Climate Change Challenges: The Effect of Shade and Herb Competition on the Regeneration of *Quercus suber* L. and *Quercus rotundifolia* Lam.

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Resumo

A reduzida taxa de regeneração das espécies *Quercus suber* L. (sobreiro) e *Quercus rotundifolia* Lam. (azinheira) são consequência de más ou inadequadas práticas de gestão e das alterações climáticas em curso, ameaçando a sustentabilidade ecológica e económica do *Montado*. O efeito facilitador da copa de árvores e arbustos é crucial para a sobrevivência das jovens árvores, no entanto o efeito da vegetação herbácea na sobrevivência é pouco compreendido. Com o objetivo de avaliar o efeito da copa e da vegetação herbácea na dinâmica de recrutamento do sobreiro e da azinheira, foram estabelecidas, em 2003, 18 parcelas combinando diferentes condições de copa (presente, aberto) e vegetação herbácea (presente, removida). Foram periodicamente medidos a altura e o diâmetro das árvores, e calculada a taxa de crescimento para diferentes períodos. A análise de sobrevivência foi realizada usando a regressão de Cox considerando os períodos de tempo 2004-2006 e 2004-2015, entrando em linha de conta com o SPEI (*Standardized Precipitation Evapotranspiration index*). Este estudo mostra que a presença de copa de árvores e valores elevados de SPEI (i.e. anos húmidos) têm um efeito positivo na sobrevivência do sobreiro e da azinheira em fases iniciais de desenvolvimento, especialmente para o sobreiro. A copa das árvores também afetou positivamente a sobrevivência considerando o período 2004-2015, e a interação da copa com a vegetação herbácea não afetou significativamente a sobrevivência das árvores em quaisquer condições testadas. Os resultados apresentados mostram que condições sem copa e valores elevados de SPEI tiveram um efeito benéfico no crescimento (altura). A vegetação teve um efeito negativo na taxa de crescimento das árvores, particularmente nas fases iniciais de desenvolvimento, assim como valores baixos de SPEI (mais claramente para o sobreiro). Os resultados sugerem que as taxas de crescimento mais elevadas para o sobreiro predominam nas fases iniciais, enquanto a azinheira cresce a taxas mais elevadas em fases posteriores. A perpetuação deste património natural e cultural apenas será possível através da implementação de medidas de redução da taxa de mortalidade de árvores adultas e de aumento da regeneração, como, por exemplo, a gestão ativa de vegetação herbácea e promoção da sanidade de árvores adultas.

Palavras-chave: *Quercus suber*; *Quercus rotundifolia*, efeito facilitador; gestão da vegetação; SPEI.

Abstract

Low recruitment of *Quercus suber* L. (cork oak) and *Quercus rotundifolia* Lam. (holm oak) woodlands are a consequence of inadequate land-use practices and ongoing climatic changes, threatening the ecological and economical sustainability of Mediterranean ecosystems. Increasing evidence shows the critical positive role of the canopy nurse effect on seedling survival, however the role of herb vegetation in seedling establishment is seldom understood. Aiming to address the effect of canopy and herb vegetation on cork and holm oak recruitment dynamics, 18 plots were established in 2003 under different combinations of canopy cover (present, open) and herb vegetation (present, removed). Height and diameter were measured periodically, and growth rate was calculated. Survival analysis was performed using Cox Regression for 2004-2006 and 2004-2015 time periods, considering SPEI (Standardized Precipitation Evapotranspiration index). This study shows that nurse tree canopies and high SPEI values have a positive effect on cork and holm oak seedling survival ratio, especially for cork oak. Canopy also positively affected trees, considering the period 2004-2015, and canopy interaction with herb vegetation did not significantly affect tree survival in any of the conditions tested. Our results show that open conditions and high SPEI (high moisture level) had a beneficial effect on growth (height). Presence of herb vegetation had a negative effect on tree growth rate, particularly in early development stages and when SPEI values were low, and more clearly for cork oak. The results suggest that higher growth rates predominate for cork oak in early stages, while holm oak grows at a higher rate for later stages. Only by ameliorating the causes of adult mortality and improving regeneration by management practices (e.g., active management of herb vegetation, promoting healthy tree canopy) will it be possible to assure the permanence of this valuable and important part of the natural and cultural heritage.

Key words: *Quercus suber*; *Quercus rotundifolia*; nurse effect; herb management; SPEI.

Resumo alargado

O Montado é um ecossistema agrosilvopastoril caracterizado por um coberto arbóreo de baixa densidade composto por *Quercus suber* L. (sobreiro) e *Quercus rotundifolia* Lam. (azinheira). Principalmente encontrado na região do Alentejo, Portugal, o Montado apresenta elevada importância social, ecológica e económica devido à extração e comercialização da cortiça. Nas últimas décadas, tem-se observado uma redução da área de azinheira e sobreiro devido a um declínio significativo de regeneração e à perda de vitalidade e mortalidade de árvores adultas. A reduzida taxa de regeneração de sobreiro e azinheira são consequência de más ou inadequadas práticas de gestão e das alterações climáticas em curso, ameaçando a sustentabilidade ecológica e económica do Montado. A sustentabilidade dos povoamentos de sobreiro e azinheira dependem de uma taxa de recrutamento de sucesso. Para tal, a taxa de sobrevivência deve ser superior à taxa de mortalidade. O efeito facilitador da copa de árvores e arbustos é crucial para a sobrevivência das jovens árvores, no entanto o efeito da vegetação herbácea na sobrevivência é pouco compreendido. A humidade do solo e temperatura são fatores críticos para a sobrevivência durante a fase de estabelecimento, e a intensidade da radiação tem influência no crescimento. O efeito facilitador da regeneração é o equilíbrio entre interações negativas (competição) e positivas (facilitação), sendo que a facilitação domina em níveis intermédios de stress, e a competição prevalece em condições de stress severo. Na ausência de copa, a mortalidade é superior na presença de vegetação. Com o objetivo de avaliar o efeito da copa e da vegetação herbácea na dinâmica de recrutamento do sobreiro e da azinheira, realizaram-se ensaios de regeneração na Tapada Real de Vila Viçosa, localizada no sudeste de Portugal. A área é explorada para extração de cortiça e caça desportiva. A área de sobreiro e azinheira apresenta uma densidade baixa, de 30 a 80 árvores por hectare, e um sub-coberto composto, essencialmente, por *Cistus ladanifer*. O clima é tipicamente mediterrânico com verões quentes e invernos frios e húmidos. Foram estabelecidas, em 2003, 18 parcelas combinando diferentes condições de copa (presente, aberto) e vegetação herbácea (presente, removida). A altura e o diâmetro das árvores foram medidas quase mensalmente de Abril de 2004 a Junho de 2005, uma vez a cada 2-4 meses até Julho de 2006, e uma vez nos anos 2008, 2009 e 2015. A taxa de crescimento foi calculada para diferentes períodos e, sempre que possível, o cálculo teve em consideração momentos equivalentes do ano. A análise de sobrevivência foi realizada usando a regressão de Cox considerando os períodos 2004-2006 e 2004-2015, entrando em linha de conta com o SPEI (*Standardized Precipitation Evapotranspiration index*). A análise do crescimento foi realizada considerando os períodos 2004-2006 e 2008-2009 em que anos adjacentes foram agrupados para simplificar a análise dos resultados, calculando a altura e

diâmetro médio em cada data de medição. Esta análise permite abordar simultaneamente a prevalência da competição herbácea (2004-2006) e a presença de copa (2008-2009). A caracterização climática mostra que o SPEI anual mais baixo foi registado em 2005 (-1,98) e foi o mais baixo alguma vez observado em Vila Viçosa, o SPEI verão mais elevado foi registado em 2007 (0,68) e o mais baixo em 2003 (-1,97), e o SPEI primavera mais elevado foi registado em 2013 (1,39) e o mais baixo em 2009 (-1,78). Este estudo mostra que a presença de copa de árvores e valores elevados de SPEI (i.e. anos húmidos) têm um efeito positivo na sobrevivência do sobreiro e da azinheira em fases iniciais de desenvolvimento (2004-2006), especialmente para o sobreiro, uma vez que a importância relativa facilitação-competição em condições de stress climático é mais importante para plântulas do que para árvores jovens. A copa das árvores também afetou positivamente a sobrevivência considerando o período 2004-2015 uma vez que a sobrevivência das plântulas sob copa é superior devido à diminuição do stress térmico e hídrico. Este benefício é mais evidente no caso do sobreiro devido a uma maior vulnerabilidade à seca. Registou-se, ainda, que a interação entre copa e vegetação não afetou significativamente a sobrevivência em quaisquer condições testadas, e valores baixos de SPEI estão associados a reduções significativas de sobrevivência. Apesar de a interação da copa com a vegetação herbácea não ter afetado significativamente a sobrevivência das árvores, os resultados apresentados mostram que condições sem copa e valores elevados de SPEI tiveram um efeito benéfico no crescimento (altura), uma vez que elevados índices de radiação permitem um maior crescimento das árvores estabelecidas e a progressão para estados de desenvolvimento superiores. A característica heliófila do sobreiro resultou numa altura superior à altura da azinheira em estados iniciais de desenvolvimento e fora de copa, e a altura final da azinheira (2015) foi superior sob copa e na ausência de vegetação devido a uma maior tolerância à sombra. O crescimento dos sobreiros e azinheiras aumentou de 2005 para 2006 devido a uma combinação de efeitos limitadores de crescimento de 2005 (baixo SPEI) e elevados valores de SPEI anual e de verão em 2006. A vegetação teve um efeito negativo na taxa relativa de crescimento das árvores, particularmente nas fases iniciais de desenvolvimento, assim como valores baixos de SPEI. Este efeito foi mais evidente para o sobreiro devido à competição por água e luz. Os resultados sugerem que as taxas de crescimento mais elevadas para o sobreiro predominam nas fases iniciais, enquanto a azinheira cresce a taxas mais elevadas em fases posteriores. Observaram-se taxas relativas de crescimento superiores para Julho de 2006 comparando com Junho de 2005, efeito observado para as duas espécies, possivelmente explicado por elevados valores de SPEI de verão. A copa das árvores tem um efeito facilitador na sobrevivência do sobreiro e da azinheira em fases iniciais de desenvolvimento, pelo que se torna importante distinguir os diferentes estados de crescimento, o que pode justificar uma alteração na gestão. O recrutamento poderá ser aumentado através da gestão ativa de espécies competitivas (e.g. *Cistus ladanifer*) e de árvores e arbustos facilitadores (e.g. *Retama sphaerocarpa*). Os resultados sugerem que SPEI tem um efeito superior sobre o sobreiro em estados inicias de desenvolvimento. Torna-se, por isso, necessário adotar uma gestão diferenciada de modificação espacial e temporal das intervenções silvícolas considerando o efeito do SPEI sobre o sobreiro em estados inicias de desenvolvimento. Gestão através do melhoramento genético e produção de sementes de qualidade são medidas complementares a considerar. Compreender os fatores bióticos e abióticos, ambientais e de gestão envolvidos no declínio do montado é a chave para formular e executar opções de gestão sustentável. Tradicionalmente, a manipulação de plantas como medida de restauro de ecossistemas tem-se concentrado essencialmente na redução da competição por remoção da vegetação existente. No entanto, o crescente reconhecimento do efeito da facilitação levou à implementação de melhores práticas de conservação da vegetação envolvente. A perpetuação deste património natural e cultural apenas será possível através da implementação de medidas de redução da taxa de mortalidade de árvores adultas e de aumento da regeneração. O futuro do montado irá depender da vontade e da capacidade de tomar medidas concertadas de gestão e de implementar programas de restauro. É neste contexto que se devem tomar as decisões de gestão, combinando práticas que melhoram as condições do solo e promovem a mitigação dos constrangimentos de recrutamento como, por exemplo, a gestão ativa de vegetação herbácea e promoção da sanidade de árvores adultas.

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Introduction

Montado is a Mediterranean agro-silvopastoral type ecosystem characterized by a sparse tree cover of *Quercus suber* L. (cork oak) and/or *Quercus rotundifolia* Lam. (holm oak), and understory vegetation ranging from shrub formations to grasslands.

Cork oak is a strictly Mediterranean evergreen species, of high economic, social, and ecological importance in Portugal (Oliveira and Costa, 2012). Cork, its main product, is a highly valuable non-timber forest product, periodically removed from the main trunk and branches throughout the cork oak tree's lifetime. Cork and holm oak are evergreen oaks that constitute keystone species for biodiversity and ecosystem services in western Mediterranean countries.

Man-made *Montado* ecosystems require active management and use to ensure their continued existence. Cork and holm oak agro-silvopastoral ecosystems are mainly found in the province of Alentejo, on flat terrain, and tree density is typically low (40 to 80 trees/ha), often determined according to the need for pasture or crop space (Costa et al., 2010).

Loss of tree vitality and mortality, strong regeneration decline and a decrease in the density of mature trees has been observed in Mediterranean evergreen oak forests in the last decades (Plieninger et al., 2010; Aubard et al., 2019). Disturbances such as wildfires, drought and intensive or inadequate human management act together to affect natural regeneration, seedling establishment and tree recruitment (Catry et al., 2010), and can contribute to the development of new forest plagues and diseases and increased pest attack (Bergot et al., 2004; Nunes et al., 2019; Huang et al., 2020). Degraded and dry sites frequently result in persistent patches commonly colonized by monospecific stands of pioneer shrubs (e.g., *Cistus* spp.) (Acácio and Holmgren, 2014), reducing biodiversity and leading to decreased ecosystem services provision (Bugalho et al., 2011).

In the Mediterranean climate regions, lack of economic incentives to management is leading to land abandonment, biodiversity losses, and degradation of ecosystem services (Acácio and Holmgren, 2014; Bugalho et al., 2016). Additionally, climate projections for the Mediterranean basin foresee warmer and drier springs, an increase in the length and severity of seasonal summer drought, with more frequent and intensive extreme events, such as heat waves, severe droughts, and wildfires (Giorgi and Lionello, 2008; Perkins-Kirkpatrick and Gibson, 2017). Extreme climate events will have a more pronounced influence on ecosystems than gradual shifts of mean temperature and precipitation (Jentsch and Beierkuhnlein, 2008; Acácio et al. 2009, 2017).

Montado has shown in the last decades, a trend of decreasing cover (Aubard et al., 2019), which indicates that cork and holm oak woodlands in southwestern Portugal will face high challenges in a global warming scenario (Costa et al., 2016; Parente et al., 2019). Recent modeling studies predict that up to 40% of current environmentally suitable areas for cork oak may be lost by 2070, mainly in northern Africa and southern Iberian Peninsula, and almost 90% of new cork oak stands are predicted to lose suitability by the end of the century (Correia et al., 2018).

Cork oak and holm oak mortality is consistently associated with water-stressed sites. Studies highlight cork oak's sensitivity to the amount and timing of late spring precipitation, since drought before early summer increases the risk of xylem embolism at the peak of the drought period (Besson et al., 2014). Also, long term experimental drought reduced holm oak stem growth by 17.5% and increased stem mortality rates by 42.3% (Barbeta et al., 2013). This can be critical as future climate scenarios predict a reduction of spring and summer precipitation (−20 to −40%, depending on the climate change scenarios) (Giorgi and Lionello, 2008) and greater concentration of temperature and precipitation anomalies during spring and early summer months are expected (Nunes et al., 2019).

Adaptive management is a key strategy to mitigate impacts of climate change considering future climate scenarios of increasing temperatures, reduced precipitation, and decreased productivity (Palma et al., 2015). Future climatic scenarios call for a differential type of conservation planning of cork oak/holm oak by anticipating future conditions, considering local settings and human disturbances. Unless such actions are undertaken in the short-term, the *Montado* systems will not be sustainable (Acácio and Holmgren, 2014).

State-of-the-art

Biotic and abiotic factors affecting tree recruitment

The structure and age of cork and holm oak stands are very important for their regeneration. The ongoing change in climate is decreasing the success of the regeneration of oak trees primarily through limitations in acorn dispersal and seedling germination and survival (Gómez-Aparicio et al. 2008; Simões et al., 2016). A hampered transition from seedling to adult (Matías et al., 2019) leads to the aging of the stands and threatens the future of *Montado* ecosystems. The sustainability of cork and holm oak stands depends on a successful recruitment rate, that is, a survival rate of young plants higher than adult tree mortality rate (Costa and Pereira, 2007; Acácio and Holmgren, 2014; Garcia-Fayos et al., 2020).

Although cork oak and holm oak can grow in similar Mediterranean conditions, the two species have different ecological features in terms of needs and tolerance to drought stress. The heliophilous cork oak has a higher growth capacity when not limited by water, dominating the landscape on wetter soils. The shade tolerant holm oak prevails in drier and mesophilous sites.

