UNIVERSIDADE DE ÉVORA

Mestrado em Biologia da Conservação

Dissertação

"Estratégias adaptativas de C*istus* a diferentes condições de secura e insolação"

Elsa Fonseca

Orientadora:

Dr.ª Margarida Vaz

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A natureza é o único livro que oferece um conteúdo valioso em todas as suas folhas.

Johann Goethe

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A/**PPFD** - Curves of photosynthetic response to photosynthetic photon flux density

ALE - Accumulated leaf emergence (n^{er})

ALS - Accumulated leaf shedding (n^{er})

A_{max} - Light-saturated photosynthetic rate (μmol CO_2 m^{-2} s^{-1})

BB - Brachyblasts

Ca – Leaf Calcium concentration (mg g^{-1})

CLAD - *Cistus ladanifer* L.

CMON - *Cistus monspeliensis* L.

CN - Climatological normals

CPOP - *Cistus populifolius* L.

CPSI - *Cistus psilosepalus* Sweet

DB - Dolichoblasts

gs - Stomatal conductance (mol m^{-2} s^{-1})

K – Leaf Potassium concentration (mg g^{-1})

LLF - Leaf litterfall (g m^{-2})

Mg – Leaf Magnesium concentration (mg g^{-1})

Mn – Leaf Manganese concentration (mg g^{-1})

N – Leaf nitrogen concentration (per area, mg cm^{-2}, and per mass, mg g^{-1})

OLF - Other litterfall (g m^{-2})

P - Leaf Phosphorus concentration (mg g^{-1})

PPFD - Photosynthetic photon flux density (μmol photons m^{-2} s^{-1})

$PPFD_{max}$ - Maximum photosynthetic photon flux density (μmol photons m^{-2} s^{-1})

R - Rainfall (mm)

R_d - Rate of respiration in the light (exclusive of photorespiration) (μmol CO_2 m^{-2} s^{-1})

Rs - Solar radiation (W m^{-2})

SE - Standard error

SLA - Specific leaf area (cm^2 g^{-1})

SWC - Soil water content (%)

T - Average air temperature (ºC)

TLF - Total litterfall (g m^{-2})

Tr - Transpiration rate (mmol H$_2$O m^{-2} s^{-1})

VPD - Vapour pressure deficit (kPa)

VPD$_L$ - Vapour pressure deficit based on leaf temp (kPa)

WS - Whole shoot

ΔΨ - Delta leaf water potential (MPa)

Φ - Initial slope (quantum yield) (μmol CO$_2$ m^{-2} s^{-1}/μmol photons m^{-2} s^{-1})

Ψ$_{IMD}$ - Mid-day leaf water potential (MPa)

Ψ$_{IPD}$ - Predawn leaf water potential (MPa)

D - RESUMO

"Estratégias adaptativas de C*istus* a diferentes condições de secura e insolação"

Na região Mediterrânica, os efeitos das alterações climáticas esperam-se sob a forma de longos períodos de seca, em especial em ecossistemas como o montado. Em montados com baixa regeneração natural, os arbustos podem proporcionar a germinação e o crescimento das suas plântulas. De março a outubro de 2012, foram caracterizadas as estratégias feno-morfológicas e fisiológicas de *Cistus ladanifer*, *Cistus monspeliensis*, *Cistus populifolius* e *Cistus psilosepalus*, através de medições fenológicas, teor de água no solo, potenciais hídricos, trocas gasosas e concentração de nutrientes. Os resultados obtidos sugerem que as estratégias de *C. ladanifer* e *C. monspeliensis* incluem mecanismos de tolerância à seca, *C. psilosepalus* de prevenção e, os mecanismos de *C. populifolius,* parecem estar entre a prevenção e a tolerância. Entender essas estratégias e respostas à seca, poderá permitir prever as futuras comunidades de espécies em cenários de crescente secura e o estabelecimento de diretrizes na gestão do montado.

E - ABSTRACT

"Adaptive strategies of *Cistus* to different conditions of drought and insolation"

In the Mediterranean region, the effects of climate change are expected in form of long periods of drought, particularly in ecosystems such as *montado*. In *montados* with low natural regeneration of their trees, shrubs may promote their seed germination and seedling growth. During March to October 2012, it was characterized the pheno-morphological and physiological strategies of *Cistus ladanifer*, *Cistus monspeliensis*, *Cistus populifolius* and *Cistus psilosepalus*, by phenological, soil water content, water potential, gas exchange and nutrient concentration measurements. The results suggest that the strategies of *C. ladanifer* and *C. monspeliensis* include drought-tolerance mechanisms, *C. psilosepalus* a drought avoidance mechanism and *C. populifolius* seem be in-between avoidance and tolerance. Understanding these strategies and responses to drought may be important for predicting future species assemblages in scenarios of increasing dryness and for laying down guidelines in *montado* management.

1 - INTRODUÇÃO GERAL

As plantas são uma componente fundamental dos ecossistemas, constituindo a sua estrutura física e, são de importância essencial para a o funcionamento da atmosfera do planeta (Bilz et al. 2011), influenciando expressivamente o clima e os recursos hídricos (Hamilton e Hamilton 2006).

O ritmo biológico das plantas, reflete a adaptabilidade das espécies em explorar condições ambientais favoráveis, de forma a obterem ganhos de carbono e alocar produtos resultantes da fotossíntese para o crescimento e a reprodução (Correia et al. 1992; Gratani e Crescente 1997). Uma variedade de padrões fenológicos evoluiu de forma a otimizar a adaptação à flutuação sazonal da disponibilidade de água (Simões et al. 2008) e de nutrientes do solo (Correia et al. 1992), particularmente em climas marcadamente sazonais, como o tipo Mediterrânico (Gill e Mahall 1986), onde os principais pulsos de disponibilização ocorrem no início da primavera e do outono (Simões 2003), sendo a seca uma restrição para o crescimento e a produtividade das espécies perenes (Gratani et al. 2006; Mooney et al. 1974).

Nesses ecossistemas, as plantas devem conseguir resistir a um verão longo, quente e seco, quando o défice hídrico está associado a elevadas intensidades de luz e temperaturas, que impõem restrições à assimilação de carbono (Faria et al. 1998; Chaves et al. 2002; Pereira et al. 2004, 2007), sendo os défices hídricos atenuados pelas chuvas de outono (Vaz et al. 2010).

