g., protection from direct insolation and overheating, increases in soil organic matter, nitrogen content and mineralisation rates), thereby increasing above-ground biomass of the herbaceous understorey (e.g., Pugnaire et al. 1996; Moro et al. 1997). Likewise, Prieto et al. (2010) showed evidence that *Retama* is able to hydraulically lift and release water from deep to shallow soil layers during markedly dry periods, helping to maintain fine root activity and potentially accessing nutrients and occasional rain during drought.

Contrary to expectation, tree growth was significantly higher with than without *Retama* encroachment. This difference may be a reflection of higher soil nutrient supply in the presence of *Retama*. For example, Delgado-Baquerizo et al. (2010) found that, in semiarid grasslands, the two-year average accumulation of inorganic-N in *Retama* microsites was 5.3 times higher than that in open areas lacking *Retama*. The authors also showed that nitrate was the dominant N form under *Retama* microsites, while dissolved organic nitrogen was dominant in open areas. The latter N species could be an advantage for tree growth since nitrate is the preferential N-uptake form of trees (Pallardy 2008). However, we believe that any *Retama*-related nutritional facilitation was outweighed during the summer, when soil water deficits became more intense. This supposition was revealed by the fact that mean acorn dry mass was lower in the presence of *Retama* understorey compared to its absence. Indeed, soil water depletion in mid-summer may have a negative effect on early acorn ripening and, ultimately, on acorn yield (Carevic et al. 2010).

4.4. Pasture understorey is more responsive to shrub encroachment than tree overstorey,

especially in dry years

Our results revealed that pasture production is more responsive to shrub encroachment and year-to-year rainfall variation than is *Q. Ilex*. This finding is likely the result of a low dependence of deep-rooted *Q. ilex* and a high dependence of pasture on soil resources in the uppermost soil layer, where the most competition (*Cistus*) and facilitation (*Retama*) are expected to occur. Moreno et al. (2007), for example, did not find any significant response of *Q. ilex* growth and acorn production to soil fertilisation and irrigation. In contrast, pasture yield in fertilised open areas (i.e., 20 m from the tree trunk) was 2.3 to 2.6 times higher than that in unfertilised plots. These differences in soil resource dependence are likely epitomised by a certain degree of spatial segregation between grass and tree root systems in dehesas. This assumption is supported by results from Moreno et al. (2005), who observed that root length density of grasses was five times higher than that of trees in the first 40-cm of soil depth. The relatively low responsiveness of *Q. ilex* to shrub encroachment and year-to-year rainfall variation may also be explained by its high internal N-use efficiency and low phenotypic plasticity (Silla and Escudero 2004)

Interestingly, the importance of shrub encroachment effects on pasture yield increased in the driest year (2009). This finding is relevant in the face of climate change scenarios predicted for Mediterranean climate regions that are likely to experience more frequent and severe droughts over the next several decades (IPCC 2007). Our results suggest that, as drought pressure increases abiotic stress in Mediterranean silvopastoral systems, facilitation by *Retama* and competition with *Cistus* on pasture will become more important. The increased facilitative effect of *Retama* in the driest year may be due to increased hydraulic lift magnitude, although probably at resource costs to *Retama* (Ludwig et al. 2003; Prieto et al. 2010). The increased competitive effects of *Cistus*

under high water stress conditions are likely to occur because the level of the most limiting resource (i.e., water) is so low that the potential benefits provided by *Cistus* (e.g., reductions in temperature and light intensity) cannot overcome its own resource uptake demands (Maestre and Cortina 2004).