While soil moisture and temperature are critical factors determining survival during the establishment phase, light, which influences growth rate (along with soil moisture), may become more important in later plant life stages (Puerta-Pinero et al., 2007; Caldeira et al., 2014). Most studies that have focused on the positive effects on regeneration by trees and shrubs (i.e., canopy nurse effect) suggest that this results from ameliorating stress conditions such as reducing maximum temperatures (Gomez and Valladares, 2007) and increasing water availability (Cuesta et al., 2010; Leiva et al., 2013), especially during the establishment phase (Caldeira et al., 2014).

High temperatures can directly inflict physiological damages to seedlings (e.g., denature of proteins), but also increase the need of seedlings to dissipate heat energy through transpiration (Kolb and Robberecht, 2006; Caldeira et al., 2014). Recruitment occurs in full sun only when annual precipitation is high, but as precipitation decreases, seedlings need shade to compensate for evapotranspiration demand, until reaching a lower limit of annual precipitation (Garcia-Fayos et al., 2020).

In some studies, seedling growth was positively associated with increasing soil moisture and light (Caldeira et al., 2014), while in other studies maximal growth was found at intermediate irradiance (Puerta-Pinero et al., 2007). Plant light requirement is affected by stress factors like drought, flooding, nutrient availability, or herbivory (Gómez-Aparicio et al., 2006; Pinto et al., 2011). Thus, minimum light availability tolerated by any given species can vary in different ecosystems or experimental conditions (Valladares and Niinemets, 2008), affecting facilitative and competitive plant–plant and plant–animal interactions in a complex and dynamic manner (Valladares et al., 2016). In the absence of canopy openings, low light levels may not allow the established oaks (particularly holm oak) to grow and progress to higher developmental stages (Martín-Alcón et al., 2015).

Increasing tree mortality in forests is attributed to the combined effects of climate change, inappropriate management practices and proliferation of pests and diseases (Choat et al., 2012). Transitions from cork and holm oak woodlands to savannas and shrublands are triggered by both ecological (e.g., climatic extremes (Moreno et al., 2019; Andrade and Contente, 2020), wildfire frequency (Acácio and Holmgren, 2014)) and land use mechanisms (e.g., population decline (Acácio et al., 2017)) that act together to affect natural regeneration, seedling establishment and tree recruitment (Ogaya et al., 2020). Degraded and dry sites often have persistent patches colonized by monospecific layers of pioneer *Cistus* spp. shrubs (Acácio and Holmgren, 2014), consequently reducing biodiversity and leading to the degradation of ecosystem services (Bugalho et al., 2011). Moreover, drought reduces trees' ability to produce sap, which protects them from destructive insects and disease, contributing to the development of new forest plagues and diseases (Huang et al., 2020).

Decreased economic income related to global market devaluation of cork and low economic value of holm oak forests is leading to land abandonment, biodiversity loss, and degradation of ecosystem services (Acácio and Holmgren, 2014; Acácio et al., 2017; Bugalho et al., 2016). Management plans promoting maintenance of a healthy adult tree canopy cover may be critical to assure regeneration of the Mediterranean evergreen oak woodlands. Also, using pioneer species, such as pines, may promote *Quercus spp.* seedling establishment in areas without mature tree canopies. For example, in Portuguese cork woodlands, *Pinus pinea* L. has been successfully used as a nurse species (Vallauri, Aronson and Barbero 2002; Gomez-Aparicio et al., 2009). However, extreme summer droughts can prevent the success of any silvicultural practice (Gómez Aparicio et al., 2008; Rodríguez-Calcerrada et al., 2010; Caldeira et al., 2014).

Positive and negative interactions

Improved understanding of facilitation and competition processes has direct relevance for the development of tools for ecosystem restoration, and for improving our understanding of how plant species and communities respond to environmental changes.

Facilitation may be direct or indirect: one species may directly beneficiate other species by ameliorating abiotic conditions (Caldeira et al., 2014), and a third species may indirectly increase the performance of the target species by mediating interactions between the nurse and the target species (Cuesta et al., 2010). Amelioration of extreme temperatures, protection from herbivores, and increasing nutrient availability (Cuesta et al., 2010; Caldeira et al., 2014) are some examples of direct facilitation. On the other hand, plants may directly modify the environment of other plants by competing for resources like water or light (Caldeira et al., 2014).

The net facilitation effect on regeneration by tree and shrub cover is the balance between negative (competition) and positive (facilitation) interactions on plant communities through interactions between abiotic (e.g., soils, weather) conditions and biotic (e.g., herb biomass) factors (Acácio and Holmgren, 2014; Caldeira et al., 2014), with facilitation dominating at intermediate levels of environmental stress and competition prevailing under stressful conditions (Rolo et al., 2013; Caldeira et al., 2014). Other factors such as seedling-specific traits (e.g., seedling size) can also affect the outcome of the balance between negative and positive interactions. The presence of nurse shrubs and trees and active management of herbs (e.g. mowing, controlled grazing) can facilitate the natural establishment of cork and holm oak (Gómez-Aparicio, 2005, 2009; Caldeira et al., 2014; Vaz et al., 2019), especially in clearing areas or in very sparse stands where there is a greater negative effect of air and soil dryness during the summer (Smit et al., 2008; Caldeira et al., 2014), while offering physical protection from animal predation (Gómez et al., 2008; Leiva et al., 2013).

Nurse canopies have a positive effect on cork and holm oak seedling survival at low range of soil moisture levels (below 15%) by indirectly reducing herb competition for water and light (Cuesta et al., 2010; Caldeira et al., 2014). Even without water limitation, survival of cork oak and holm oak seedlings are higher in the shade, probably due to decreased thermal and water stress during the typical Mediterranean summer drought (Gómez-Aparicio et al., 2008; Acácio and Holmgren, 2014; Caldeira et al., 2014). Several studies in open oak woodlands showed that canopy cover decreases soil moisture during winter and early spring but has no effect on soil moisture during late spring and summer when environmental conditions are critical for seedling survival (Quilchano et al., 2008; Cuesta et al., 2010; Caldeira et al., 2014).

The facilitating effect of the shrubs depends on the edaphic-climatic conditions and is species-specific, as some shrubs species may compete with young plants for environmental resources such as water or light (Acácio et al., 2007, Pausas et al., 2006, Pérez-Devesa et al., 2008). Several studies point to a negative effect on the survival of cork oaks by xerophytic shrub species such as *Cistus ladanifer* (Acácio et al., 2007; Pausas et al., 2006). On the other hand, Rolo et al. (2013) showed a beneficial effect of the shrub *Retama sphaerocarpa* on early development stages of holm oak, and other studies refer to the facilitating effect of *Genista hirsuta* on holm oak (Smit et al., 2008) and *Erica arborea* on cork oak (Pérez-Devesa et al., 2008).

The indirect facilitative effects of nurse canopies on seedlings result from their interaction with herb vegetation, which are highly competitive for water in Mediterranean ecosystems (Rey Benayas et al., 2002, 2005; Cuesta et al., 2010), and from nitrogen fixation, in the case of nitrogen-fixing shrubs (Rolo et al., 2013). Seedling mortality under trees or shrubs is less affected by herb vegetation whereas in gaps it is significantly higher in presence of herb vegetation (Cuesta et al., 2010, Caldeira et al., 2014; Gavinet et al., 2016). Even if seedlings benefited directly from high soil water availability in wet years, higher soil water availability may not be sufficient to overcome increased competition from the herb layer, resulting in net negative effects on seedling survival (Caldeira et al., 2014).

The relative importance of facilitation and competition in ecosystems stressed by climate and herbivores depends on its life stage (Callaway and Walker, 1997), and this association is stronger for saplings than for juveniles. Indeed, cork and holm oak are known to have a relative tolerance to shading in early development stages. Shading provided by some species of shrubs (e.g., *Retama sphaerocarpa*) or artificial structures, have a beneficial effect on cork and holm oak seedlings (Smit et al., 2008; Alias et al., 2010; Rolo et al., 2013). Allowing the growth of certain species of shrubs should be considered whenever possible in the management of cork and holm oak stands, especially in the early stages of recruitment. However, a shrub layer can increase the risk of fire and competition for water and light, which should be considered on a case-by-case basis. For this reason, it is important to distinguish different stages of growth, namely the transition from young plants to young trees, which could justify a change in management.

Objectives

In this study, we aimed to understand the effect of canopy nurse trees and herb vegetation on the recruitment dynamics of cork oak and holm oak, as well as to determine the effects of drought periods on tree survival and growth. We used a 12-year field experiment to test these effects.

Material and Methods

Study area

The study took place at Tapada Real de Vila Viçosa (38°47′N, 7°22′W), a 900-ha estate in south-east Portugal. The study area is privately owned by Fundação da Casa de Bragança. The area is dominantly covered by cork and holm oak, exploited for cork, and primarily managed for deer hunting (e.g., food-supplementation, selective culling).

The evergreen cork and holm oak woodland is relatively open (30 to 80 trees per ha), with an almost mono-specific understory of the shrub *Cistus ladanifer* interspersed with annual herbaceous species that set seed and die in late spring (Bugalho et al., 2011). The site is browsed by herbivore ungulates, red deer (*Cervus elaphus*), fallow deer (*Dama dama*), and wild boars (*Sus scrofa, L.*).

The local climate is typically Mediterranean, characterized by hot, dry summers and cool, wet winters. Mean annual precipitation is mostly distributed between October and April. Mean annual temperature reaches its lowest value in January (3.4 °C) and the highest values are typically registered in August (32.7 °C). Soils are poorly developed haplic leptosols (WRB, 2006) with dominant bedrock of schist (Caldeira et al., 2014).

Experimental design

Plots were established in five homogeneous fenced areas (blocks) of a mixed cork oak and holm oak savannah-type ecosystem. The field experiment was held within five 25 m × 25 m (625 m^2) fenced areas established in previous studies (Bugalho et al., 2011; Caldeira et al., 2014). There were 3–4 cork oak and 3–5 holm oak trees in each fenced area. These fenced areas were established in homogeneous areas with similar slopes (4.6° ± 0.5° SE) at NW-SE orientations. Distance between fenced areas was 250–400 m (Lecomte et al., 2019). Fences were 2.20 m heigh to exclude large herbivores (red deer, fallow deer, and wild boar) and thus facilitating tree regeneration.

Eighteen paired plots (2 m x 4 m) were established (Figure 1), ten beneath the canopy of mature *Quercus spp.* trees and eight in open grassland areas. To establish an herb presence treatment (present, removed), each plot was halved into two subplots (2 m × 2 m), in one of which the herb vegetation was removed by hand thrice a year. Owing to space constraints, the number of plots was not the same in all fences.

Figure 1 - Paired subplots with and without herbaceous vegetation under the canopy of mature trees (left) and in open areas (right). Photos by MC Caldeira.

Acorns were collected in the study area from at least five different cork and holm oak trees. Cork and holm oak acorns were germinated in a greenhouse until the radicles were 0.5 cm long. In mid-November of 2003, 36 acorns of each species were sowed per subplot interspersing pre-germinated acorns of the two species (totaling 1296 acorns) in lines. Acorns were buried 2 cm deep into the soil and 30 cm apart in field experimental plots.

Cork and holm oak acorns weighed, on average, 3.5 g ± 0.9 and 2.8 g ± 0.8, respectively. Different seed sizes may have different impacts on growth (Urbieta et al., 2008). However, this effect was excluded by initially choosing acorns of similar size.

The 1296 planted seedlings were tagged and monitored thereafter. The experiment extended to 2015 with aperiodic seedling monitoring.

Measurements

Total height (length of main stem) and crossed stem diameters (2 cm above-ground) of seedlings were measured 21 times from April 2004 to December 2015: nearly monthly from April 2004 to June 2005, every 2–4 months until July 2006 and once in the years 2008, 2009 and 2015.

Daily relative growth rates were calculated for 2015 living trees by the quotient of the Napierian logarithm (ln) of the difference between final (H_t) and initial (H_0) plant total height by the number of days of growth (t) (Eq. 1). Whenever possible, the relative growth rate calculation was performed considering equivalent moments of the year (e.g., April 2004 and April 2005).

(*Eq. 1*) $RGR = ln(H_t - H_o)/t$

Daily relative growth rates were analyzed to account for different periods between measurements, assuming that the growth was linear in the period between measurements. Thus, possible differences in growth between consecutive years originated, for example, by annual variations in climate, are not considered. It was decided to accept the annual linear growth for the period between measurements, since the trees are in a regeneration phase, where the growth curve is translated into a linear phase.

Data analysis

Tree growth (height and diameter) was analyzed considering two different time periods of death: (1) trees that died in the first three years (2004, 2005 or 2006) and (2) trees that died in the fifth and sixth years of the experiment (2008 or 2009). Adjacent years were grouped to simplify the analysis of the results and allowed to simultaneously address the prevalence of herb competition (first three years) and the canopy/open treatments (fifth and sixth years). Trees that died within the same period were grouped, and in each measurement date the average height and diameter was calculated. Tree growth during the two different periods were compared to mean values of the living trees by 2015, for each experimental condition and species.

Early in the experiment, seedlings that experienced above-ground tissue mortality but resprouted within a 384-day period were recorded. Seedlings that did not resprout for 384 days by the end of the experiment were assumed to be dead. This cutoff was defined as only 5% of observed resprouting events occurred after 384 days.

Statistical analyses of survival analysis were conducted using the SPSS® software package (IBM Corp. Released 2019. IBM SPSS Statistics for Windows, Version 26.0. Armonk, NY: IBM Corp). Survival analysis was performed with Cox Regression using two different approaches: the first considering the data related to the first three years of the experiment (2004 and 2006) to assess how tree canopy cover and removal of herbs affected trees survival early in the experiment, and the second considering the total trial period (2004 to 2015) to assess the effect of the different treatments on tree's survival 12 years later.

The Standardized Precipitation Evapotranspiration index (SPEI) was used to characterize the study years. SPEI represents a simple climatic water balance index that has been formulated based on precipitation and PET - Potential Evapotranspiration (Vicente-Serrano and Beguería, 2016).

Each survival analysis was performed separately for the two species, using the *Enter* method, and for two different periods using May of 2004 as the time of greater germination: (1) considering the measurements of September of 2004 (310 days), January of 2005 (415 days), September of 2005 (675 days) and January of 2006 (781 days), using canopy (categorical), vegetation (categorical), the interaction between canopy and vegetation, the initial height (measured in April of 2004) and SPEI as covariates, and (2) considering all the measures between 2004 and 2015, using canopy (categorical), vegetation (categorical), the interaction between canopy and vegetation, and the initial height as covariates. The SPEI of the period of 12 months before allows the evaluation of the accumulated effect of previous spring and summer climatic conditions on the tree's survival, as direct physiological damages induced on seedlings by drought periods may lead to tree death only detected some months later.

Results

Climatic characterization

Mean annual precipitation during the 2003-2015 period was 524 mm, ranging from 300 mm in 2015 to 777 mm in 2010 (Figure 2), and mostly distributed between October and April. Mean annual temperature between 2003 and 2015 was 15.0 °C, ranging from 13.7 °C (2008) to 16.6 °C (2015) (Figure 2). The highest value of average daily maximum temperature was 32.7 °C (in August) and the lowest was 3.4 °C (in January) (Mitra - www.cge.uevora.pt).

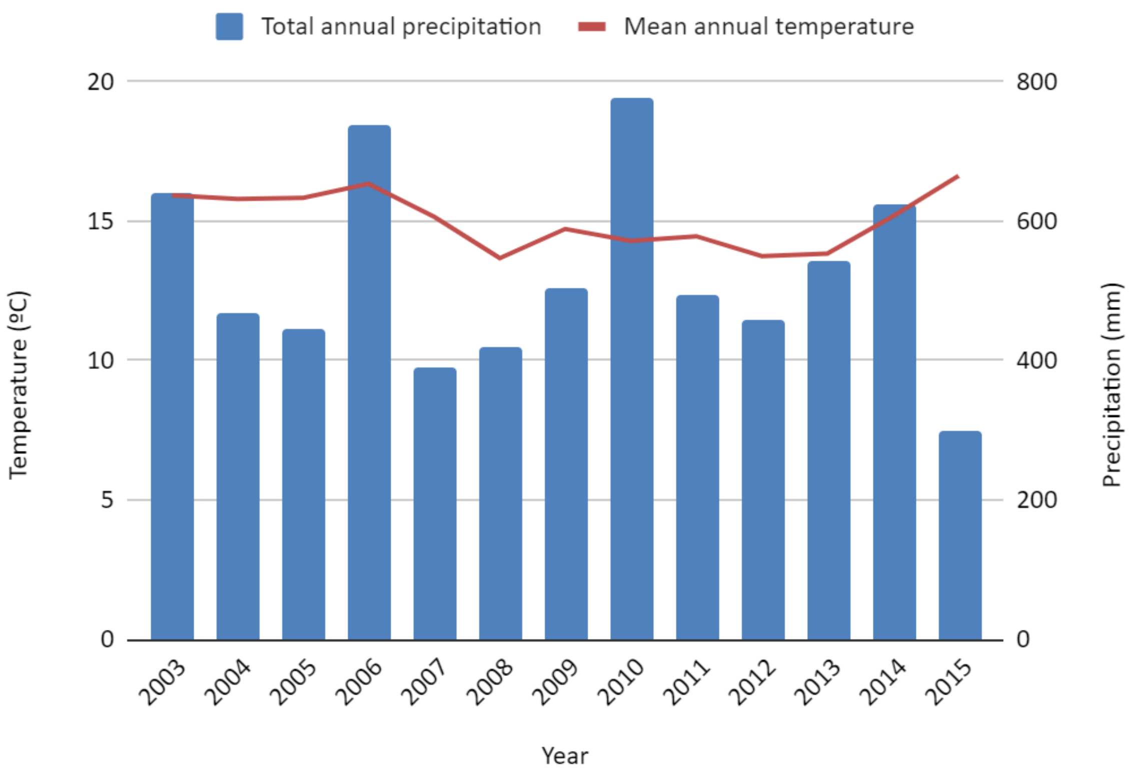


Figure 2 - Mean annual temperature (ºC) and total annual precipitation (mm) during the 2003-2015 period.