As respostas da fotossíntese à redução da água do solo compreendem duas fases distintas: a primeira, caracterizada por uma diminuição da condutância estomática (Faria et al. 1998; Chaves et al. 2002, 2003; Centritto et al. 2003; Flexas et al. 2006, 2007) e uma diminuição da condutância no mesófilo (Flexas et al. 2006, 2007; Galmés et al. 2007a, 2007b) e, uma segunda fase, em que continuadas reduções da condutância estomática podem conduzir a prejuízos metabólicos (Flexas et al. 2006). Quando o stresse hídrico se desenvolve progressivamente ao longo de semanas ou meses, alterações bioquímicas na folha, que resultam numa diminuição da regulação do metabolismo fotossintético, podem ocorrer como resposta à redução de substratos de carbono (Chaves e Oliveira 2004; Flexas et al. 2007), causada pela restrição estomática (Vaz et al. 2010).

1.1 - Alterações climáticas previstas

Na Europa e, em especial na região mediterrânica, os efeitos das alterações climáticas prevêem-se sob a forma de aumento da temperatura média anual, redução da precipitação média anual, acentuação da mediterraneidade (sazonalidade climática) e, aumento da frequência de episódios de precipitação intensa e de períodos longos de seca. Prevê-se que as temperaturas médias aumentem 2–4 °C nos próximos 50 anos e causem alterações consideráveis nos padrões regionais e sazonais de precipitação (IPCC 2007).

No continente europeu, Thuiller et al. (2005) preveem que em 2080 as alterações climáticas resultarão numa perda de 27–42 % das espécies, com extremos potenciais variando de 2,5–86 % de perda da diversidade florística atual. Assim, a longo prazo, pensa-se que as alterações climáticas se tornem um fator expressivo que ameace as espécies vegetais. As alterações na temperatura e, mais importante a disponibilidade de água, poderão resultar em modificações na distribuição das espécies e das comunidades e numa forte pressão seletiva para mais genótipos com maior capacidade de adaptação (Maxted et al 2008). A água é um dos fatores mais limitantes para o crescimento das plantas em ambientes semiáridos e regula muitos processos ecológicos, não só devido à sua escassez, mas também por causa da sua variabilidade no espaço e no tempo e, pela imprevisibilidade das chuvas (Ehleringer et al 1999; Lázaro et al. 2001; Schwinning e Sala 2004; Sher et al. 2004).

Supõem-se que as alterações climáticas previstas venham a influenciar diretamente as relações planta-inseto que co-evoluíram (Harrington et al. 1999), e consequentemente a fenologia, o ciclo de vida, o crescimento e as taxas de desenvolvimento das plantas (Bornman e Teramura 1993), podendo desta forma resultar em alterações dramáticas na sua distribuição (Bale et al. 2002), nomeadamente, em ecossistemas muito particulares como o montado.

1.2 - O montado

O montado, enquanto ecossistema mediterrânico, encontra-se sob a influência de um clima húmido, com a precipitação concentrada no inverno, em que os meses mais quentes apresentam temperaturas médias superiores a 22 ºC (Pereira et al. 2009). Nas

regiões em que se situa este ecossistema a variabilidade inter-anual da precipitação é elevada, apresentando um coeficiente de variação da ordem dos 30 % para o Alentejo, traduzindo-se na ocorrência frequente de secas, especialmente nas regiões mais a Sul (Pereira e Paulo 2004). Por outro lado, a repartição da precipitação e da evapotranspiração potencial ao longo do ano apresentam características marcadamente sazonais (Pereira et al. 2009).

Os montados encontram-se seriamente ameaçados pelo pouco cuidado que tem sido dedicado à regeneração natural de sobreiros e azinheiras. Em Portugal, os povoamentos denotam uma idade avançada, uma menor densidade devida à intensidade das práticas agrícolas e a uma incidência preocupante de pragas e doenças. As práticas agrícolas e a condução dos animais em pastoreio que se têm desenvolvido nos montados não são adequadas aos processos de dispersão, estabelecimento de jovens plantas e ao seu desenvolvimento até árvores adultas. Em montados mais densos, o pastoreio pode até ter efeitos benéficos no vigor da recuperação do arvoredo, pela remoção da vegetação herbácea e de algum mato potenciadores de incêndios. Noutros casos, dever-se-á excluir o pastoreio durante períodos variáveis, em função da espécie pecuária e da situação de partida, ou conciliar os matos com o pastoreio, de forma a permitir a germinação das bolotas e proceder posteriormente à proteção dos renovos (Pereira et al. 2009).

Sendo o montado um ecossistema com elevado número de árvores adultas, comparativamente à sua taxa de regeneração, a manutenção e gestão dos arbustos são de grande importância, uma vez proporcionarem um microclima e um substrato vegetal favorável às plântulas que ocorram sob as suas copas. Desta forma, torna-se relevante determinar quais os arbustos a manter, tendo em conta a sua eficiência e os que s supõe melhor resistirem às alterações climáticas previstas, como o aumento da temperatura do ar e da seca na região Mediterrânica (Miranda et al. 2002). Assim, tornam-se necessários mais estudos acerca de onde e, porque motivos, determinadas espécies poderão prevalecer sobre outras (Simões et al. 2008).

1.3 - Objetivos

A presente dissertação, apresentada sob a forma de artigo científico e a submeter a uma revista indexada ao sistema *ISI web of knowledge*, tem como objetivo caracterizar as estratégias feno-morfológicas e fisiológicas subjacentes ao crescimento e sobrevivência de quatro espécies de *Cistus*, *Cistus ladanifer* L., *C. monspeliensis* L., *C. populifolius* L. e *C. psilosepalus* Sweet, que coocorrem nas atuais condições de seca no Mediterrâneo. Entender essas estratégias e respostas à seca, pode ser importante para prever as futuras comunidades de espécies em cenários de crescente secura e o estabelecimento de diretrizes na gestão do montado. Para o efeito, foram efetuadas medições fenológicas, de teor de água no solo, potencial hídrico foliar, medições de trocas gasosas foliares e análise de curvas de resposta à luz, área foliar específica, quantificação de folhada e concentração de nutrientes.