Conclusion

We found that sign and magnitude of shrub encroachment effects on pasture and tree production in Iberian dehesas were shrub species-specific. Our results indicate that the strong competitive effects of *Cistus* may reduce substantially the overall system forage productivity (pasture, tree browse and acorn). In contrast, we found evidence that the facilitative effects of *Retama* may increase this system's forage productivity, especially by increasing pasture yield. The importance of competition by *Cistus* and facilitation by *Retama* on pasture yield increased in the driest year. This result is consistent with the strength of plant-to-plant interactions that may modulate the responses of plant communities to climate change in dry environments (Brooker 2006; Suttle et al. 2007). The highly contrasting effects of *Cistus* and *Retama* on pasture and tree production raise important management questions. We recommend that future research be guided towards determining whether or not the management of shrub cover (e.g., promoting *Retama* understorey and clearing *Cistus*, while retaining only some patches of the latter) may aid early tree recruitment without compromising overall productivity of the system.

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Table 1. Main characteristics of the tree and shrub layers of the 29 silvopastoral sites studied in central-western Spain.

Variable analyzed	Type of site	Plot	Replications	Tree layer			Shrub layer	
				Density (tree/ha)	Canopy cover[b] (%)	DBH[c] (cm)	Canopy cover[d] (%)	Height (m)
Pasture yield (n = 6)[a]	Cistus (n = 3)	Control	6	16.3 ± 3.2	13.5 ± 1.0	42.5 ± 4.1		
		Encroached	6	26.3 ± 3.9	10.8 ± 0.2	41.5 ± 1.6	73.3 ± 8.8	2.1 ± 0.1
	Retama (n = 3)	Control	8	22.0 ± 2.9	21.4 ± 4.2	60.1 ± 9.5		
		Encroached	8	14.3 ± 2.8	19.6 ± 6.4	48.4 ± 15.1	30.0 ± 0.5	1.9 ± 0.4
Acorn yield (n = 20)	Cistus (n = 10)	Control	10	28.2 ± 4.4	17.0 ± 2.2	45.0 ± 2.4		
		Encroached	10	35.6 ± 3.2	18.8 ± 2.5	41.7 ± 3.3	75.0 ± 4.3	2.1 ± 0.1
	Retama (n = 10)	Control	10	18.8 ± 2.4	18.2 ± 3.4	48.7 ± 3.8		
		Encroached	10	18.5 ± 3.7	17.0 ± 2.7	45.0 ± 4.2	33.5 ± 3.4	1.8 ± 0.1
Shoot elongation (n = 29)	Cistus (n = 14)	Control	6	27. 9 ± 3.3	18.2 ± 2.3	44.6 ± 1.1		
		Encroached	6	35.1 ± 3.2	18.8 ± 2.2	42.0 ± 2.6	76.1 ± 3.3	2.0 ± 0.1
	Retama (n = 15)	Control	6	20.4 ± 2.3	20.3 ± 3.3	47.9 ± 2.6		
		Encroached	6	20.1 ± 3.5	21.6 ± 4.7	44.5 ± 3.1	32.3 ± 3.3	1.9 ± 0.1

[a] Number of sites (n).
[b] Cover estimated as the percentage of land cover by tree canopy.
[c] Diameter at breast height (130 cm).
[d] Cover estimated as the percentage of land cover by shrub canopy.

Figure Captions

Figure 1. Monthly average precipitation (filled bars) and air temperature (line) at the Aldehuela del Jerte station (40º00' N, 6º13'W) in central-western Spain. *O*, *J*, *A*, *Jl*, October, January, April, July.

Figure 2. Pasture yield in 2007, 2008, 2009 and 2010 as influenced by position with respect to *Quercus ilex* canopy in silvopastoral systems of central-western Spain. Vertical lines represent +1 SE ($n = 42$ per position). Probability values (p) for repeated measures ANOVA, involving Position as between-subject factor, Year as within-subject (repeated) factor, and their interaction, are summarised in the upper right corner. Within Year, means not sharing the same letter are significantly different at $p = 0.05$.

Figure 3. Pasture yield in 2007, 2008, 2009 and 2010, as influenced by (A) *Retama sphaerocarpa* and (B) *Cistus ladanifer* encroachment in silvopastoral systems of central-western Spain. Vertical lines represent +1 SE (a, $n = 18$; b, $n = 24$ per treatment). Probability values (p) for repeated measures ANOVA, involving shrub Encroachment as between-subject factor, Year as within-subject (repeated) factor, and their interaction, are summarised in the upper right corner. Within Year, means not sharing the same letter are significantly different at $p = 0.05$.