The average annual SPEI in Vila Viçosa decreased from -0.05 in the period 1971-2000 to -0.58 during the period 2001-2015. Specifically, during the experiment (2003-2015), annual SPEI ranged from 0.68 in 2014 to -1.98 in 2005, spring SPEI from 1.39 in 2013 to -1.78 in 2009, and summer SPEI from 0.68 in 2007 to -1.97 in 2003 (Figure 3) (SPEI Database - www.spei.csic.es/database.html).

Following Isbell et al (2015), years can be classified as extremely dry (when SPEI is lower than -1.28), moderately dry (from -1.28 to -0.67), normal (from -0.67 to 0.67), moderately wet (from 0.67 to 1.28), and extremely wet (higher than 1.28). According to this classification, a few important results are listed below:

- 2004, 2005, 2007 and 2015 were extremely dry years.
- 2008, 2009 and 2012 were moderately dry years.
- 2003, 2006, 2010, 2011 and 2013 were normal years.
- 2014 was the only wet year (moderate).
- The lowest annual SPEI (-1.98) was observed in 2005 and was the lowest value ever recorded in Vila Viçosa.
- The highest summer SPEI was in 2007 (0.68) and the lowest was in 2003 (-1.97).
- The highest spring SPEI was in 2013 (1.39) and the lowest was in 2009 (-1.78).

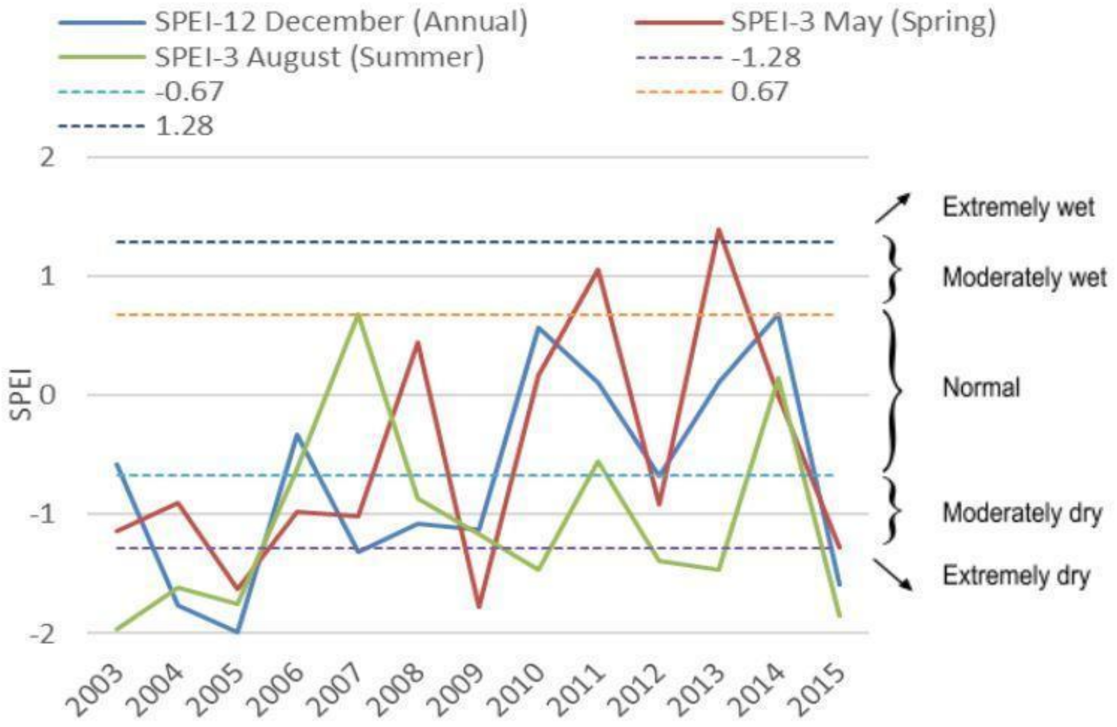


Figure 3 - SPEI-12 of December (annual), SPEI-3 of May (spring) and SPEI-3 of August (summer) for the period 2003-2015, and SPEI thresholds (< -1.28 - extremely dry; -1.28 to -0.67 - moderately dry; -0.67 to 0.67 - normal; 0.67 to 1.28 - moderately wet; > 1.28 - extremely wet (Isbell et al., 2015)).

Survival

For the first three years of seedling establishment (2004-2006), vegetation had a non-significant effect on cork oak survival ($p = 0.733$) and on holm oak survival ($p = 0.346$) (Table 1, Figure 4. a, c). Canopy had a significant positive effect on cork oak survival ($b = 0.480$, $p = 0.005$) and had a non-significant effect on holm oak survival ($p = 0.138$) (Table 1, Figure 4. b, d). Indeed, cork oak seedlings under the canopy were almost two-fold less likely to die than seedlings in the open (HR = 1.616). By January 2006, survival of cork oak under the canopy was ≈ 40%, whereas in the open survival was only ≈ 27%. Holm oak seedlings that were initially taller had an almost nearly significant lower survival probability ($b = -0.042$, $p = 0.088$) (Table 1). Higher annual SPEI values had a significant positive effect on cork oak ($b = 4.056$, $p < 0.001$) and holm oak survival ($b = 4.179$, $p < 0.001$) (Table 1). Survival decreased sharply between January 2004 (day 414) and September 2005 (day 675). For both species and all experimental conditions, survival decreased by 42-52% during that period.

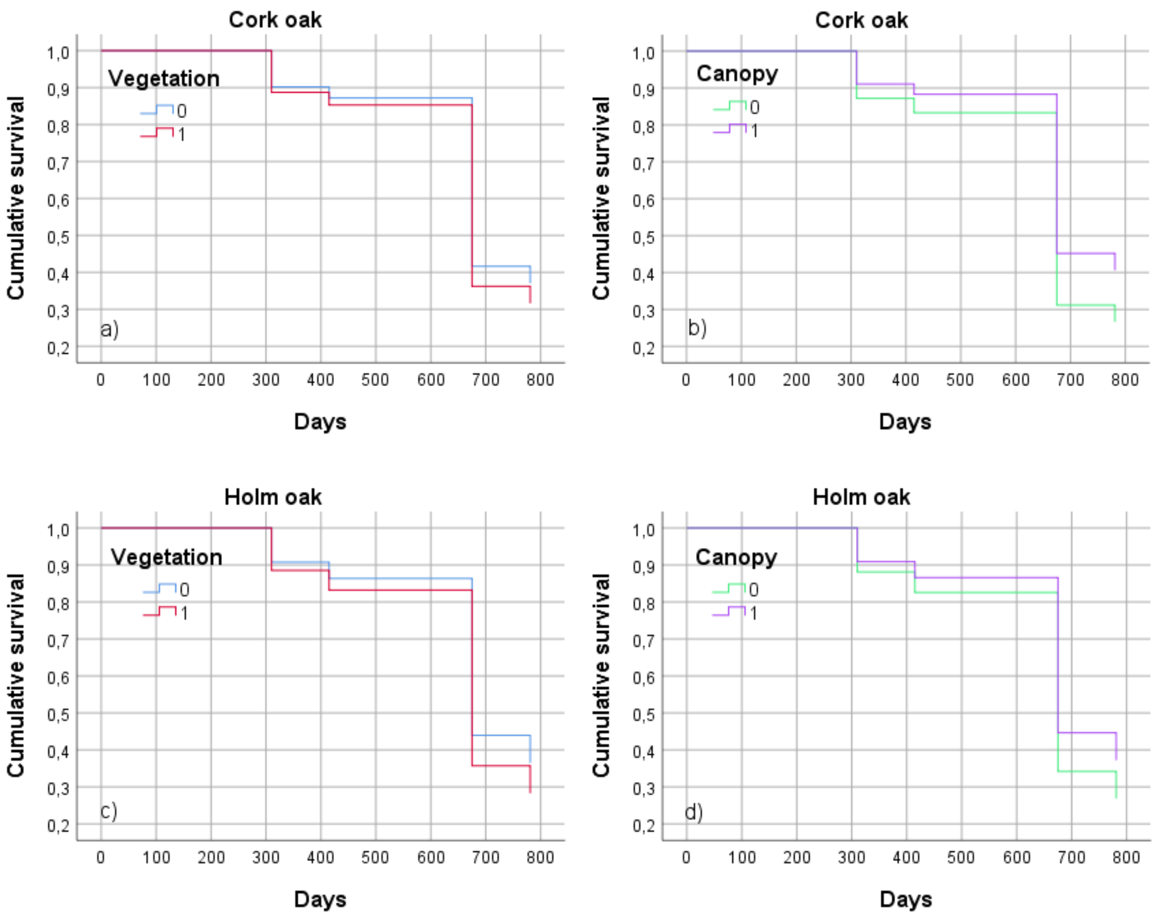
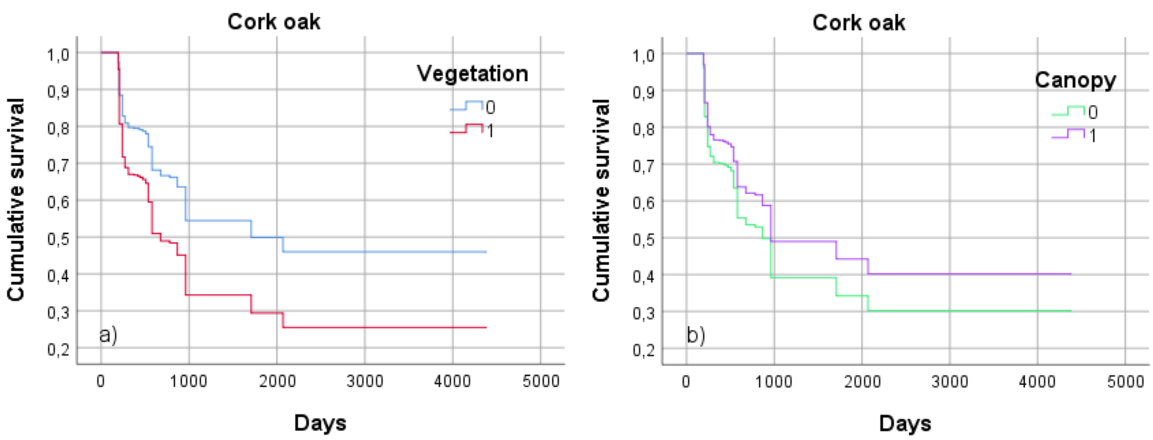


Figure 4 - Survival analysis by Cox multiple regression for the 2004-2006 period (in days) for cork oak (separate lines for vegetation (**a**) and canopy (**b**)) and holm oak (separate lines for vegetation (**c**) and canopy (**d**)).

Table 1 - Survival analysis for the 2004-2006 period by Cox multiple regression for cork oak and holm oak-seedlings (SE = standard error; χ^2 = Chi-Square; HR = Hazard Ratio; CI = effect size confidence intervals).

Species	Co-variables	ß-coef	SE	χ^2	p-value	HR (95%CI)
Cork oak	Canopy	0.480	0.172	7.814	0.005	1.616 (1.154-2.262)
	Vegetation	-0.063	0.185	0.116	0.733	0.939 (0.654-1.348)
	Can*veg	-0.191	0.256	0.552	0.457	0.826 (0.500-1.366)
	Initial_Height	-0.014	0.019	0.526	0.468	0.987 (0.951-1.023)
	SPEI-year	4.056	0.490	68.585	< 0.001	57.748 (22.113-150.809)
Holm oak	Canopy	0.292	0.197	2.196	0.138	1.339 (0.910-1.969)
	Vegetation	-0.218	0.232	0.887	0.346	0.804 (0.510-1.266)
	Can*veg	-0.014	0.303	0.002	0.963	0.986 (0.544-1.787)
	Initial_Height	-0.042	0.025	2.903	0.088	0.958 (0.913-1.006)
	SPEI-year	4.179	0.625	44.637	< 0.001	65.270 (19.158-222.369

The survival analysis for the period 2004-2015 (Figure 5, Table 2) shows that vegetation had a significant negative effect on cork oak survival (b = -0.455, p = 0.002) and a non-significant effect on holm oak survival (Figure 5. a, c). By the end of 2015, survival of cork oak without vegetation was ≈ 46%, whereas with vegetation survival was only ≈ 25%. The presence of canopy positively affected cork oak (b = 0.398, p = 0.003) and holm oak (b = 0.874, p < 0.001) survival (Figure 5. b, d). By the end of 2015, survival of cork oak under the canopy was ≈ 40%, whereas in the open survival was ≈ 30%, while survival of holm oak under the canopy was ≈ 50%, whereas in the open survival was only ≈ 25%. Interaction between canopy and vegetation did not significantly affect cork oak survival (p = 0.231) and had a nearly negative effect on holm oak survival (b = -0.444, p = 0.074). Initial height had a significantly negative effect on cork oak (b = -0.061, p < 0.001) and holm oak survival (b = -0.084, p < 0.001).



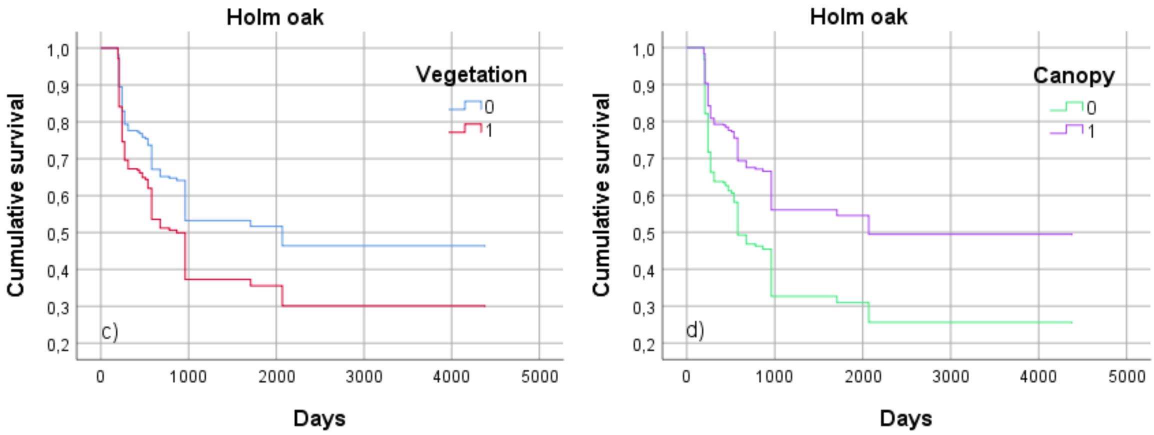


Figure 5 - Survival analysis by Cox multiple regression for the 2004-2015 period for cork oak (separate lines for vegetation (**a**) and canopy (**b**)) and holm oak (separate lines for vegetation (**c**) and canopy (**d**)).

Table 2 - Survival analysis for the 2004-2015 period by Cox multiple regression for cork oak and holm oak-seedlings (SE = standard error; χ^2 = Chi-Square; HR = Hazard Ratio; CI = effect size confidence intervals).