1.4 - Plantas em estudo: *Cistus*

Na Bacia do Mediterrâneo, a vegetação nativa é caracterizada por um matagal denso com espécies anuais, de folha caduca e semi-decídua, tolerantes à seca e por espécies esclerófilas lenhosas perenes (Mooney e Dunn 1970). Espécies esclerófilas estão adaptadas à baixa disponibilidade de água durante o verão, por meio de folhas pequenas, coriáceas e escuras cobertas por pequenas e grossas cutículas (Read e Sanson 2003). Pequenas folhas e área foliar específica reduzida têm sido vistas como adaptações ao clima do tipo Mediterrânico em muitas espécies de plantas perenes (Ackerly 2004).

Componentes arbustivas significativas nos ecossistemas Mediterrânicos pertencem à família Cistaceae, sendo o género *Cistus* um dos mais característicos, particularmente predominantes em matagais (Carlier et al. 2008). A maioria dos *Cistus* têm uma vida útil relativamente curta (10–20 anos), apesar de *Cistus ladanifer* L. ter maior longevidade, com uma vida útil de 30–50 anos (Arianotsou-Faraggitaki e Margaris 1982; Roy e Sonie 1992; Patón et al. 1998).

Para além da sua importância ecológica, este género inclui espécies que produzem metabolitos com importância económica e/ou têm grande potencial para aplicações industriais ou medicinais (Carlier et al. 2008). Arbustos *Cistus* melhoraram os níveis

hídricos, de nutrientes, taxas de assimilação de carbono e de crescimento, criando condições microclimáticas e propriedades físico-químicas no solo para as plântulas que ocorrem sob as suas copas (Armas e Pugnaire 2005). Além disso, a sombra destas plantas reduz as amplitudes térmicas e a evaporação da água do solo (Domingo et al. 1999), podendo ainda facilitar a germinação de sementes e o crescimento de plântulas. A sombra proporcionada também reduz o stresse térmico e a transpiração das plantas de sub-bosque, protegendo-os da foto-inibição (Nobel 1980; Fuentes et al. 1984; Vetaas 1992; Moro et al. 1997).

A conservação e a gestão, nomeadamente dos matos são, assim, fundamentais para uma redução da erosão dos solos, devido à acumulação de matéria orgânica por parte destes (Andreu et al. 1998). Os matos proporcionam regeneração natural de árvores e sobrevivência de plântulas que ocorrem sob a proteção da cobertura arbustiva (Plieninger et al. 2003, 2004), assim como promovem biodiversidade, constituindo um habitat para muitas espécies (Simões et al. 2009).

Arbustos como *Cistus* podem, desta forma, ser associados não apenas a estágios de sucessão regressiva mas, também, à regeneração e a estágios de sucessão progressiva secundária. Manchas de solo sob a copa de arbustos podem ser importantes locais sumidouros de nutrientes que influenciam a estrutura da comunidade. Desta forma, a manutenção do estrato arbustivo pode promover o desenvolvimento de espécies mais exigentes uma vez que, áreas de elevada fertilidade, são suscetíveis de serem locais privilegiados para a regeneração da vegetação (Simões et al. 2009).

1.4.1 - *Cistus ladanifer* Linnaeus (1753)

C. ladanifer ocorre no sul da França, na metade ocidental da Península Ibérica e no norte de África (Marrocos e Argélia). É uma espécie de clima quente e seco, com invernos chuvosos e ocorre em solos siliciosos (Castroviejo et al. 1993). Frequentemente, é a única espécie lenhosa a resistir no matagal tipicamente seco, em solos ácidos e pobres em nutrientes (Carlier et al. 2008). Desenvolve-se a uma altitude ente os (0) 300–1000 (1500) m (Guzmán et al. 2009) e, em termos de condições de insolação, é uma espécie subheliofila (Dansereau 1958), predominando em florestas degradadas de *Quercus suber/ilex* (Guzmán et al. 2009). As suas folhas possuem uma

forma linear-lanceolada (Figura 1) de comprimento entre os 40–80 mm e de largura 6–21 mm (Guzmán et al. 2009). As suas folhas são de margem plana, venação pinada e de superfície lisa e textura coriácea (Guzmán et al. 2009).

C. ladanifer tem sido utilizada na região Mediterrânica desde a antiguidade (Deforce 2006) pela sua produção de resina aromática, o labdanum, cuja secreção é de cerca de 12,5 % (Gülz et al 1996).

Figura 1. *Cistus ladanifer* L. (Detalhe das folhas à esquerda e da flor à direita).

1.4.2 - *Cistus monspeliensis* **Linnaeus (1753)**

C. monspeliensis ocorre na região mediterrânica, Madeira e Tenerife e, assim como *C. ladanifer,* é uma espécie de clima quente e seco, e de invernos chuvosos (Castroviejo et al. 1993) e ocorre em solos siliciosos (Guzmán et al. 2009). É uma espécie arbustiva de pequeno porte, semi-decídua de verão com dimorfismo foliar entre o verão e o inverno (Correia et al. 1992; de Lillis e Fontanella 1992). Desenvolve-se a uma altitude ente os 0–800 (1200) m (Guzmán et al. 2009) é uma espécie subheliofila (Dansereau 1958), predominando em florestas degradadas de *Quercus suber/ilex* e de *Pinus* (Guzmán et al. 2009). As suas folhas possuem uma forma linear-lanceolada (Figura 2) de comprimento entre os 15–45 mm e de largura 2–7 mm (Guzmán et al. 2009). As suas folhas são de margem plana ligeiramente revolutosa, venação paralela e de superfície lisa e textura coriácea (Guzmán et al. 2009). A secreção de labdanum, ronda os 10,7% (Gülz et al 1996).

Figura 2. *Cistus monspeliensis* L.

1.4.3 - *Cistus populifolius* **Linnaeus (1753)**

C. populifolius está restrito à Península Ibérica e Narbonne, Aude (França) (Castroviejo et al. 1993). É de clima seco (Guzmán et al. 2009), mas, em termos de condições de insolação, é uma espécie submesófila (Dansereau 1958), ocorrendo em locais mais sombrios e barrancos frescos (Castroviejo et al. 1993). Desenvolve-se em solos siliciosos (Guzmán et al. 2009), é uma espécie calcífuga (Castroviejo et al. 1993) e ocorre numa altitude entre 200–1500 m (Guzmán et al. 2009) em florestas degradadas de *Quercus* e *Pinus* (Guzmán et al. 2009). As suas folhas possuem uma forma ovado-lanceoladas (Figura 3) de comprimento entre os 50–95 mm e de largura 25–55 mm (Guzmán et al. 2009). De margem plana e venação pinada, as suas folhas possuem uma superfície lisa de textura coriácea (Guzmán et al. 2009). A secreção de labdanum, ronda os 5,6 % (Gülz et al 1996).