Figure 4. *Quercus ilex* shoot elongation in 2007, 2008, and 2009, as influenced by (A) *Retama sphaerocarpa* and (B) *Cistus ladanifer* encroachment in silvopastoral systems of central-western Spain. Vertical lines represent +1 SE (a, $n = 90$; b, $n = 84$ per treatment). Probability values (p) for repeated measures ANOVA, involving shrub Encroachment as between-subject factor, Year as within-subject (repeated) factor, and their interaction, are summarised in the upper right corner. Within Year, means not sharing the same letter are significantly different at $p = 0.05$.

Figure 5. Mean acorn dry mass, number of acorns per m^2 of canopy, and acorn yield per m^2 of canopy in 2007, 2008, 2009 as influenced by (A, C, E) *Retama sphaerocarpa* and (B, D, F) *Cistus ladanifer* encroachment in silvopastoral systems of central-western Spain. Vertical lines represent +1 SE ($n = 100$ per treatment). Probability values (p) for repeated measures ANOVA, involving shrub Encroachment as between-subject factor, Year as within-subject (repeated) factor, and their interaction, are summarised in the upper right corner. Within Year, means not sharing the same letter are significantly different at $p = 0.05$.

Figure 6. Interactions between shrub encroachment (*Retama sphaerocarpa* and *Cistus ladanifer*) and pasture (yield) and *Quercus ilex* (shoot elongation and acorn yield) in 2007, 2008 and 2009 in silvopastoral systems of central-western Spain. Pasture and *Quercus ilex* responses are expressed relative to the control (unencroached) plots and normalised to 1. An asterisk indicates significant differences between shrub encroachment and control; see Figures 2, 3 and 4 for repeated-measures ANOVA p-values.