Species	Co-variables	ß-coef	SE	χ^2	p-value	HR (95%CI)
Cork oak	Canopy	0.398	0.136	8.528	0.003	1.489 (1.140-1.946)
	Vegetation	-0.455	0.147	9.553	0.002	0.635 (0.476-0.847)
	Can*veg	-0.250	0.211	1.402	0.236	0.779 (0.515-1.178)
	Initial_Height	-0.061	0.015	16.138	< 0.001	0.940 (0.913-0.969)
Holm oak	Canopy	0.874	0.171	26.197	< 0.001	2.395 (1.714-3.347)
	Vegetation	-0.234	0.184	1.619	0.203	0.791 (0.552-1.135)
	Can*veg	-0.444	0.248	3.197	0.074	0.642 (0.395-1.044)
	Initial_Height	-0.084	0.022	14.807	< 0.001	0.919 (0.881-0.960)

Tree growth

Height of seedlings that died between 2004-2006 clearly decreased in spring 2005 under open and herb vegetation conditions (Figure 6), reaching a minimum value in the month of April, for cork oak (6.19 cm ± 0.55) and holm oak (7.23 cm ± 0.76).

Holm oak living trees in 2015 under open conditions (Figure 6) were substantially higher when herb vegetation was present early in the experiment, specifically until the month of January of 2006.

Under canopy conditions, the presence of vegetation had a positive effect on cork and holm oak seedlings' height growth during the period 2004-2006 (Figure 6), although this difference is not as clear for holm oak seedlings growing under canopy and that died in the period 2004-2006.

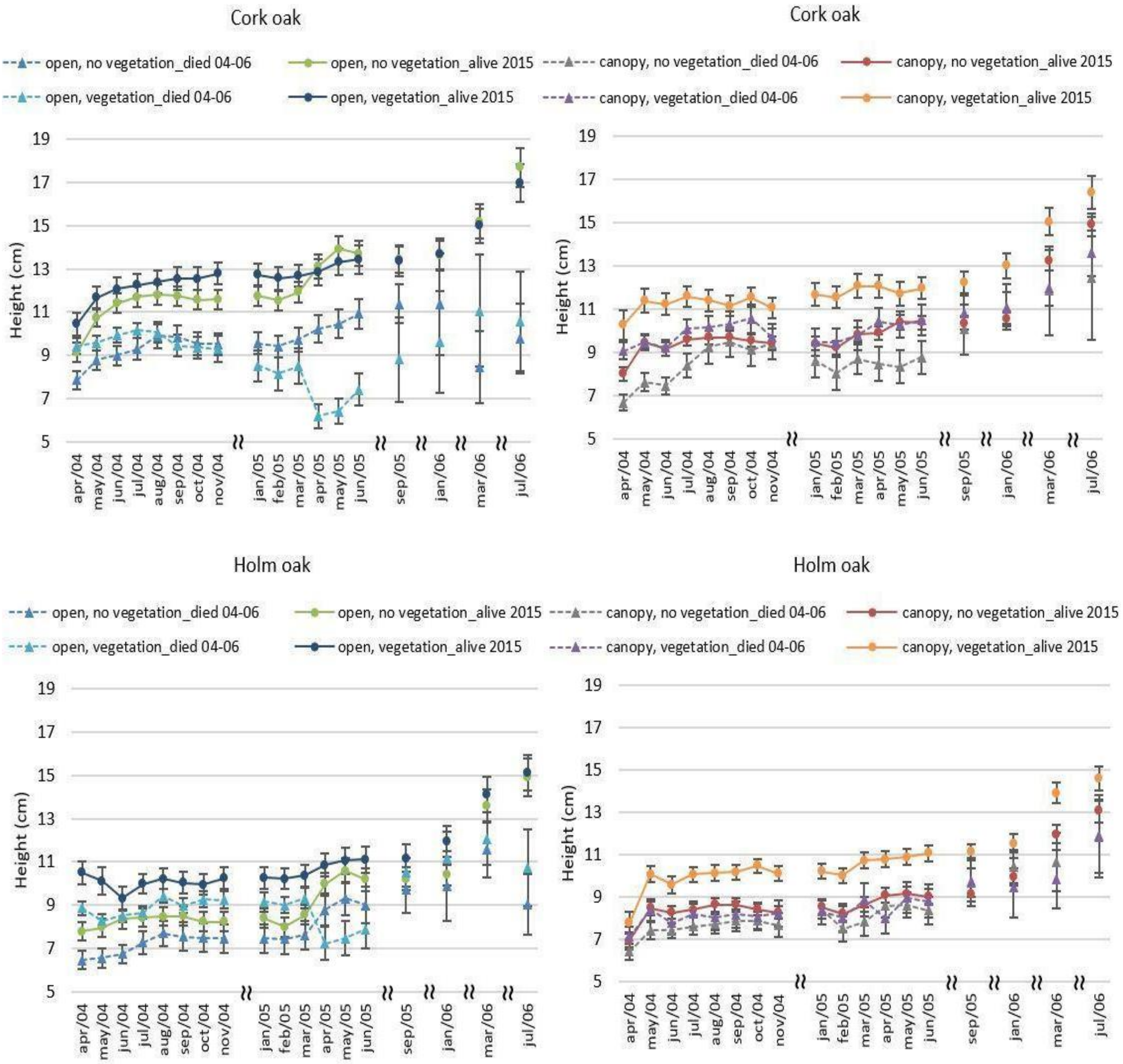


Figure 6 - Height (mean ± SE) of cork oak seedlings in the open (top left) and under canopy (top right), and holm oak seedlings in the open (bottom left) and under canopy (bottom right) that died in the 2004-2006 period and living trees in 2015.

Height of the cork oak saplings in the open and without herb vegetation that died in 2004-2006 was smaller when compared to trees that died in 2008-2009 and live trees for the period of April 2004 to July 2006 (Annex I, Figure I.1). On the other hand, no clear relations can be seen between diameter measurements (Annex I, Figure I.2). The height of living cork oak trees under open and herb vegetation conditions are clearly higher than the other two situations considered, during a significant number of moments of the experiment (Annex I, Figure I.3). For example, in June 2005 saplings that died in 2004-2006 (7.41 cm ± 0.75) were smaller than saplings that died in 2008-2009 (12.35 cm ± 1.62) and alive saplings in 2015 (13.44 cm ± 0.66). Also, in July 2006 alive saplings in 2015 (16.95 cm ± 0.86) were taller than saplings that died in 2008-2009 (10.71 cm ± 1.59) and saplings that died in 2004-2006 (10.56 cm ± 2.30). Height of trees that died between 2004-2006 clearly dropped during the months of late spring and early summer 2005. Moreover, the height of trees that died in 2008-2009 decreased from 2005 to 2006. The results for the diameter (Annex I, Figure I.4) are not as clear, although in some moments the same analysis is valid for the diameter. In the case of cork oak under canopy and no herb vegetation conditions (Annex I, Figures I.5 and I.6), lower cork oak height values were obtained in June of 2005 for trees dead in the period 2004-2006 (8.75 cm ± 0.76) compared to trees dead in 2008 and 2009 (10.90 cm ± 1.02) and alive trees (10.36 cm ± 0.33). The height of the living cork oak trees under canopy and herb vegetation treatment was significantly higher, in several dates, compared to trees that died in the previous two periods (Annex I, Figure I.7). Although this relation is true for some cases regarding diameter analysis (Annex I, Figure I.8), the difference was not as consistent.

Holm oak trees dead in 2004-2006 growing under open and no herb vegetation conditions (Annex I, Figures I.9 and I.10) generally showed lower height and diameter values compared to the other situations tested; in July of 2006, lower tree heights (9.02 cm ± 1.41) were observed compared to trees dead in 2008 and 2009 (17.02 cm ± 1.84) and alive trees (14.92 cm ± 0.88). Living holm oak trees under open and herb vegetation conditions were higher and had larger diameters throughout the study period (Annex I, Figures I.11 and I.12), however, this difference is more evident for height. Similarly, to cork oak analysis of height and diameter, under open and herb vegetation conditions, holm oak also showed a clear decrease of height and diameter during the months of April, May, and June of 2005. The height and diameter of holm oak trees under canopy and no herb vegetation (Annex I, Figures I.13 and I.14) were higher for trees that died in the period 2008-2009, particularly during and after 2006. For example, in July 2006 higher heights were measured for saplings that died in 2008-2009 (15.49 cm ± 1.48) compared to saplings that died in 2004-2006 (11.88 cm ± 1.94) and living trees in 2015 (13.06 cm ± 0.54). The same tendency was registered for the cork oaks although not as consistent and only for height. Trees that died between 2004-2006 under canopy and herb vegetation conditions showed lower height than saplings that remained alive (Annex I, Figure I.15). On the other hand, the diameter was higher for the living trees when last measured (Annex I, Figure I.16).

Cork oak trees living in the open with no vegetation were overall taller than trees in the other treatments (Figure 7). For holm oak, differences between treatments were not as clear for most of the measurement periods. However, in December 2015 trees living in the open without vegetation were taller (80.18 cm ± 5.96).

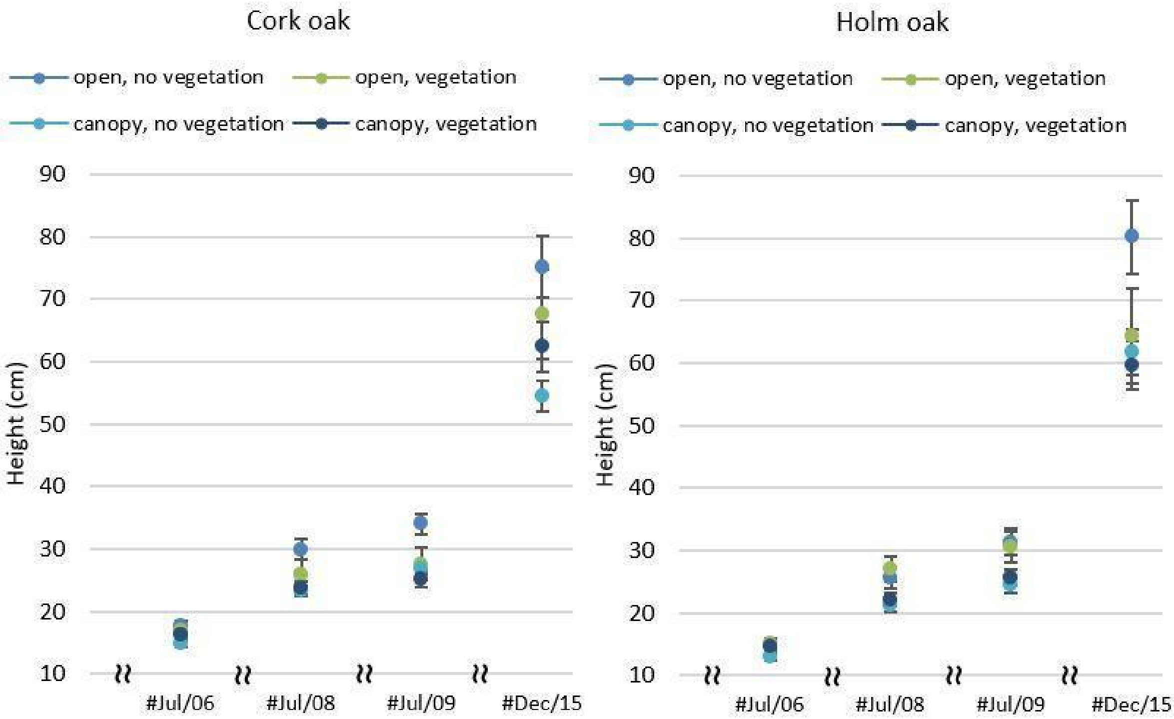


Figure 7 - Height (mean ± SE) of cork oak (left) and holm oak (right) living trees in 2015 from July of 2006 to December of 2015.

The effect of the canopy on the height of living trees was compared for herb vegetation and no herb vegetation conditions, and for both species (Annex II). Under no herb vegetation (Figure II.1), the height of cork oak trees in the open was consistently higher when compared to the trees that grew under the canopy. For example, in June 2005 and July 2006, saplings growing in the open were significantly higher (13.71 cm ± 0.59 and 17.69 cm ± 0.90, respectively) than saplings growing under the canopy (10.36 cm ± 0.33 and 14.89 cm ± 0.53, respectively). Mean holm oak height under no herb vegetation conditions was generally higher in the open than under the canopy (Figure II.2), although not as consistently as in the case of cork oak. For example, in June 2005 and July 2006, saplings growing in the open (10.18 cm ± 0.53 and 14.92 cm ± 0.88, respectively) were higher than saplings growing under the canopy (9.00 cm ± 0.34 and 13.06 cm ± 0.54, respectively). Specifically, in July 2006, cork and holm oak trees that were alive in 2015 were taller than trees that died in 2004-2006.

Under no herb vegetation conditions, canopy had a negative effect on trees' final average height whereas this difference was clearer for cork oak (Table 3). Thus, open and no herb vegetation conditions led to taller cork (75,17 ± 4,89) and holm oak trees (80,18 cm ± 5,96). Trees' diameter in 2015 was also consistently higher in the open, both for cork and holm oak trees (Table 3). Particularly, in the case of cork oak growing under the canopy, herb vegetation had a positive effect on trees' final average height (62.38 cm ± 3.96). Holm oak trees' height was higher for canopy and no herb vegetation conditions (61.74 cm ± 3.67) compared to cork oak trees' height under the same conditions (54.49 cm ± 3.67), while the opposite was true for diameter.

Table 3 - Height (mean ± SE) and diameter (mean ± SE) of cork and holm oak living trees in 2015.

Para-meter	Cork oak				Holm oak			
	open		canopy		open		canopy	
	no vegetation	vegetation	no vegetation	vegetation	no vegetation	vegetation	no vegetation	vegetation
Height (cm)	75.17 ± 4.89	67.60 ± 7.09	54.49 ± 2.51	62.38 ± 3.96	80.18 ± 5.96	64.39 ± 7.55	61.74 ± 3.67	59.69 ± 3.86
Diameter (cm)	14.55 ± 1.52	14.66 ± 2.50	8.76 ± 0.61	8.40 ± 0.72	11.34 ± 1.02	11.06 ± 1.35	6.88 ± 0.45	7.41 ± 0.49

Relative Growth Rates

Higher relative growth rates were observed for cork oak under open and without herb vegetation compared to open and herb vegetation conditions in April (0.00116 ± 0.00016 and 0.00063 ± 0.00015, respectively), May (0.00073 ± 0.00007 and 0.00032 ± 0.00010, respectively) and June (0.00048 ± 0.00005 and 0.00023 ± 0.00011, respectively) of 2005 (Figure 8). Apart from June of 2005, the same was true for holm oak (Figure 9).

Higher relative growth rates were observed for holm oak compared to cork oak under canopy and herb vegetation conditions in April (0.00130 ± 0.00021 and 0.00074 ± 0.00023, respectively), May (0.00023 ± 0.00005 and 0.00005 ± 0.00012, respectively) and June (0.00040 ± 0.00007 and 0.00016 ± 0.00007, respectively) of 2005 (Figure 8 and 9). Comparing specifically June of 2005 and July of 2006, relative growth rate was consistently higher for July of 2006 for both species and tested conditions.

Two maximum relative growth rates are worth noticing: cork oak trees under open and no herb vegetation conditions reached 0.00116 ± 0.00016 in April of 2005 (Figure 8) and holm oak under canopy and herb vegetation conditions reached 0.00130 ± 0.00021 in April of 2005 (Figure 9). For both species, relative growth rates were overall higher in April 2005, March 2006, and July 2006.