Figura 3. *Cistus populifolius* L. (Detalhe das folhas à esquerda e da flor à direita).

1.4.4 - *Cistus psilosepalus* Sweet (1826)

C. psilosepalus ocorre a N, NW e W da Península Ibérica. É uma espécie de climas húmidos e de zonas de influência oceânica e de verões secos (Castroviejo et al. 1993) e, é uma espécie submesófila (Dansereau 1958). Ocorre sobre solos siliciosos (Guzmán et al. 2009) sendo, tal como *C. populifolius*, uma espécie calcífuga (Castroviejo et al. 1993). Pode ser encontrado a uma altitude entre 0–800 (1100) m em matagais (Guzmán et al. 2009). As suas folhas possuem uma forma lanceolado-elíptica (Figura 4) de comprimento entre os 30–65 mm e de largura 10–23 mm (Guzmán et al. 2009). Estas são de margem plana, venação reticulada e de superfície lisa e textura macia (Guzmán et al. 2009). A secreção de labdanum, é de apenas 2,0 % (Gülz et al 1996).

Figura 4. *Cistus psilosepalus* Sweet.

1.5 - Área de estudo

O estudo foi realizado no sul de Portugal, perto de Évora, (38° 32' N; 8° 01' W; 240 m de altitude), em ambiente de montado, onde o clima é tipicamente mediterrânico, com invernos húmidos e verões secos (Simões et al. 2009). A média da quantidade de precipitação total é 609,4 milímetros, a temperatura média anual é de 15,9 ° C (normais climatológicas para 1971–2000) e, o período seco pode durar até cinco meses (Simões et al. 2008).

Em termos da tipologia bioclimática, a área de estudo encontra-se no macroclima mediterrâneo (Rivas-Martínez et al. 2004), apresentando um período seco bem definido, nos meses de verão, com precipitação inferior ao dobro da temperatura, em pelo menos

dois meses do ano (Capelo 1996). O bioclima é Mesomediterrânico Pluviestacional oceânico (Rivas-Martínez et al. 2004).

Biogeograficamente localiza-se no Reino Holárctico, Região Mediterrânica, Subregião Mediterrânica Ocidental, Província Mediterrânica Ibérica Ocidental, Sub-província Luso-Extremadurense, Sector Marianico-Monchiquense, Subsector Araceno-Pacense e Distrito Alentejano (Costa et al. 1998; Rivas-Martínez et al. 2002).

A paisagem é suavemente ondulada, com inclinações variando entre os 3 e os 8% e o substrato geológico consiste em granitos e gnaisses (Carvalhosa et al. 1969). Os solos são de origem granítica e correspondem a Leptossolos e Cambissolos Quartzosos (WRB 2006), com uma textura de argila-arenosa a areia-argilosa (Driessen et al., 2001).
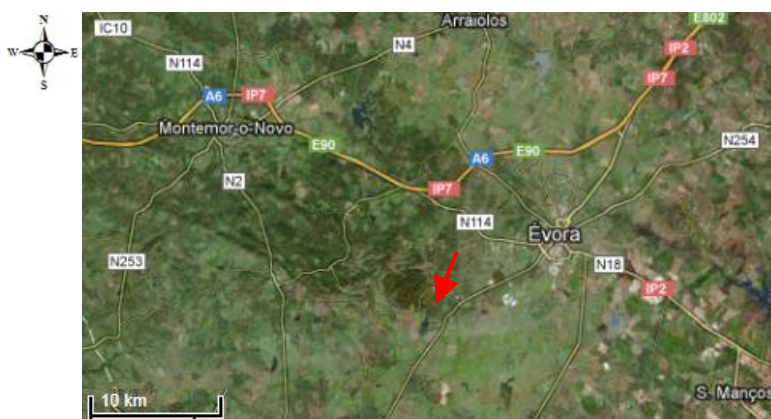
Figura 5. Localização da área de estudo (fonte: Google maps 2013)

2 - ARTIGO CIENTÍFICO

Plant/Leaf traits and adaptive strategies of *Cistus* species to Mediterranean drought and insolation

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Abstract

In the Mediterranean region, the effects of climate change are expected in the form of increase in mean annual temperature, mean annual precipitation decreased and long periods of drought, particularly in very specific ecosystems such as *montado*. The *montados* are seriously threatened by the reduced attention that has been dedicated to natural regeneration and shrubs may promote their seed germination and seedling growth. In this context, it was characterized, during March to October 2012, the pheno-morphological and physiological strategies of *Cistus ladanifer*, *Cistus monspeliensis*, *Cistus populifolius* and *Cistus psilosepalus*, by phenological, soil water content, water potential, gas exchange, specific leaf area, litterfall and nutrient concentration measurements. The results suggest that the strategies of *C. ladanifer* and *C. monspeliensis* include drought-tolerance mechanisms, *C. psilosepalus* a drought avoidance mechanism and *C. populifolius* seem be in-between avoidance and tolerance. It seems that the diversity of *Cistus* may decrease in scenarios of dryness and *C. ladanifer* and, in particularly, *C. monspeliensis,* among the studied species, will be dominant shrub species. Understanding these strategies and responses to drought may be important for predicting future species assemblages in scenarios of increasing dryness and for laying down guidelines in *montado* management.

Introduction

In Europe, and especially in the Mediterranean region, the effects of climate change are expected in the form of increase in mean annual temperature, mean annual precipitation decreased, accentuation of mediterraneaty (climatic seasonality) and increased frequency of episodes of intense precipitation and long periods of drought. An increase of 2–4 °C in average temperatures is predicted in the next 50 years, with considerable changes in the patterns of regional and seasonal precipitation (IPCC 2007). Changes in temperature and, more importantly, in the availability of water, may result in changes in the distribution of species and communities and in a strong selective pressure for more genotypes with greater adaptability (Maxted et al 2008). It is assumed that the expected climate change will directly affect plant-insect associations that co-evolved (Harrington et al. 1999), phenology, life cycle, growth and plant development rates (Bornman & Teramura 1993), which can result in dramatic consequences in their distribution (Bale et al. 2002), particularly in very specific ecosystems such as *montado*.