Figure 1
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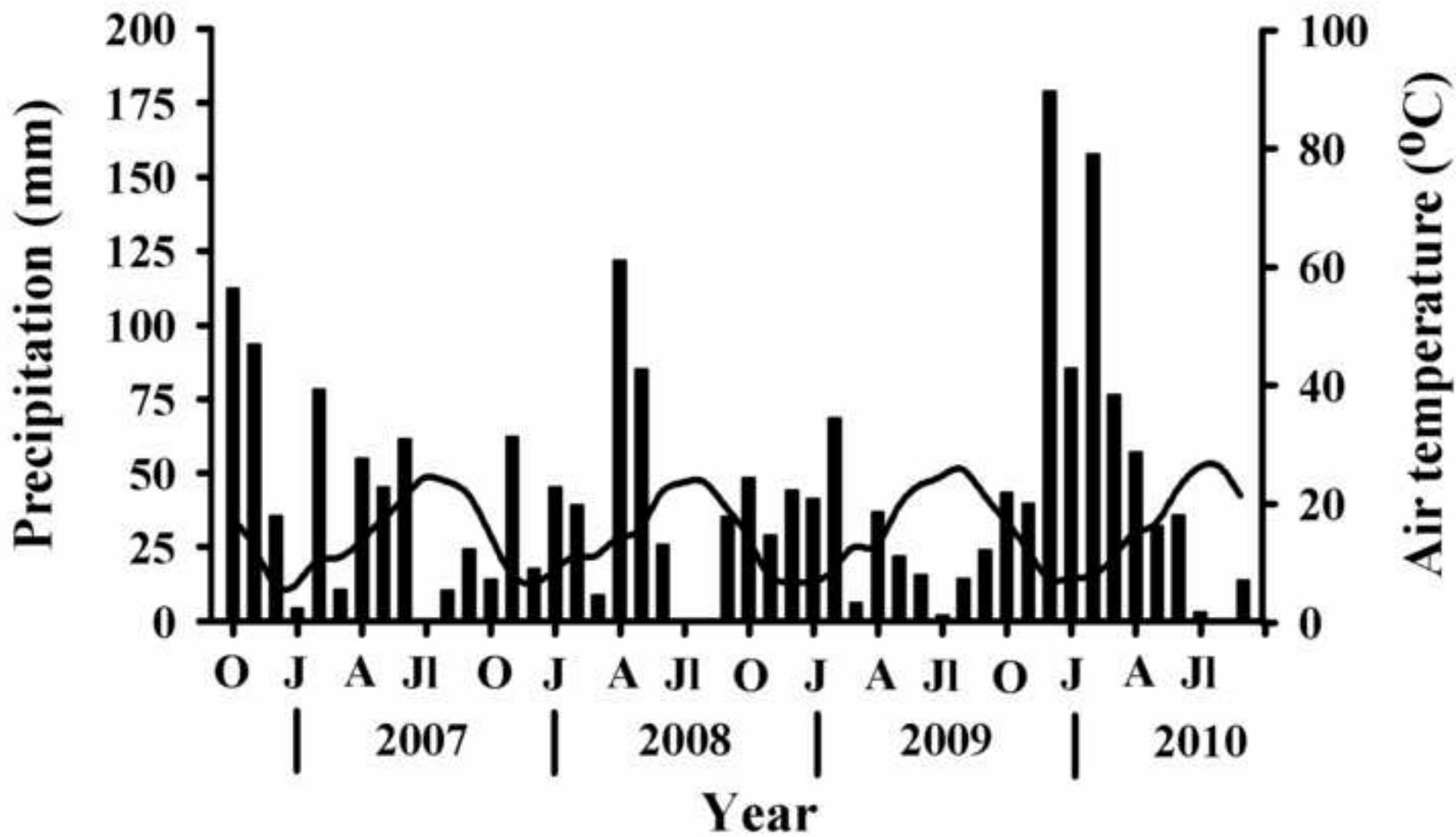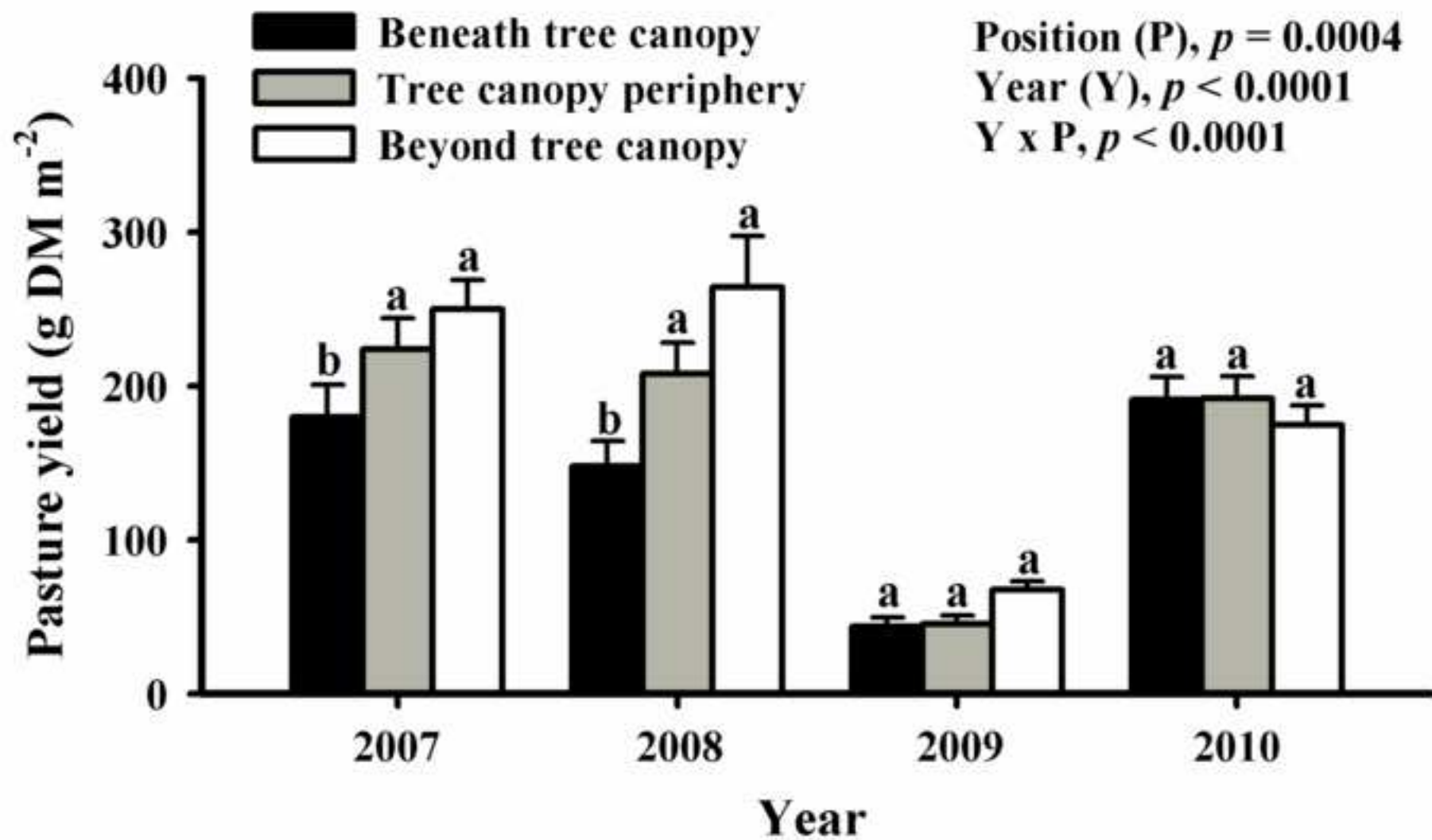