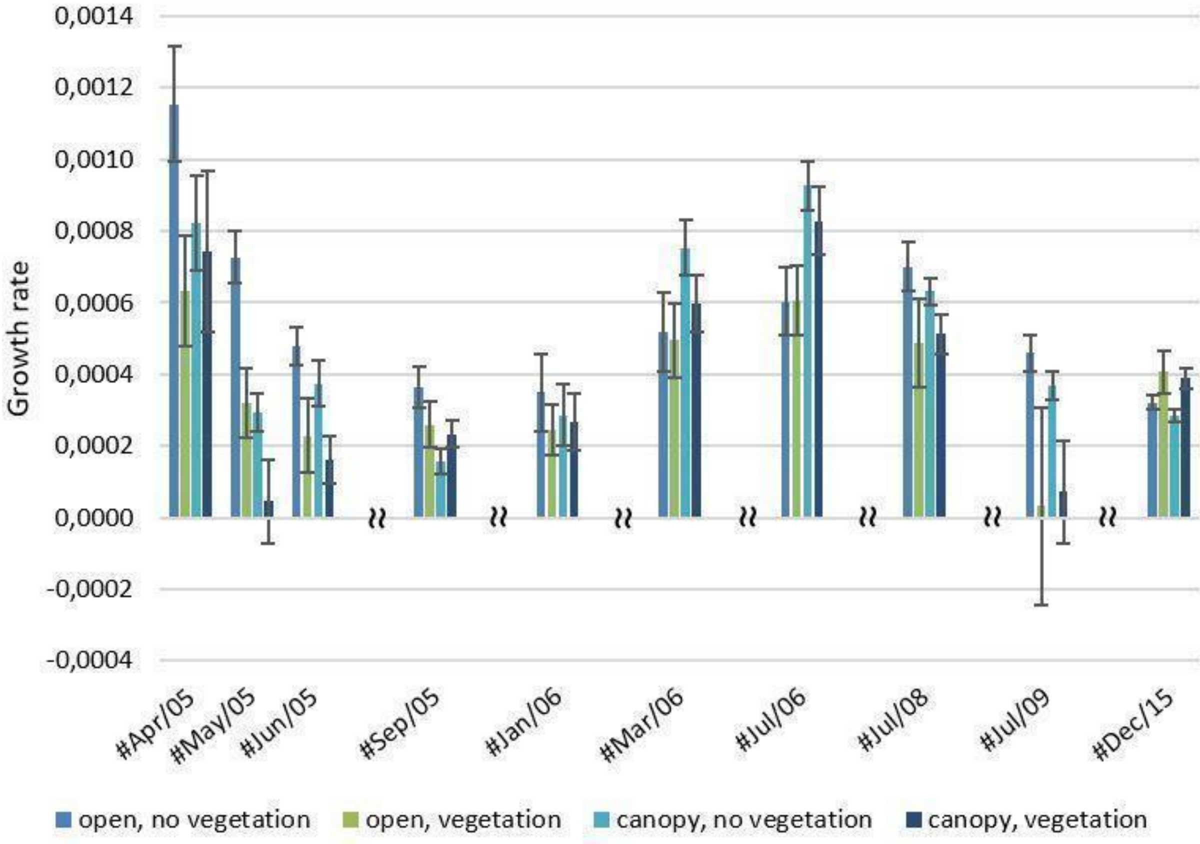


Figure 8 – Relative growth rates (mean ± SE) of cork oak living trees in 2015 under the four conditions tested.

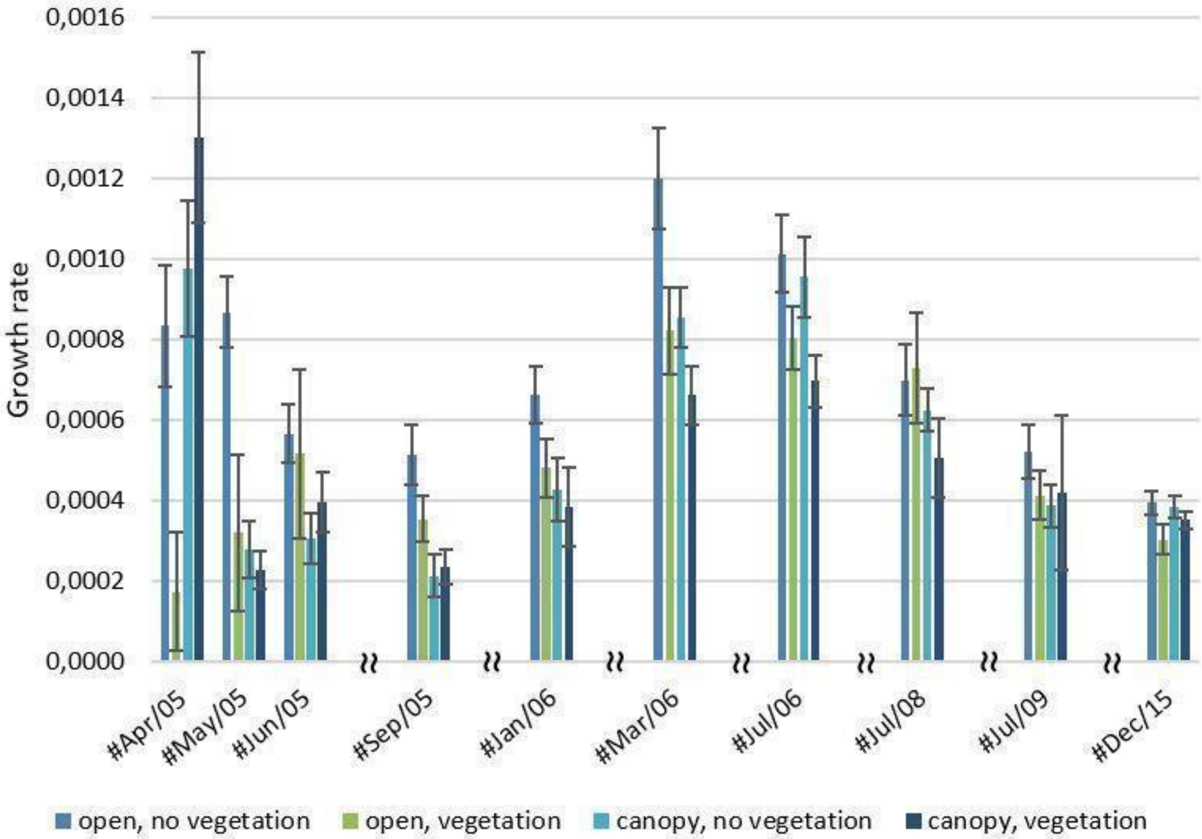


Figure 9 – Relative growth rates (mean ± SE) of holm oak living trees in 2015 under the four conditions tested.

Overall, higher relative growth rates were observed for holm oak compared to cork oak. This difference was especially clear in January 2006 (holm oak: 0.0005 ± 0.0001; cork oak: 0.0003 ± 0.0001) and March 2006 (holm oak: 0.0009 ± 0.0001; cork oak: 0.0006 ± 0.0001) (Figure 10).

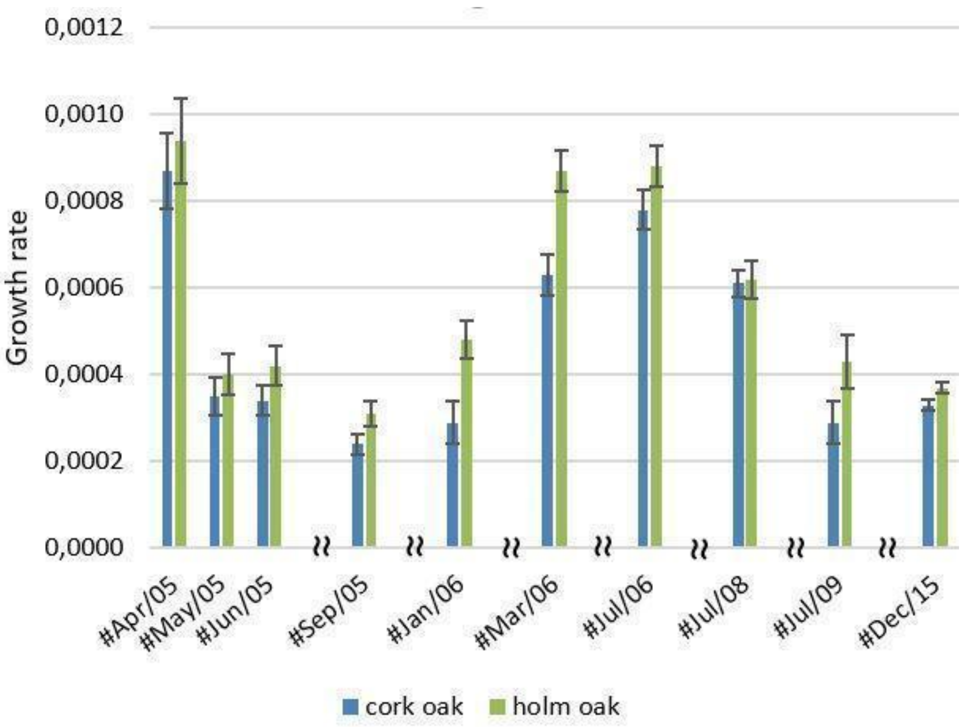


Figure 10 – Relative growth rates (mean ± SE) of the cork oak and holm oak living trees in 2015 considering the four treatments together.

Discussion

The degree of interactions between shrubs and/or trees and seedlings is very important in arid and semi-arid areas and largely depends on the balance of negative and positive effects between these different plant life-forms, ranging from facilitation to competition (Rolo et al., 2013). Seedlings' survival under the canopy is higher as shade decreases thermal and water stress (Gómez-Aparicio et al., 2008; Acácio and Holmgren, 2014; Caldeira et al., 2014). Our results show that the canopy of adult trees had a positive effect on cork and holm oak seedling survival. These results agree with previous studies that showed competition prevails under stressful conditions (Acácio and Holmgren, 2014; Caldeira et al., 2014), and are particularly important for the Mediterranean ecosystems as they are under climate change scenarios of increasing temperatures and drought (Costa, Santos, and Pinto, 2012). However, these effects are not equal for all species. Indeed, this positive effect was more beneficial for cork oak, possibly due to its higher vulnerability to drought than holm oak (Petroselli et al., 2013).

We show that the presence of herb vegetation did not decrease holm oak recruitment, however presence of vegetation decreased cork oak survival for 2004-2015, suggesting herb vegetation competition for water and light had a stronger effect on cork oak trees.

Previous studies suggest that herb vegetation does not affect seedling mortality under canopy trees whereas in gaps seedling mortality is significantly higher in the presence of herb vegetation (Cuesta et al., 2010, Caldeira et al., 2014; Gavinet et al., 2016). Contrary, survival analysis showed that interaction between canopy and vegetation did not significantly affect tree survival, although growth was clearly affected by canopy and vegetation conditions.

Previous studies show that holm oak is more xerophilous and shade tolerant than cork oak (David et al., 2007), prevailing in drier and mesophilous sites (Petroselli et al., 2013), while cork oak is more heliophilous than holm oak, especially in young stages (Petroselli et al., 2013). As expected, survival analysis for the 2004-2006 period, showed that drought periods (measured by SPEI relative to the previous 12 months of measure) had a significant negative effect on cork and holm oak recruitment, and lower SPEI values (2005) were associated with clear drops in seedling survival. These results are supported by previous studies (Gómez-Aparicio et al. 2008).

Soil moisture and temperature are critical factors for seedlings survival, while light may become more important for established oaks to grow and progress to higher development stages (Martín-Alcón et al., 2015). Our results show that open conditions (higher light levels) had a beneficial effect on growth: open and no herb vegetation conditions led to higher cork oak and holm oak trees' height when compared to any canopy condition, which is supported by previous studies (Caldeira et al., 2014) that showed that canopy has a negative effect on tree growth during the establishment phase.

For both species, during the first years of tree establishment (2004-2006), seedlings living in the open with herbaceous vegetation seemed to be overall taller, and this was consistently true for holm oak. Cork oak height was consistently higher in several moments of the experiment than holm oak height, for comparable conditions. This fact can be related to cork oak's higher heliophilous growth, especially in young stages (for open conditions), as suggested by previous studies (Petroselli et al., 2013). However, final holm oak height was higher, specifically for canopy and no herb vegetation conditions, which may indicate that, in later stages, holm oak grows at a higher rate compared to cork oak, especially under canopy conditions, due to its higher shade tolerance in opposition to the heliophilous cork oak.

This study shows that the growth of seedlings of cork oak and holm oak increased from 2005 to 2006. Trees' height and diameter clearly decreased during late spring and early summer in 2005 and higher growth rates were observed in the months of March and July of 2006. This may be related to a combination of growth-limiting effects of the dry second year and high annual and summer SPEI values observed in 2006.

Although the combined effect of canopy and vegetation did not significantly affect tree survival, relative growth rate of living trees in 2015 showed that higher growth rate values were observed for open and no herb vegetation conditions than open and herb vegetation conditions for both species, suggesting that herb vegetation may not influence seedling survival, but seedlings may grow at higher rates in early ages if vegetation is not present, especially in open conditions. Holm oak's higher tolerance to drought and herb vegetation competition may explain why the difference stated before was not as consistent as for cork oak (David et al., 2007; Petroselli et al., 2013). Herb vegetation had a negative effect on seedlings growth rate, particularly in early stages and when SPEI values were low (effect more clearly for cork oak), and later in July of 2009 for cork oak when the lowest spring SPEI was registered (-1.78). These findings are supported by previous studies (Caldeira et al., 2014). It might even be the case that drought played a higher role than herb vegetation competition as herb vegetation development may be delayed or canceled by harsh drought periods. Higher relative growth rate of cork oak seedlings under open and no herb vegetation conditions compared to holm oak in April 2005 may be due to higher heliophilous capacity while stressful conditions of drought and herb competition are not present.

Higher relative growth rates for cork and holm oak living seedlings/trees in 2015 agree with high SPEI values: growth rate in July of 2006 was generally higher than in July of 2008, and, in turn, higher than July of 2009, suggesting that higher growth rates are related to higher SPEI values (SPEI-summer observed values were -0.61, -0.86 and -1.16 for 2006, 2008 and 2009, respectively). Consistent higher relative growth rate values for July of 2006 compared to June of 2005 for both species and tested conditions may be explained by higher SPEI-summer values (-0.61 and -1,75 for 2006 and 2005, respectively).

Conclusion and General Considerations

Montado is a complex agro-silvopastoral system resulting from the interactions between climate, soil, pasture, trees, and animals. Tree decline and low recruitment of oak woodlands are a consequence of poor land-use practices and ongoing climatic changes that are threatening their ecologic and economic sustainability (Moreno et al., 2019). The future of cork and holm oak land use systems will depend on people's willingness and capacity to undertake concerted management actions and restoration programs. It is in this context that management decisions for forest recovery must be made, combining practices that improve soil conditions and mitigate recruitment constraints.

Traditionally, plant manipulation during restoration of forest ecosystems have focused on the reduction of competition by existing vegetation. However, it is well settled that regeneration of cork and holm oak seedlings is negatively correlated with low density, open woodlands (lower canopy stands) (Ibanez et al., 2015; Moreno et al., 2019), and the increasing recognition of facilitation has led to better practices of conserving neighboring vegetation (Gómez-Aparicio, 2009). Our results show that tree canopies have a nurse effect over cork and holm oak seedlings survival. Lower growth rates were obtained when herb vegetation was present, particularly in water stress conditions. For these reasons, management of competitive species such as *Cistus* (e.g., mowing, controlled grazing), nurse shrubs and trees (Gómez-Aparicio et al., 2004) considering species-specific relations (Velasco and Becerra, 2020), may increase *Quercus* seedling survival.

Management plans promoting maintenance of a healthy adult tree canopy cover are essential to assure regeneration of the Mediterranean evergreen oak woodlands. Facilitation of seedling recruitment by tree canopies in forest management practices may be essential to ensure proper regeneration of oak woodlands, especially under forecasted climate change scenarios of increasing high temperatures and drought.

Previous studies show that holm oak has more effective drought tolerance mechanisms than cork oak (David et al., 2007), such as a deeper root system that may allow for a better groundwater uptake preventing water stress (David et al., 2007; Petroselli et al., 2013). Cork oak is more heliophilous than holm oak, especially in young stages, so it is replaced by holm oak during a forest succession (Petroselli et al., 2013). Although SPEI had a significant effect on survival of both species, the results suggest that SPEI has a higher effect on cork oak in early stages. This may call for a differentiated management approach by modifying the spatial and temporal patterns of silvicultural treatments and thus contribute to the stabilization of forest structure and function (Martín-Alcón et al., 2015; Ogaya et al., 2020). Advanced forest nursery technologies (genetic management) (Sampaio et al., 2016) and high-quality seedling production should also be considered as management strategies to increase cork and holm oak adaptability to climate change in the Mediterranean (Schirone, 2016).

Understanding the biotic and abiotic, environmental and management factors involved in the current decline of Western Mediterranean basin open woodlands is key to formulate and execute sustainable management options (Moreno et al., 2019). Only by mitigating adult mortality and improving regeneration will it be possible to assure the permanence of this valuable and important part of the natural and cultural heritage of Europe (Matías et al., 2019).