The *montado*, while Mediterranean ecosystem, is under the influence of a humid climate, with rainfall concentrated in the winter, in which the warmer months present mean temperatures above 22 ºC (Pereira et al. 2009). In regions where this ecosystem is situated the inter-annual variability of rainfall is high, with a variation coefficient in the order of 30 % for the Alentejo, resulting in frequent occurrence of droughts, especially in the southern regions (Pereira & Paulo 2004). Moreover, the distribution of precipitation and potential evapotranspiration throughout the year also has markedly seasonal features (Gill & Mahall 1986; Pereira et al. 2009) with the main pulses release occurring in early-spring and -autumn (Simões 2003). Drought is a primary constraint for growth and productivity of perennial species (Gratani et al. 2006; Mooney et al. 1974) and a variety of phenological patterns occurs to optimise adaptation to the seasonal fluctuation of water availability (Simões et al. 2008) and soil nutrients (Correia et al. 1992).

In these ecosystems, plants should resist to a long, hot and dry summer, when the water deficit is associated with high light intensities and temperatures by imposing restrictions on carbon assimilation (Faria et al. 1998; Chaves et al. 2002; Pereira et al. 2004, 2007). Water deficits are alleviated by the autumn rains (Vaz et al. 2010). The responses of photosynthesis to soil water depletion comprise two distinct phases: a first stage characterized by a decrease in stomatal conductance (Faria et al. 1998; Chaves et

al. 2002, 2003; Centritto et al. 2003; Flexas et al. 2006, 2007) and decrease in mesophyll conductance (Flexas et al. 2006, 2007; Galmés et al. 2007a, 2007b) and a second stage in which further decreases in stomatal conductance may coincide with metabolic impairment (Flexas et al. 2006). When water stress develops gradually over periods comprising weeks or months, changes in leaf biochemistry that result in the downregulation of photosynthetic metabolism may occur in response to lowered carbon substrates (Chaves & Oliveira 2004, Flexas et al. 2007), caused by stomatal restriction (Vaz et al. 2010).

Significant components shrub in Mediterranean ecosystems belongs to the Cistaceae family, in which *Cistus* is one of the most characteristic genera (Carlier et al. 2008). Conservation and management of shrubs are fundamental to prevent soil erosion due to accumulation of organic material produced (Andreu et al. 1998) and improved water and nutrients levels, carbon assimilation rates and growth, creating microclimatic conditions and physico-chemical properties in the soil of seedlings that occur under their canopies (Armas & Pugnaire 2005). Furthermore, the shadow reduces the thermal amplitudes of these plants and evaporation of soil water (Domingo et al. 1999), and may also facilitate seed germination and seedling growth. The shade provided also reduces heat stress and plant transpiration from the understory, protecting them from photo-inhibition (Nobel 1980; Fuentes et al. 1984; Vetaas 1992; Moro et al. 1997). Shrubs as *Cistus* may be associated not only with stages of retrogressive succession, but also with stages of secondary progressive succession. Soil patches observed beneath shrub canopies may be important local nutrient sinks that influence community structure. Therefore, shrub development may promote the invasion of more demanding species, since local areas of high fertility are likely to be favoured sites for vegetation regeneration (Simões et al. 2009).

The *montados* are seriously threatened by the reduced of natural regeneration of cork and holm oaks (*Quercus suber* and *Quercus rotundifolia*). *Montados* denote an advanced age, a lower density due to the intensity of farming practices and an increasing incidence of pests and diseases. Since the *montado* is an ecosystem with large numbers of mature trees, compared to its rate of regeneration, the maintenance and management of shrubs are of major importance, since they provide a microclimate and a favorable vegetal substrate to plant seedlings that occur under their canopies. Thus, it becomes relevant to determine which shrubs to maintain, taking into account its efficiency and which species are expected better resist to the expected climate change.

In this context, it was compared, under the same constraints of climate, the life strategies of *Cistus ladanifer* L., *C. monspeliensis* L., *C. populifolius* L. and *C. psilosepalus* Sweet, in order to determine their potential ability to adapt and survive to the climate change expected for the Mediterranean region. Our main objective was to characterize the pheno-morphological and physiological strategies underlying growth and survival of four co-occuring *Cistus* species in current Mediterranean drought conditions. Understanding these strategies and responses to drought may be important for predicting future species assemblages in scenarios of increasing dryness and for laying down guidelines in *montado* management.

Materials and methods

Study area

The study was carried out in southern Portugal, close to Évora, (38° 32' N; 8° 01' W; 240 m a.s.l.), in an environment of *montado*. The area has the typical winter-wet, summer dry pattern of the Mediterranean-type climate. Mean annual rainfall is 609.4 mm and mean annual temperature is 15.9 °C (Climatological normals for 1971-2000, Figure 1), and the dry period lasts up to five months (Simões et al. 2008).

In terms of bioclimatic approach (Rivas-Martínez et al. 2004), it is located in the MesoMediterranean, lower dry to subhumid belt of the Mediterranean pluviseasonal-oceanic bioclimate and biogeographically stands as the Lusitan-Extremadurean Province (Marianic-Monchiquensean Sector) of the Mediterranean region. The landscape is gently undulating with slopes varying from 3 to 8 % and the geological substratum consists of granites and gneisses (Carvalhosa et al. 1969). The soils are developed from granites and correspond to dystric Leptosols and dystric Cambisols (WRB 2006), with loam sandy to sandy loam texture (Driessen et al. 2001).
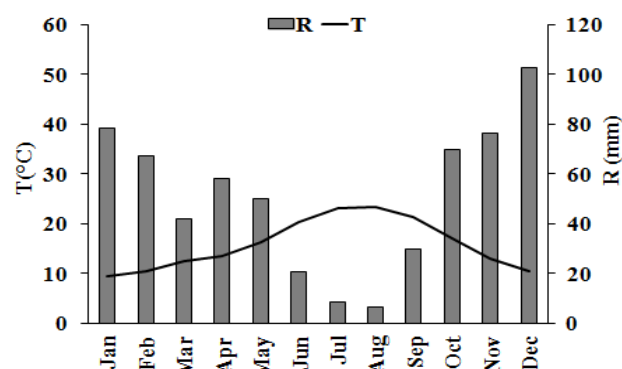
Figure 1. Climatological normals (CN) for 1971−2000 (T: average air temperature and R: total rainfall) for the study area.