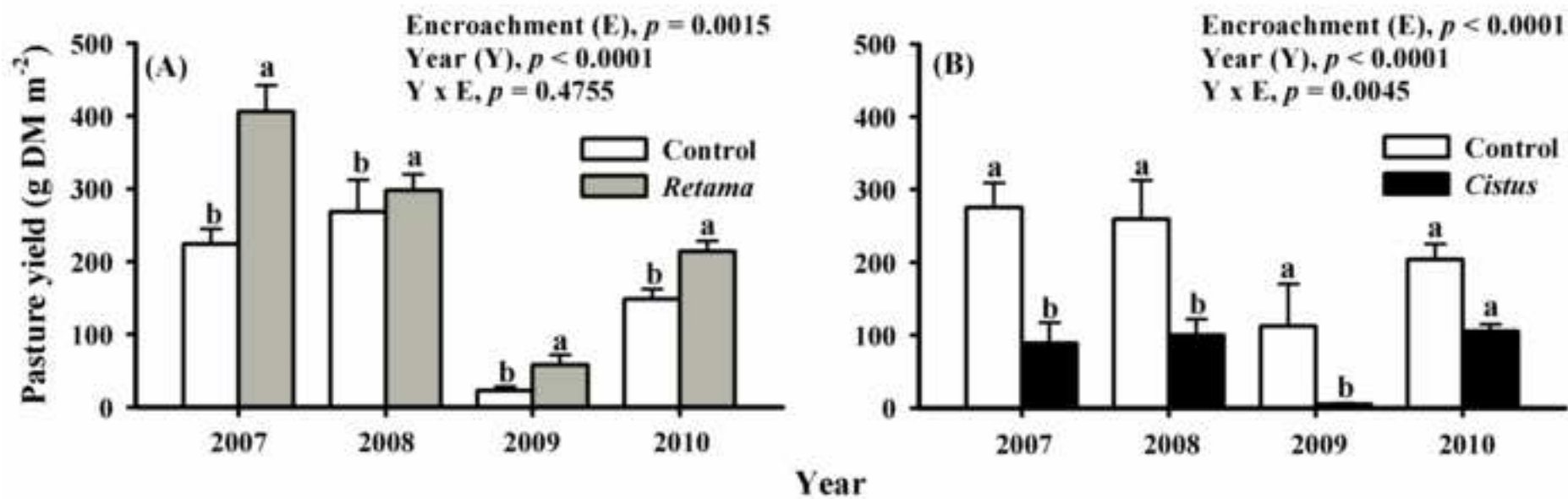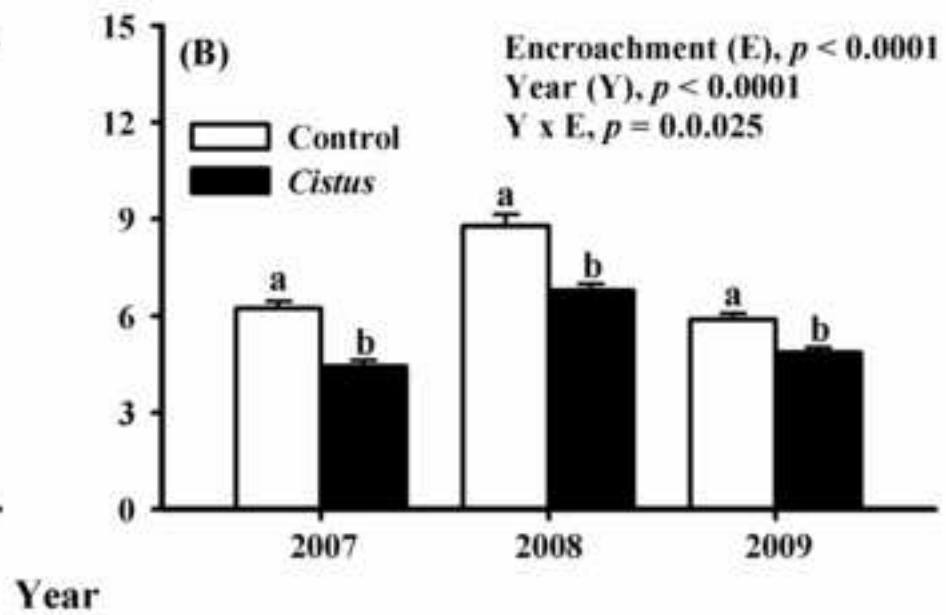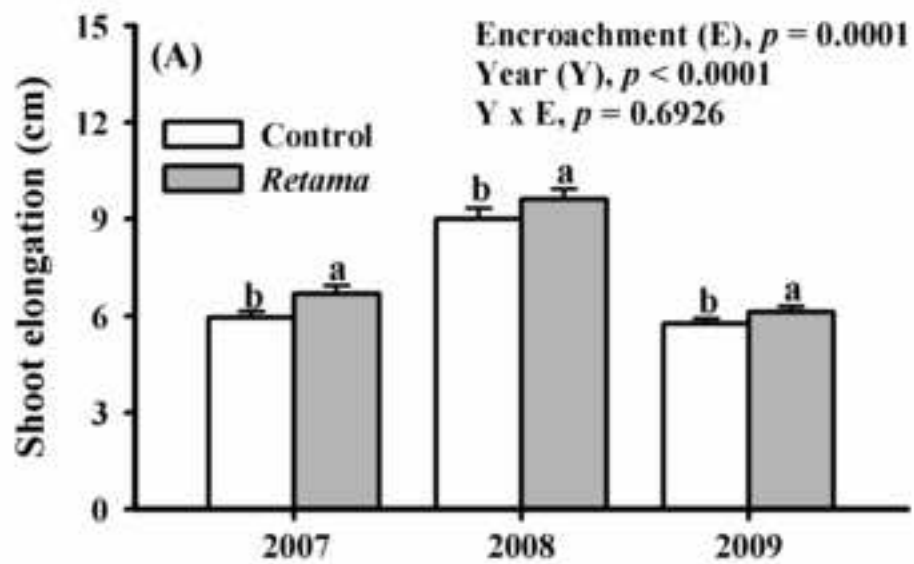
Figure 1

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Figure 5
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Figure 6