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Annex I - tree growth (height and diameter)

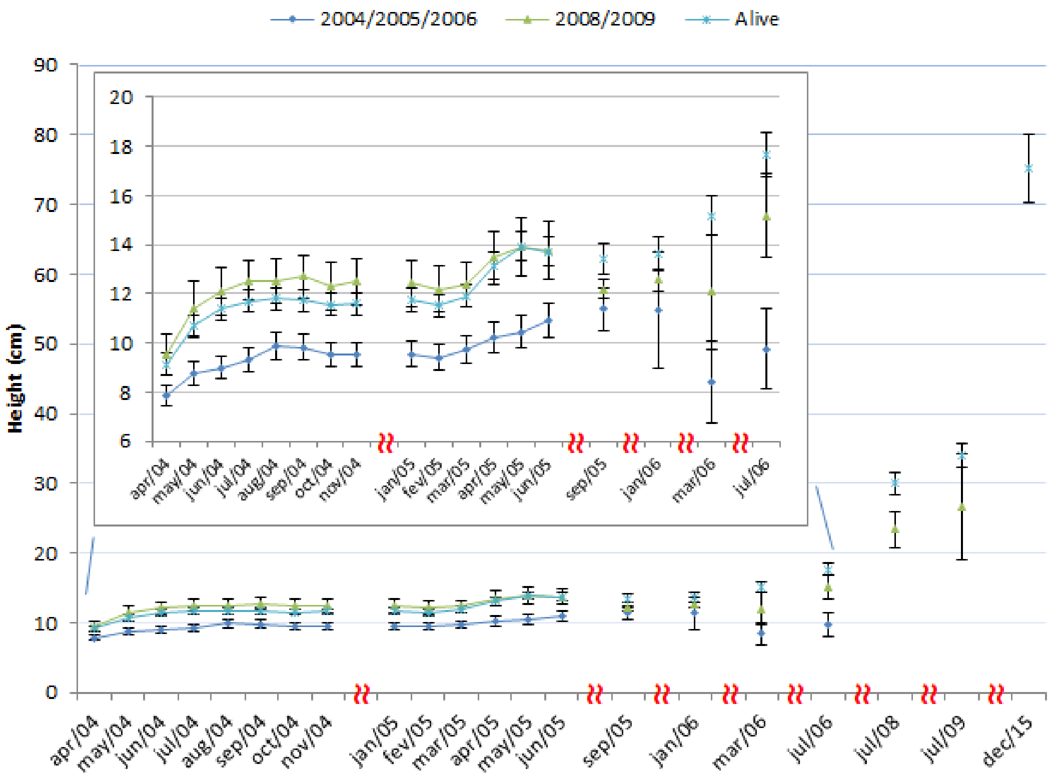

Figure I.1 - Height (mean ± SE) of cork oak trees under open and no herb vegetation conditions for (1) trees dead in 2004-2006 (dark blue), (2) trees dead in 2008-2009 (green) and (3) living trees in 2015 (light blue).

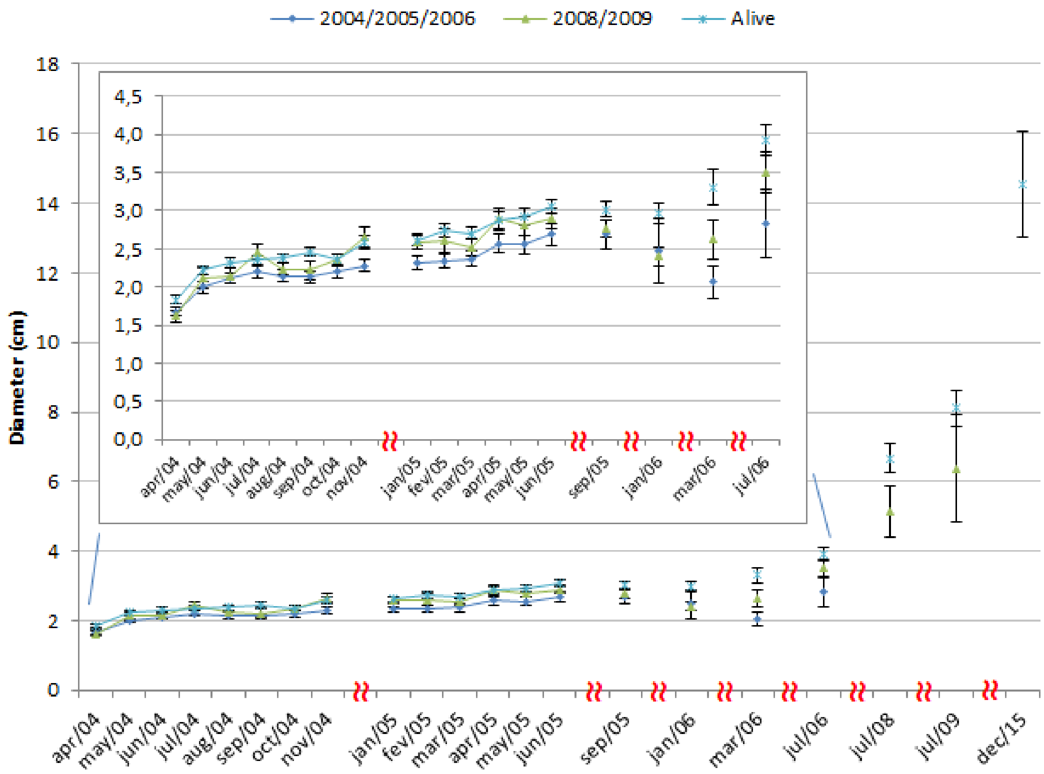

Figure I.2 - Diameter (mean ± SE) of cork oak trees under open and no herb vegetation conditions for (1) trees dead in 2004-2006 (dark blue), (2) trees dead in 2008-2009 (green) and (3) living trees in 2015 (light blue).

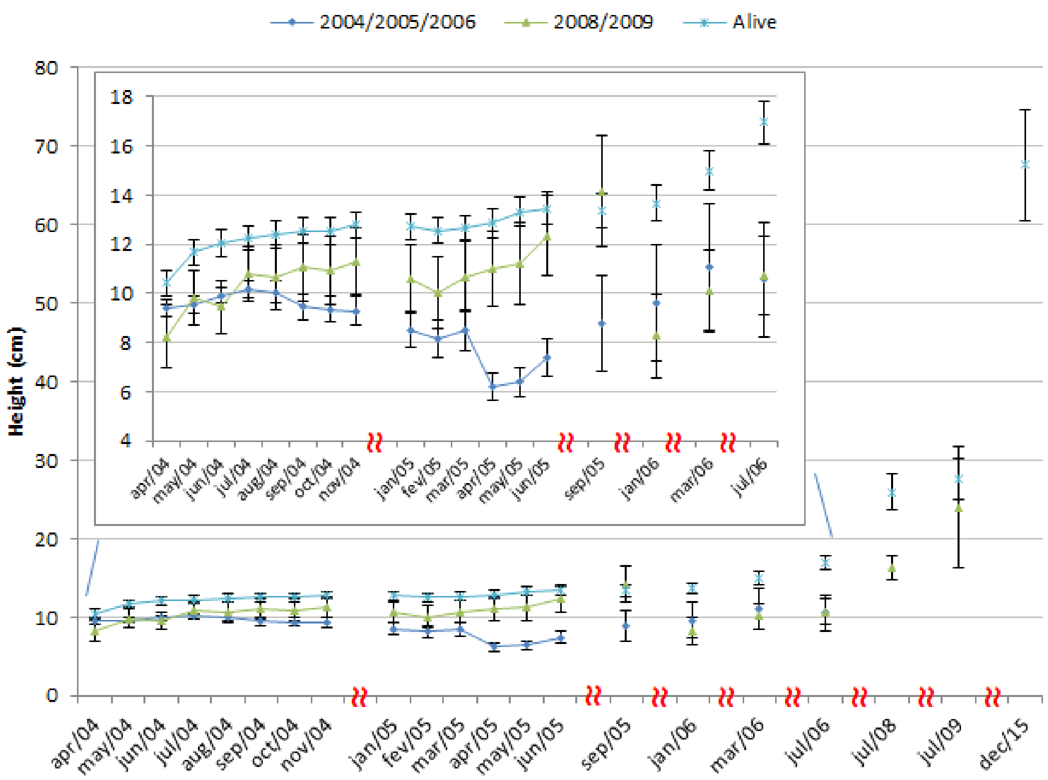

Figure I.3 - Height (mean ± SE) of cork oak trees under open and herb vegetation conditions for (1) trees dead in 2004-2006 (dark blue), (2) trees dead in 2008-2009 (green) and (3) living trees in 2015 (light blue).

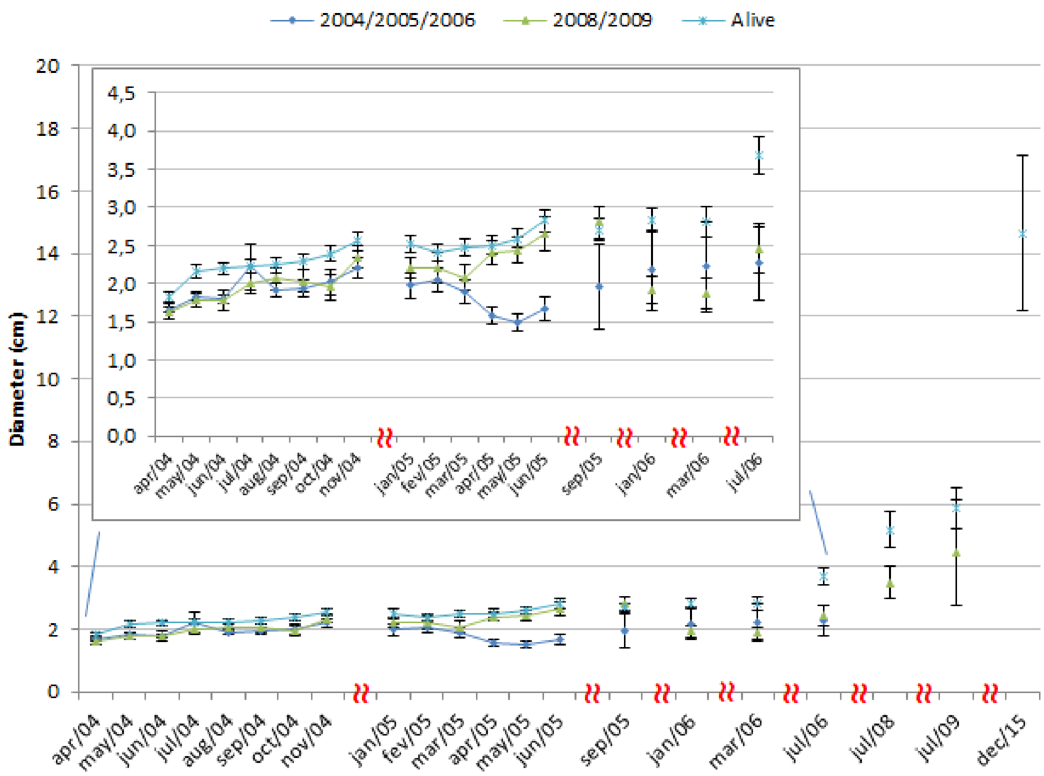

Figure I.4 - Diameter (mean ± SE) of cork oak trees under open and herb vegetation conditions for (1) trees dead in 2004-2006 (dark blue), (2) trees dead in 2008-2009 (green) and (3) living trees in 2015 (light blue).

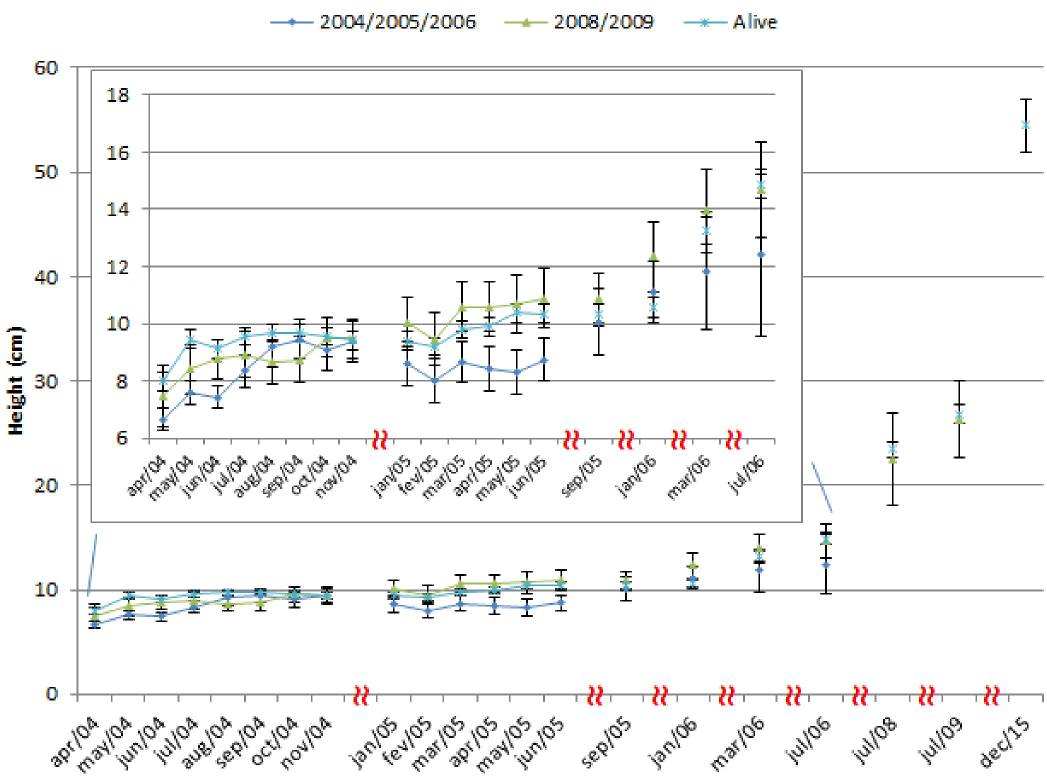

Figure I.5 - Height (mean ± SE) of cork oak trees under canopy and no herb vegetation conditions for (1) trees dead in 2004-2006 (dark blue), (2) trees dead in 2008-2009 (green) and (3) living trees in 2015 (light blue).

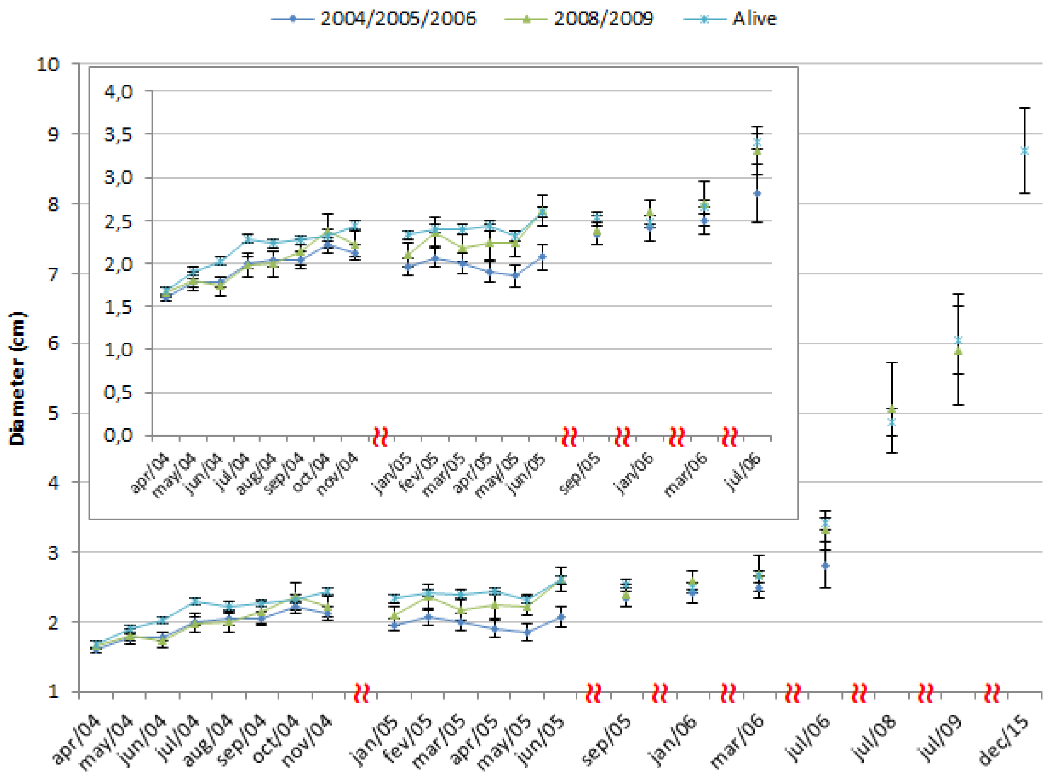

Figure I.6 - Diameter (mean ± SE) of cork oak trees under canopy and no herb vegetation conditions for (1) trees dead in 2004-2006 (dark blue), (2) trees dead in 2008-2009 (green) and (3) living trees in 2015 (light blue).