Study species

Cistus ladanifer L. (hereafter CLAD), *C. monspeliensis* L. (hereafter CMON), *C. populifolius* L. (hereafter CPOP), and *C. psilosepalus* Sweet (hereafter CPSI) are shrubs that typically occur under Mediterranean conditions. CLAD occurs in the western Mediterranean region, from Portugal and Morocco to the Côte d'Azur and Algeria; CMON in the Mediterranean region (halfway S and around the Mediterranean coast and the Balearic Islands), Madeira and Tenerife; CPOP is restricted to the Iberian Peninsula, Narbonne (Aude, France) and N Morocco; and CPSI to N, NW and W of the Iberian Peninsula. Although the four species usually inhabit regions with Mediterranean climate, where they have to endure a hot and dry summer, in terms of insolation CLAD and CMON are subheliophyllous species, while CPOP is mostly found in fresh and shadowy places and CPSI in conditions of high relative humidity and oceanic influence, both species being submesophyllous. They all occur in siliceous soils, and CPOP and CPSI are even calcifugous species. CLAD grows at altitudes between 300–1000 m, CMON and CPSI between 0–800 m and CPOP between 200–1500 m. CLAD predominates in degraded *Quercus* woodlands and CMON and CPOP in degraded *Pinus* woodlands, while CPSI is mainly found in shrublands. The four species produce long shoots or dolichoblasts (DB), and shoots characterized by much reduced internode lengths, or brachyblasts (BB), developed at the axils of DB leaves. Previous-year BB can differentiate into DB. In the present study, we consider DB as those branches longer than 3 cm and BB as those shorter than 3 cm. CLAD and CMON have coriaceous linear-lanceolate leaves (length x width: 40–80 x 6–21 mm in CLAD and 15–45 x 2–7 mm in CMON), while those of CPOP are coriaceous ovate-lanceolate (50–95 x 25–55 mm) and those of CPSI are soft and lanceolate-elliptic (30–65 x 10–23 mm). Labdanum secretion in CLAD, CMON, CPOP and CPSI is 12.5 %, 10.7 %, 5.6 % e 2.0 %, respectively (Dansereau 1958; Castroviejo et al. 1993; Gülz et al 1996).

Meteorological data

A weather station was installed in the study area for measurements of solar radiation (Rs) with a albedometer, CM7B, Germany, dry and wet bulb temperatures with a hygro-Thermo Transmitter, Germany and rainfall (R) with a tipping Bucket Rain Gauge, 52203, USA). Data were recorded as 1 hour means with a CR10 data logger (Campbell

Scientific, Utah, USA). Air vapour pressure deficit (VPD) was calculated from dry and wet bulb temperatures.

Phenological measurements

Observations and measurements were carried out during March–October 2012, on nine randomly selected shrubs per species. For phenological measurements the distinction between dolichoblasts and temporary brachyblasts proposed by Orshan (1989) was used. On 28 February, one apparently healthy dolichoblast in each individual shrub was labeled, for repeated non-destructive measurements. Different positions and exposures were taken in consideration. Since the start of the study did not coincide with the beginning of the growing season, labeling was performed at the level of a node that appeared to have begun growth in the current growing season so that all newly formed organs could be included in monitoring. Leaf emergence and shedding, brachyblast formation and shedding, flower bud formation, flowering and fruiting setting were monitored. All newly formed and shed organs were counted separately for dolichoblasts and brachyblasts. Monthly observations are considered to give a fair indication of phenology but fortnightly observations are recommended when possible Fournier & Charpantier (1975). Since both growth and phenophase shift are reported to occur faster in spring for most *Cistus* species (Pereira et al. 1987; Correia et al. 1992; Gratani & Crescente 1997; Castro-Díez & Montserrat-Martí 1998; Simões et al. 2008), sampling was conducted fortnightly from March to May and monthly from June to October.

Soil water content

The soil water content (SWC) was determined by the gravimetric method (Rundel & Jarrell 1989), in April, June, September, and October 2012. In each sampling date, three soil samples were collected beneath three individuals of each study species, at 0–10 and 10–20 cm soil depth. Samples were weighed to obtain wet soil mass, dried (105 °C during 48 h), and weighed again to obtain dry soil mass.

Leaf water potential

Predawn and mid-day (just before sunrise and around midday solar time, respectively) leaf water potential (Ψ_{IPD}, Ψ_{IMD}) was measured on a monthly basis, from April to November 2012, with a Scholander pressure chamber (PMS 1000, PMS Instruments, Corvallis, USA). A total of twelve leaves were sampled for specie (3 leaves for each shrub in 4 shrubs). It was calculated delta leaf water potential ($\Delta\Psi=\Psi_{IPD}$ -Ψ_{IMD}). At midday solar time, samples were taken in the south-facing side of the crown and at similar heights aboveground to avoid variability caused by hydrostatic water potential and immediately placed in a plastic bag to prevent further transpiration.

Leaf gas exchange measurements and micro-environmental conditions

Gas exchange measurements in environmental conditions were done with a portable steady-state photosynthetic system (Li-6400; Li-Cor, Lincoln, NE) in three seasons of 2012: spring (a pre-drought period, April-May), final summer (a drought period, August-September) and autumn (an after drought period, October-November) on fully expanded leaves from the current-year spring flushing. Photosynthetic rate (*A*), and stomatal conductance (*gs*), transpiration rate (Tr) and vapour pressure deficit based on leaf temp (VPD_L) under natural environmental conditions were measured in the morning periods (9.00h-10.00h). Leaf temperature (Lt) and photosynthetic photon flux density (PPFD) incident on the leaf surface were, respectively, measured with a 6400-04 leaf temperature thermocouple and a 9901-013 external quantum sensor coupled to an infrared gas exchange analyser (IRGA) (Li-6400, Li-Cor Inc., Lincoln, Nebraska, USA). The accuracy and reliability of both sensors were tested previously.

Curves of photosynthetic response to photosynthetic photon flux density (*A*/PPFD) were realized in the same three seasons in eight leaves of each shrubs (three shrubs of each species). The *A*/PPFD curves were conducted under a CO_2 concentration of 360 ppm, leaf temperature of around 25 ± 2 °C. The light intensity provided with a 6400-02B LED source with red and blue LEDs (665 and 470 nm, respectively), was decreasing from 2000, 1500, 1000, 500, 200, 100, 50 and 0 μmol photons m^{-2} s^{-1}. The leaves were allowed to equilibrate for 10 min before logging data in *A*/PPFD curves. These measurements were completed during the morning to avoid the midday depression of photosynthesis and stomatal conductance.