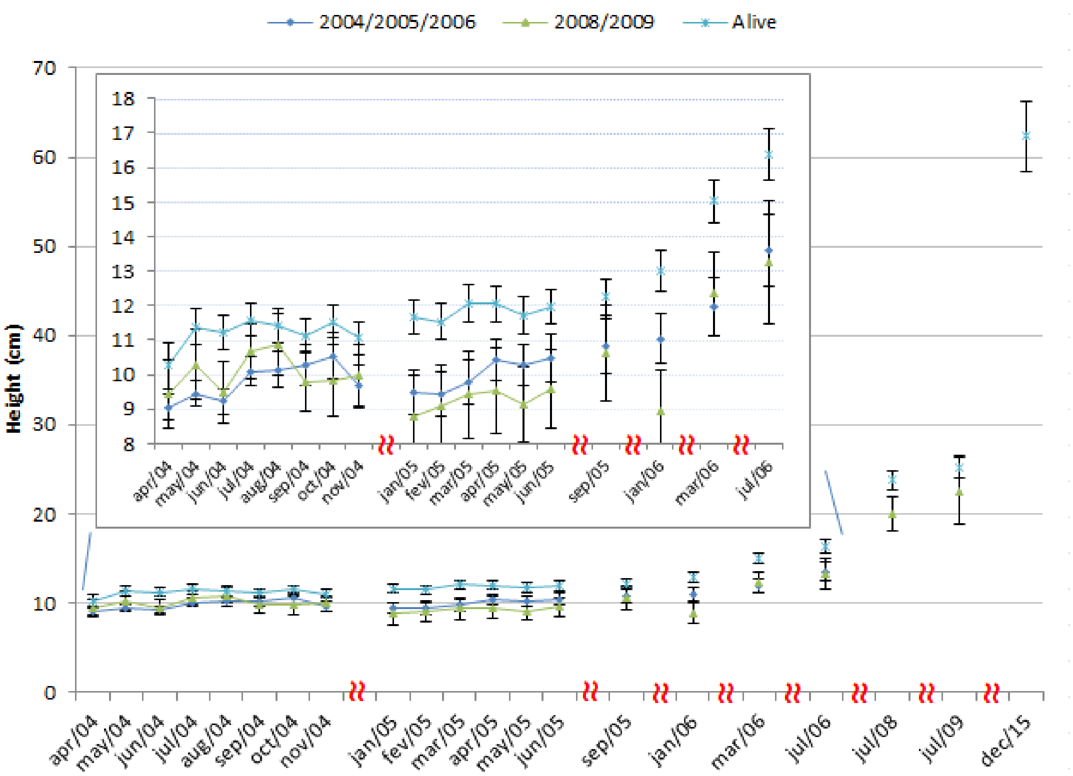

Figure I.7 - Height (mean ± SE) of cork oak trees under canopy and herb vegetation conditions for (1) trees dead in 2004-2006 (dark blue), (2) trees dead in 2008-2009 (green) and (3) living trees in 2015 (light blue).

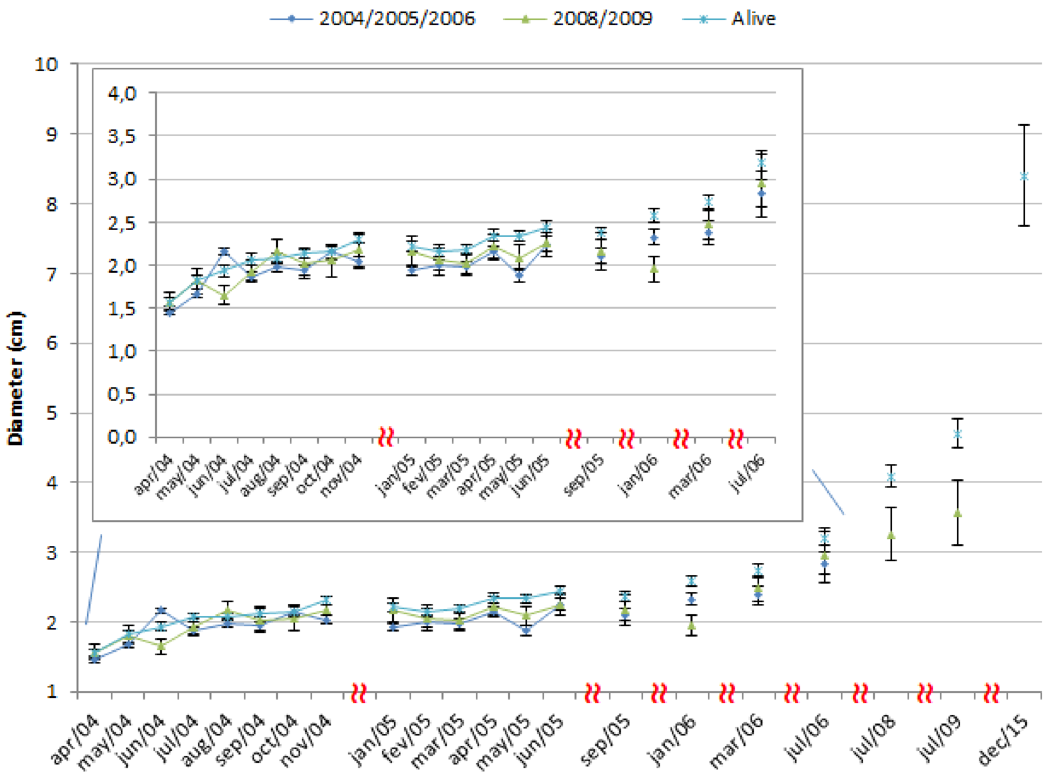

Figure I.8 - Diameter (mean ± SE) of cork oak trees under canopy and herb vegetation conditions for (1) trees dead in 2004-2006 (dark blue), (2) trees dead in 2008-2009 (green) and (3) living trees in 2015 (light blue).

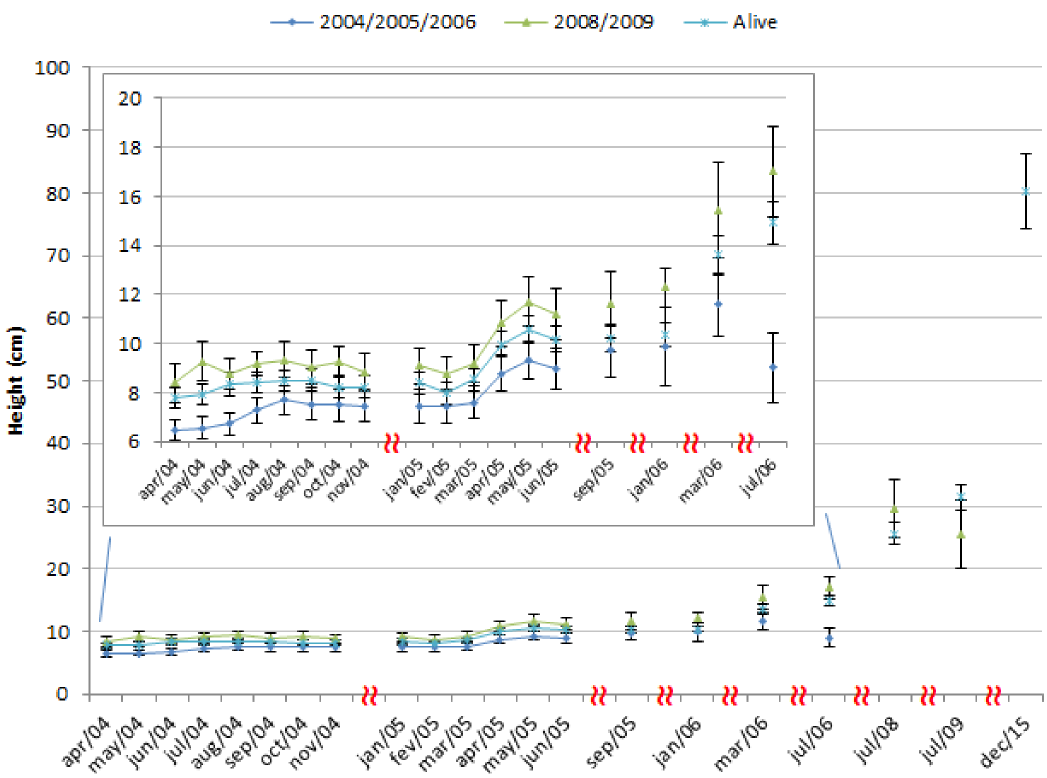

Figure I.9 - Height (mean ± SE) of holm oak trees under open and no herb vegetation conditions for (1) trees dead in 2004-2006 (dark blue), (2) trees dead in 2008-2009 (green) and (3) living trees in 2015 (light blue).

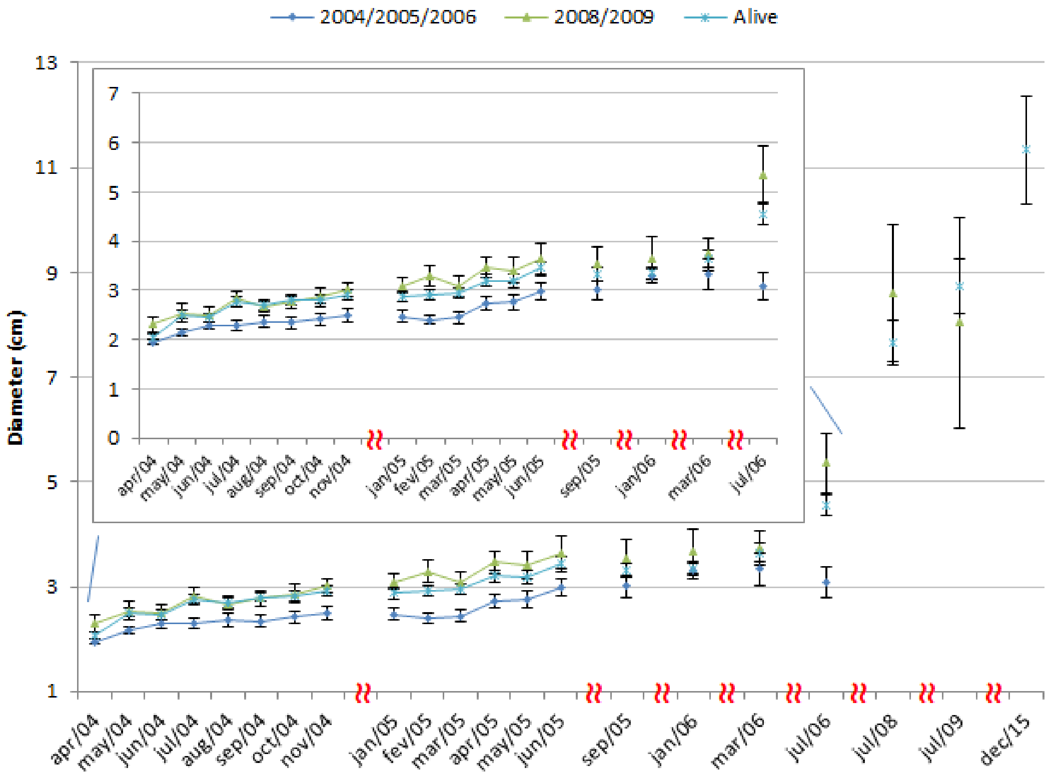

Figure I.10 - Diameter (mean ± SE) of holm oak trees under open and no herb vegetation conditions for (1) trees dead in 2004-2006 (dark blue), (2) trees dead in 2008-2009 (green) and (3) living trees in 2015 (light blue).

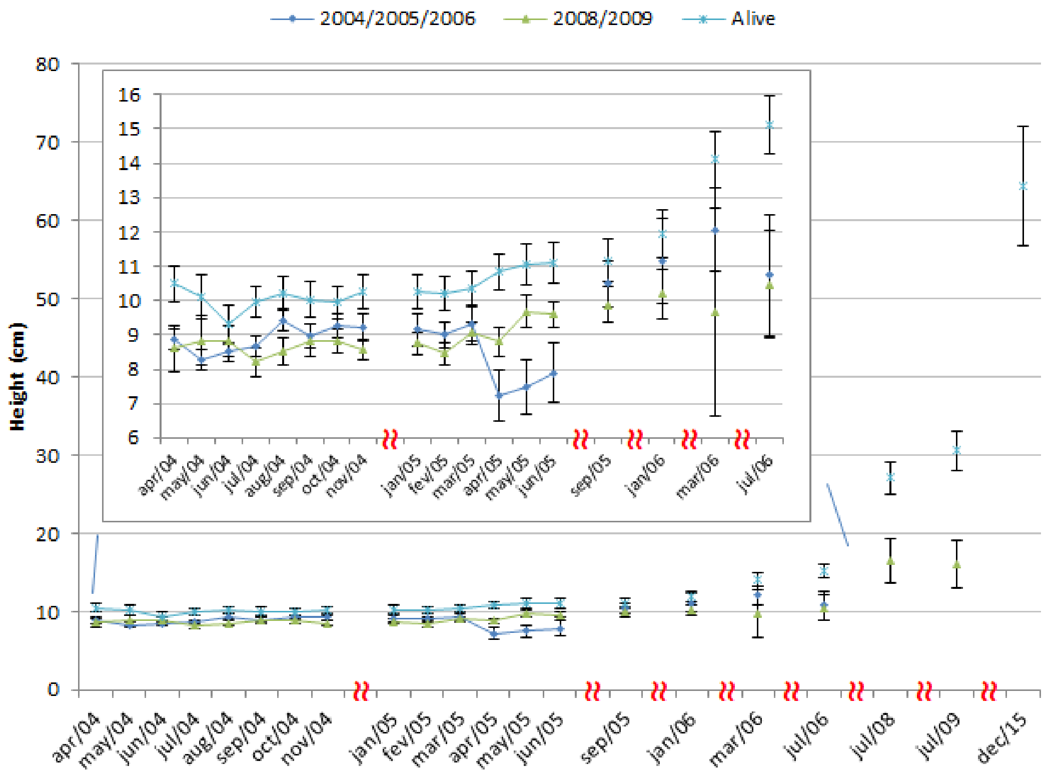

Figure I.11 - Height (mean ± SE) of holm oak trees under open and herb vegetation conditions for (1) trees dead in 2004-2006 (dark blue), (2) trees dead in 2008-2009 (green) and (3) living trees in 2015 (light blue).

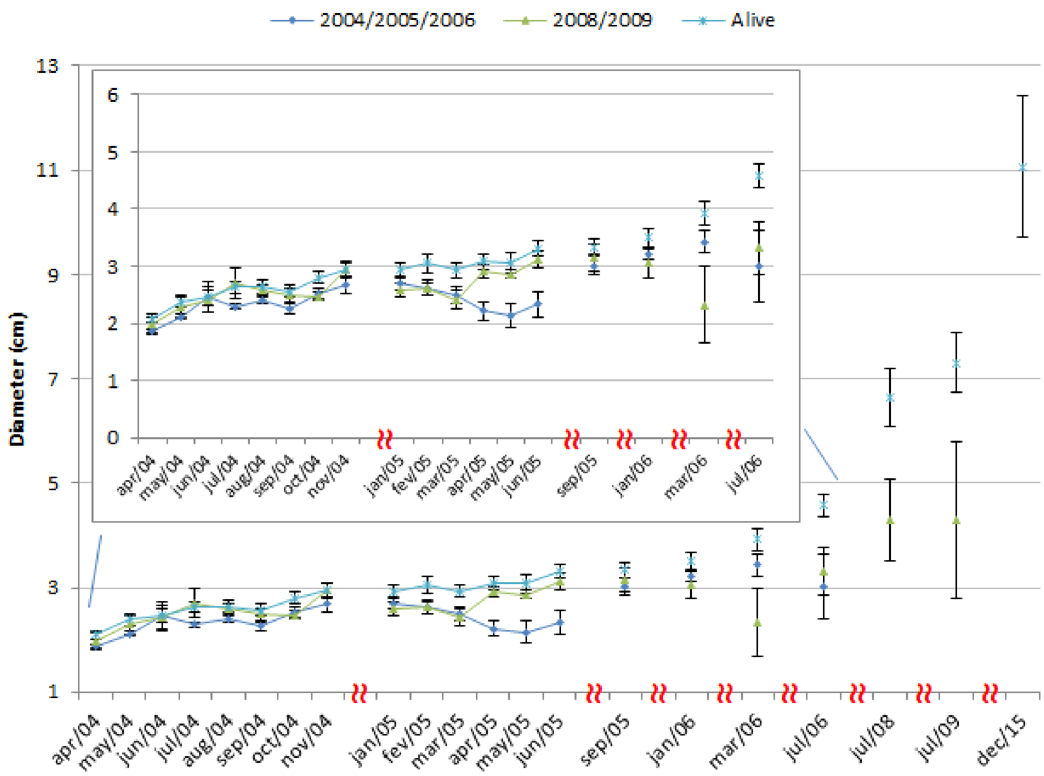

Figure I.12 - Diameter (mean ± SE) of holm oak trees under open and herb vegetation conditions for (1) trees dead in 2004-2006 (dark blue), (2) trees dead in 2008-2009 (green) and (3) living trees in 2015 (light blue).

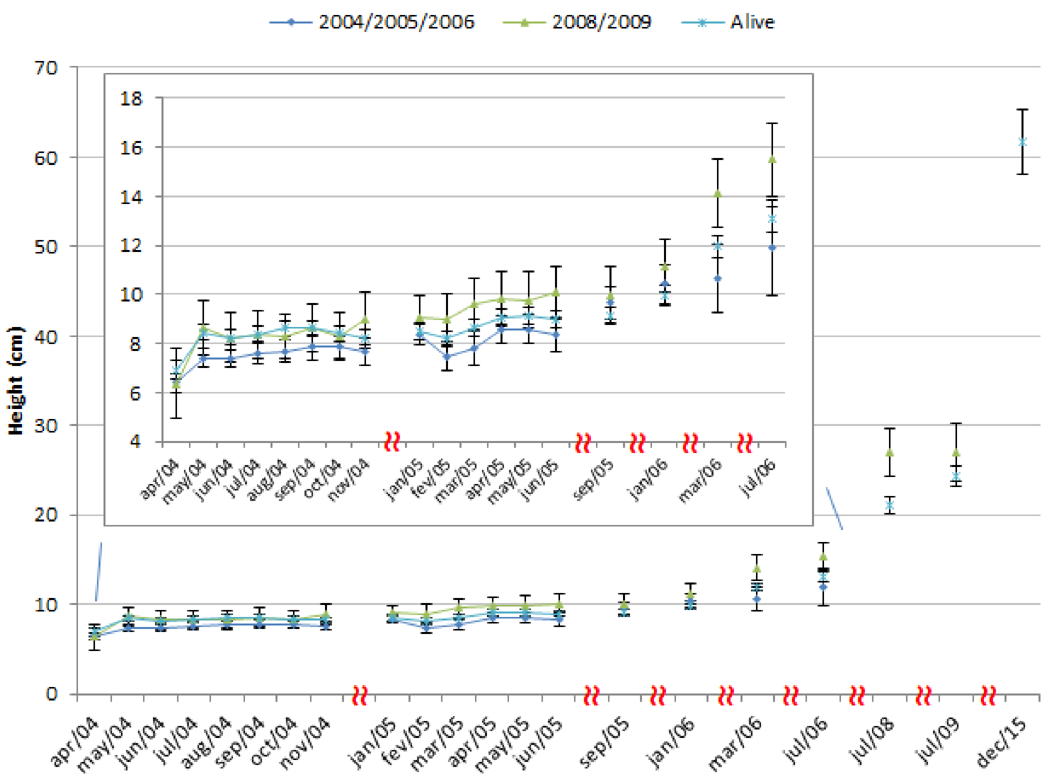

Figure I.13 - Height (mean ± SE) of holm oak trees under canopy and no herb vegetation conditions for (1) trees dead in 2004-2006 (dark blue), (2) trees dead in 2008-2009 (green) and (3) living trees in 2015 (light blue).

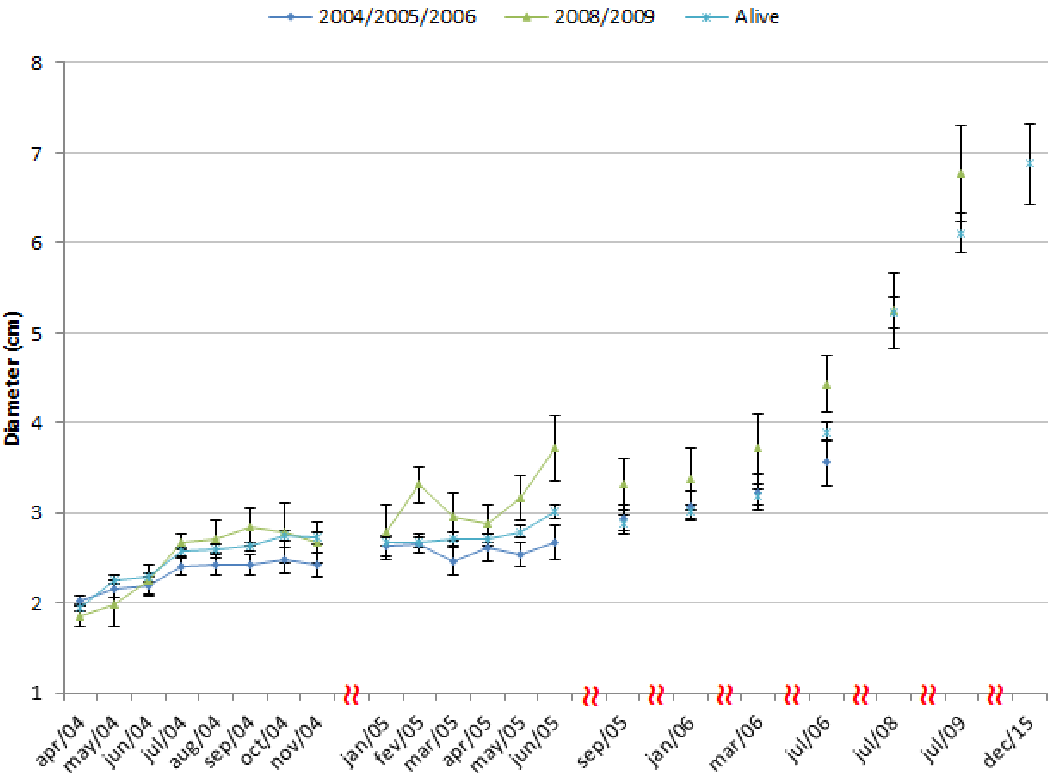

Figure I.14 - Diameter (mean ± SE) of holm oak trees under canopy and no herb vegetation conditions for (1) trees dead in 2004-2006 (dark blue), (2) trees dead in 2008-2009 (green) and (3) living trees in 2015 (light blue).

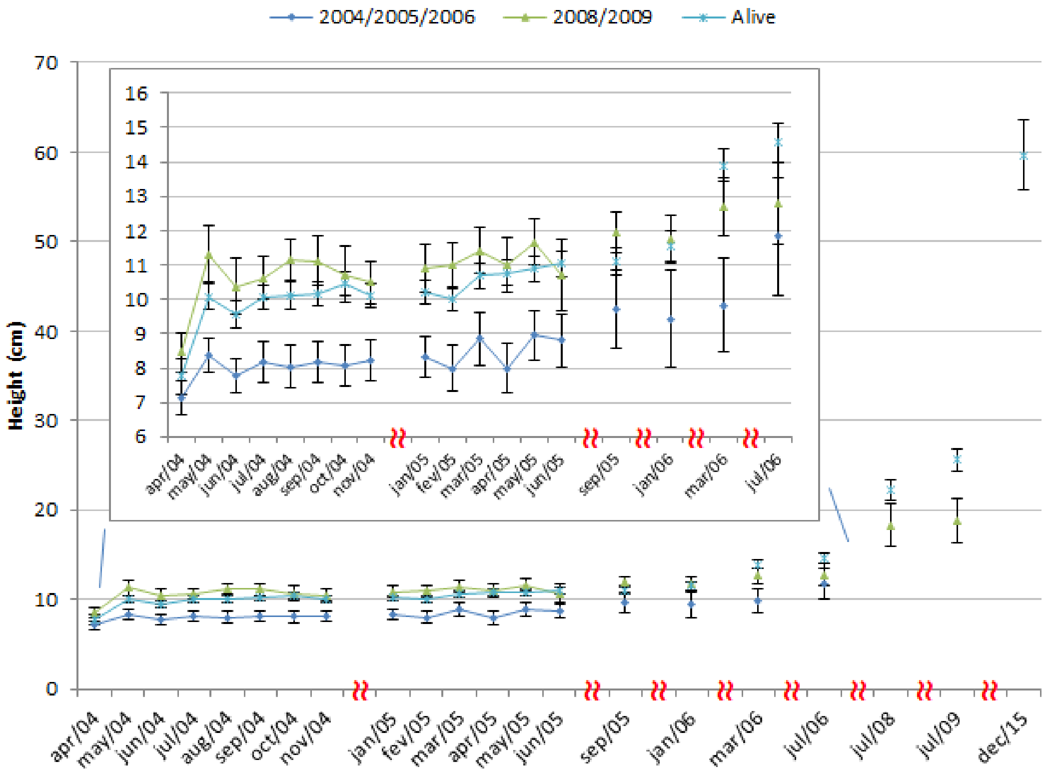

Figure I.15 - Height (mean ± SE) of holm oak trees under canopy and herb vegetation conditions for (1) trees dead in 2004-2006 (dark blue), (2) trees dead in 2008-2009 (green) and (3) living trees in 2015 (light blue).

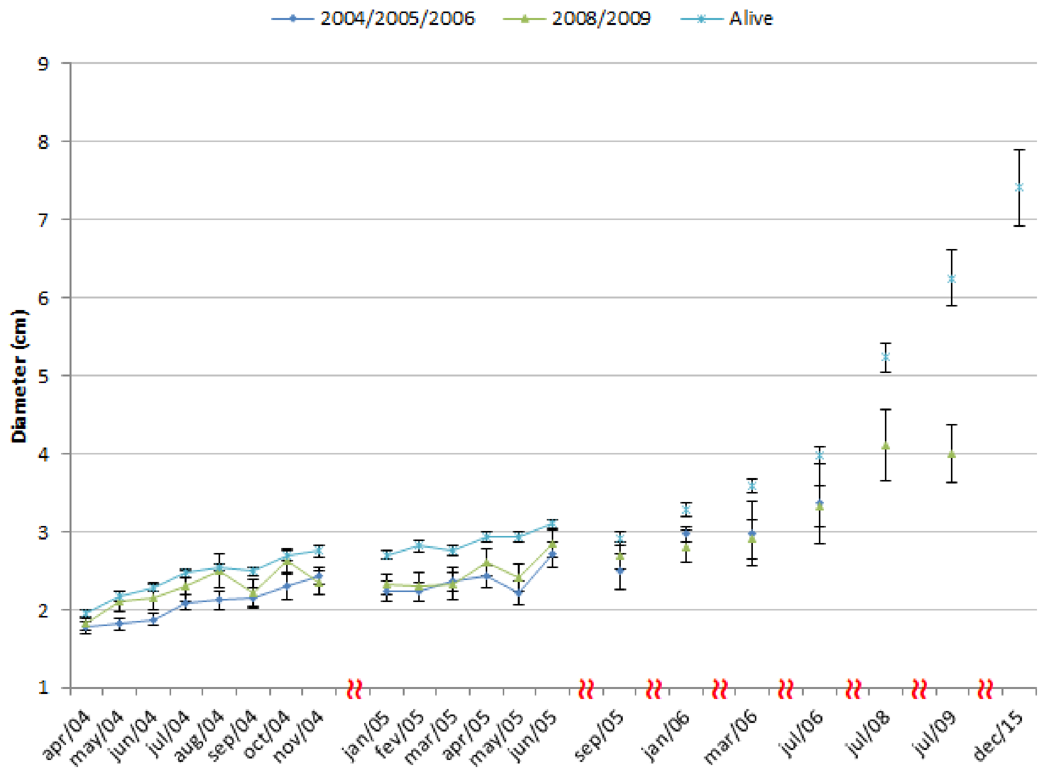

Figure I.16 - Diameter (mean ± SE) of holm oak trees under canopy and herb vegetation conditions for (1) trees dead in 2004-2006 (dark blue), (2) trees dead in 2008-2009 (green) and (3) living trees in 2015 (light blue).

Annex II - tree growth: canopy effect

The effect of the canopy on the height of living trees was compared for herb vegetation and no herb vegetation conditions, and for both species (Annex II). Under no herb vegetation (Figure II.1), the height of cork trees in the open was consistently higher when compared to the trees that grew under the canopy. For example, in June of 2005 and July of 2006 significantly higher heights were measured for saplings growing in the open (13.71 cm ± 0.59 and 17.69 cm ± 0.90, respectively) compared to saplings growing under the canopy (10.36 cm ± 0.33 and 14.89 cm ± 0.53, respectively). The mean heights of the holm oak trees under no herb vegetation conditions were generally higher in the open than under the canopy (Figure II.2), although not as consistently as in the case of cork oak. For example, in June of 2005 and July of 2006 higher heights were measured for saplings growing in the open (10.18 cm ± 0.53 and 14.92 cm ± 0.88, respectively) compared to saplings growing under the canopy (9.00 cm ± 0.34 and 13.06 cm ± 0.54, respectively).

Specifically, in July of 2006, trees' height was higher for living trees by 2015 compared to the tree's height in the same date of measure for trees that died in 2004-2006, which is valid for both cork oak and holm oak. Under no herb vegetation conditions, canopy had a negative effect on trees' final average height whereas this difference was clearer for cork oak. Thus, Open and no herb vegetation conditions led to taller cork and holm oak trees (Table 3). Trees' diameter in 2015 was consistently higher for open situations, both for cork and holm oak trees. Particularly in the case of cork oak growing under the canopy, herb vegetation had a positive effect on trees' final average height (62,38 cm ± 3,96). In the case of holm oak, the combination of open and no herb vegetation conditions led to the highest trees' average height in 2015 (80,18 cm ± 5,96). Generally, the same trend was observed for diameter. When comparing equivalent situations for cork and holm oak final heights, holm oak trees' height was higher for canopy and no herb vegetation conditions, while the opposite is true for diameter.

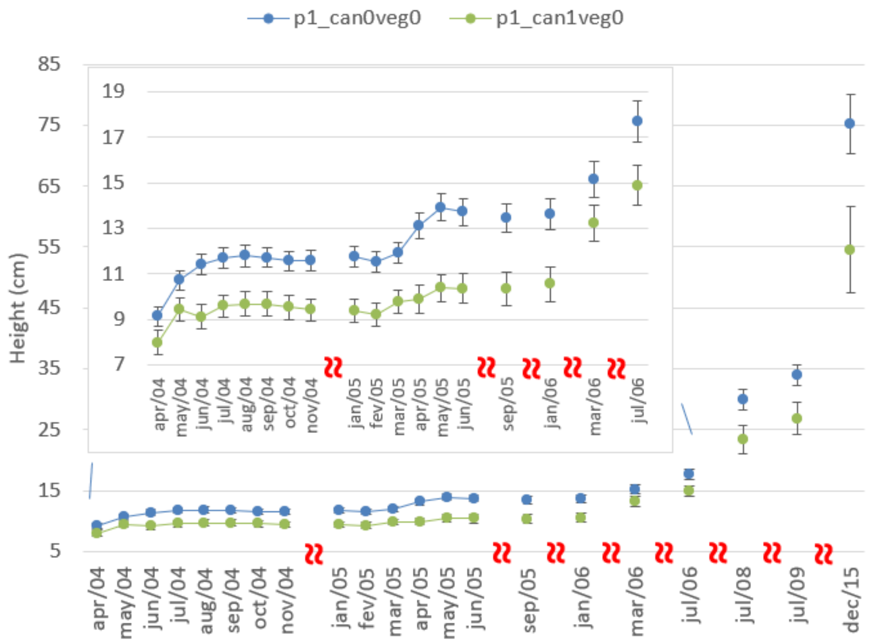

Figure II.1 - Height (mean ± SE) of living cork oak trees in 2015 under no herb vegetation conditions in the open (blue curve) and in the canopy (green curve).

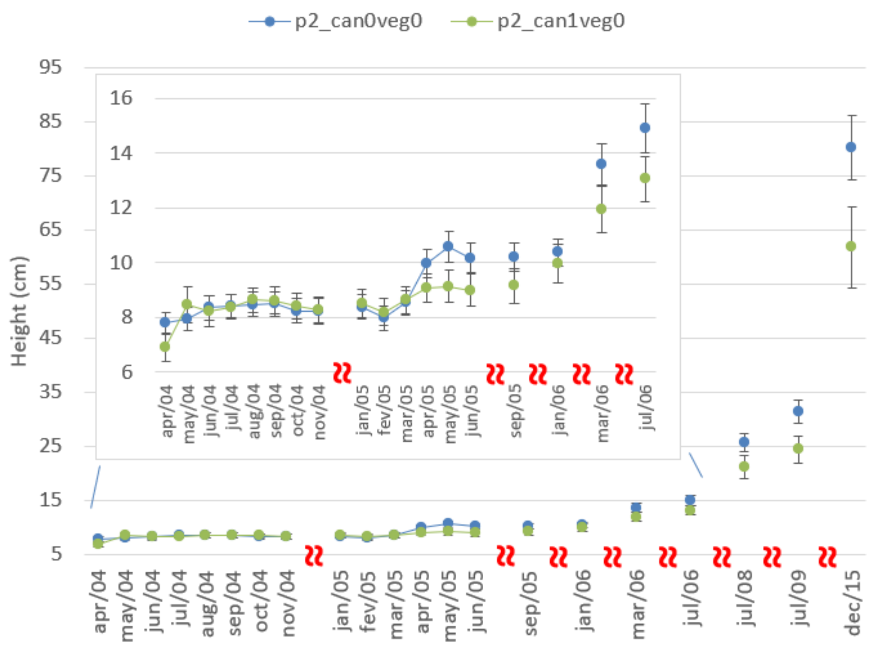

Figure II.2 - Height (mean ± SE) of living holm oak trees in 2015 under no herb vegetation conditions in the open (blue curve) and in the canopy (green curve).