Specific leaf area

To assess the specific leaf area (SLA) of leaves monitored for measurements, leaf area was measured using imaging software (Image J, 1.32 J, USA Institutes of National Health) and leaf weight was measured after drying at 70 ºC until stable weight.

Litterfall

Litterfall was assessed using litter traps (1.5 mm mesh screen with 80 x 80 cm^2 collecting surface) placed under shrub canopies, elevated ca. 6 cm above the ground. Shrubs (nine per species) and litter collecting dates (fortnightly, from March to May 2012, and monthly during the remaining study period) were those used for phenological measurements. Litterfall collections were sorted into leaves and other components. After drying (80 ºC), leaf litterfall and other litterfall were weighed. Leaf litterfall samples were pooled resulting in one sample per species and month, and a subsample was taken for chemical analysis.

Nutrient concentrations

Samples of leaves used for gas exchange measurements and of leaf litter were dried and ground to pass through a 0.5 mm mesh screen. Nitrogen in both green leaves and leaf litter was determined using Kjeldhal digestion (Digestion System 40, Kjeltec Auto 1030 Analyzer). The C amount was calculated assuming an average 50 % C content of ash-free mass. The mineral elements (P, K, Ca, Mg and Mn) in leaf litter were determined after ashing (6 hr at 450 ºC) and taken up in HCl. K, Ca, Mg and Mn were determined by atomic absorption spectrophotometry. Concentration of P was measured colorimetrically following the method described by Watanabe & Olsen (1965).

Data analysis

Soil water content (SWC) was determined by the equation SWC (%) = [(mass of wet soil - mass of dry soil) / mass of dry soil] * 100. Delta leaf water potential ($\Delta\Psi$) was calculated by $\Delta\Psi = \Psi_{lMD} - \Psi_{lPD}$ and specific leaf area (SLA) was determined by the equation SLA = fresh leaf area/leaf dry weight.

For the analysis of photosynthetic responses to light, leaf photosynthesis (A) versus PPFD curves were fitted with Sigma Plot 11.0 for Windows by nonlinear regression as hyperbolic equations (Harley et al. 1986): $A = \Phi\text{PPFD} / \sqrt{(1+\Phi^2\ \text{PPFD}^2/A^2_{max})} - R_d$ where A is the net photosynthetic rate, PPFD is the incident photon flux density, A_{max} is the light-saturated photosynthetic rate, R_d is the rate of respiration in the light, exclusive of photorespiration, and Φ is the initial slope (quantum yield). The parameters Φ and A_{max} were obtained from eight curves of three shrubs of each species. Apparent quantum yield (Φ) was estimated as the initial slopes of the A/PPFD.

All statistical analyses were performed using the SPSS software package (Statistical Package for the Social Sciences for Windows, Version 20.0, Chicago, IL, USA). One-way analysis of variance (ANOVA) was used to test the differences between means. Significant differences (P=0.05) between means of SWC, Ψ, Φ, A_{max} and R_d were evaluated with Fisher's Least Significant Difference (LSD). Significant differences (P=0.05) between means of leaf gas exchange *(gs, A* and Tr), phenological measurements, litterfall production and nutrient concentrations in leaf litter were evaluated with Tukey test. Some data were transformed (natural log) for homogeneity of variances and, when it was not obtained, nonparametric Kruskal Wallis tests were used, as in vapour pressure deficit based on leaf temp (VPD_L), maximum photosynthetic photon flux density ($PPFD_{max}$) and specific leaf area (SLA), and in a few data on soil water content and leaf water potential. All measurements are shown as means±SE. Correlations between leaf litterfall mass and nutrient concentrations were determined by the Pearson correlation coefficient.

Results

Meteorological data

Figure 2A shows the monthly values of average air temperatures (T) and rainfall (R) from March to November 2012, recorded for the study area. In spring, (March-May) rainfall values were around 40–60 mm per month and rainfall reached its minimum in summer (July) with 0.3 mm. In autumn, (October and November) rainfall were 87.9 mm and 149.5 mm respectively. Spring was dryer than CN (fig. 1) whereas autumn was wetter than CN. Monthly average air temperature ranged from 9.8 ºC in April and

November to 21.6 ℃ in August. Solar radiation (Rs) (Figure 2B) reached its maximum in July (349.6 Wm^{-2}) and the maximum vapour pressure deficit (VPD) occurred in August (1.3 kPa). The minimum value of solar radiation and vapour pressure deficit was 90.4 Wm^{-2} and 0.3 kPa, respectively, in November.
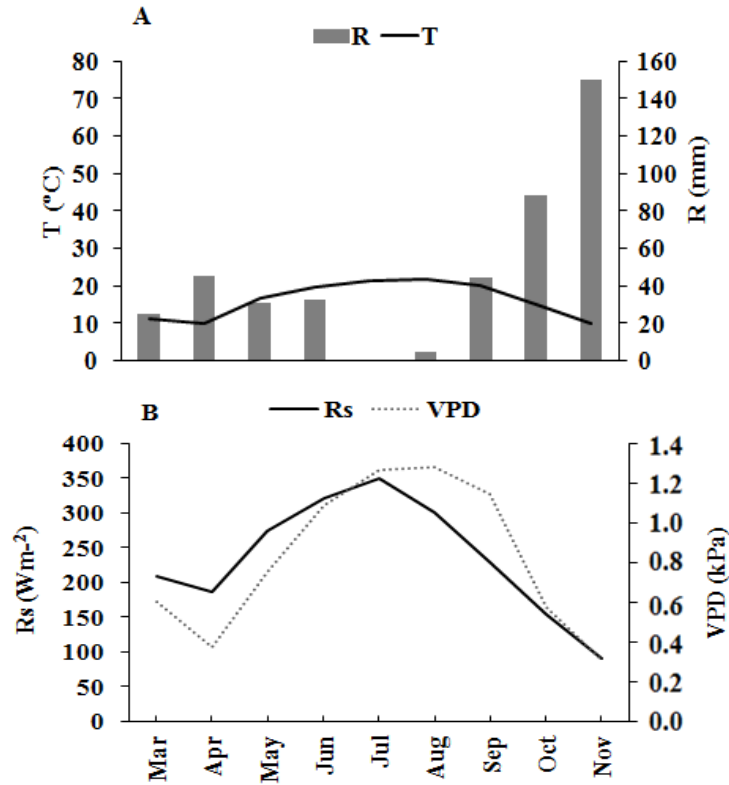
Figure 2. **(A)** Average air temperature (T) and total rainfall (R); **(B)** Solar radiation (Rs) and vapour pressure deficit (VPD) in the study period (March–November 2012), by a meteorological station located in the study area.

Phenological measurements

Some differences were observed between the phenological cycles of the four studied species (Figure 3). Leaf production in CLAD, CMON and CPSI was an almost continuous process, mainly in brachyblast that displayed leaves all year round. Dolichoblast vegetative growth occurred during a longer period in CLAD and CPOP (suspended during August and September, and July and August, respectively) than in CMON and CPSI (suspended from July to October). CPOP showed the shortest period for brachyblast growth. Flower buds developed in CLAD and CPOP from March to mid-May, in CMON from April to mid-May, and CPSI in May. Flowering of CLAD, CMON, and CPOP occurred in May and that of CPSI from mid-May to June. Fruit setting began immediately after anthesis. Leaf shedding from CMON and CLAD

dolichoblast started in April and May, respectively, and finished in September, in those of CPSI occurred from April to August, and in CPOP from June to August. Leaf shedding from brachyblasts occurred from mid-April to September in CLAD, and started in May for CPSI and in June for CMON, respectively, and continued until October, and in CPOP occurred only from mid-May to June.
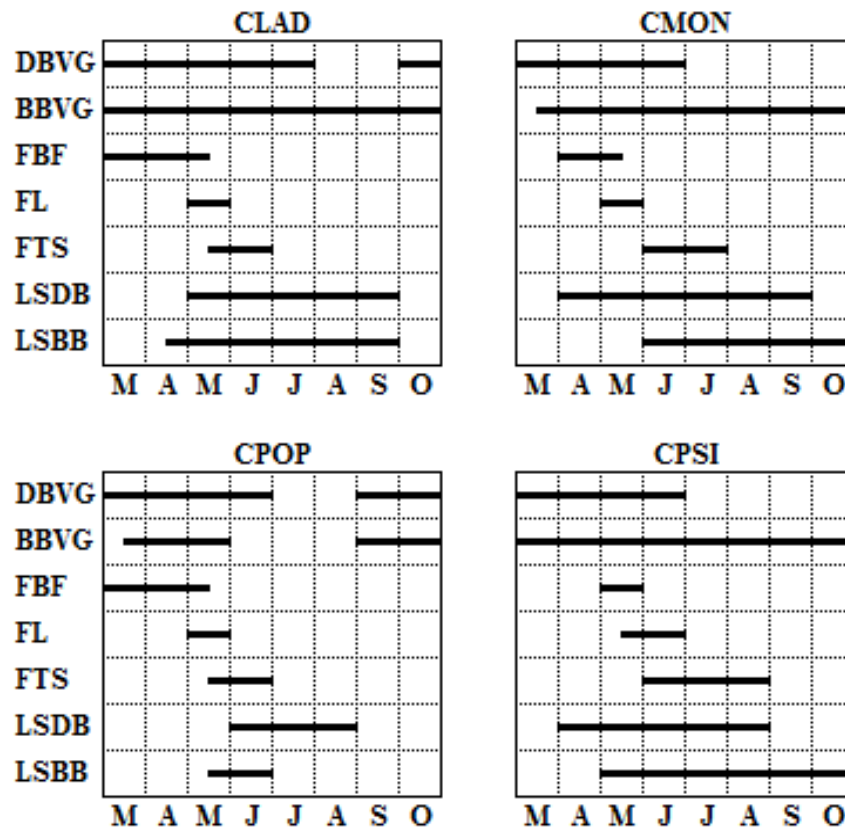
Figure 3. Phenological diagram of *Cistus ladanifer* (CLAD), *C. monspeliensis* (CMON), *C. populifolius* (CPOP) and *C. psilosepalus* (CPSI) for the study period (DBVG – dolichoblast vegetative growth; BBVG – brachyblast vegetative growth; FBF – flower bud formation; FL – flowering; FTS – fruit setting; LSDB – leaf shedding of dolichoblast; and LSBB – leaf shedding of brachyblast), from March to October 2012 (n=9 shoots).

Accumulated leaf production throughout the study period (Figure 4) shows that the number of leaves emerged on CLAD, CMON, and CPSI dolichoblast stabilized from the end of June until the end of the study period and that of leaf shedding stabilized from August for CPSI and September for CLAD and CMON. Leaf production by CLAD brachyblast stabilized between July and September, with a further increase in October, after the first autumn rains. Leaf emergence from CMON and CPSI brachyblast was continuous. Leaf shedding from CLAD, CMON, and CPSI brachyblast increased in June, but while stabilization was observed in CLAD by September,

shedding was still taking place at the end of the study period for CMON and CPSI. Leaf emergence and shedding on both dolichoblast and brachyblast of CPOP was low, but slight increases were observed for leaf emergence in October, after the first autumn rains, and for leaf shedding in June.

The number of both emerged and shed leaves on dolichoblast was significantly greater for CMON than for CLAD and CPSI (Figure 4 and Table 1). Leaf production by brachyblast and by the whole shoot was higher for CMON and CPSI than for CLAD, but the number of leaves shed by these species brachyblast did not differ significantly. The lowest leaf emergence and shedding values were observed in CPOP dolichoblasts and brachyblasts. CLAD showed the highest brachyblast production and CPOP and CPSI showed the lowest (Table 1). Brachyblast shedding was significantly higher in CMON than in the other three species, which did not differed significantly.

Table 1. Accumulated number of brachyblasts (BB) and leaves produced and shed on dolichoblast (DB), brachyblast, and whole shoot (WS), of *Cistus ladanifer* (CLAD), *C. monspeliensis* (CMON), *C. populifolius* (CPOP), and *C. psilosepalus* (CPSI), from March to October 2012.

| | **Production** (n^{er}) | | | | **Shedding** (n^{er}) | | | |
| | | **Leaves** | | | | **Leaves** | | |
	BB	**DB**	**BB**	**WS**	**BB**	**DB**	**BB**	**WS**
CLAD	10±0 a	20±2 b	36±1 b	56±2 b	1±0 b	22±1 b	32±2 a	54±3 a
CMON	8±0 b	28±2 a	46±3 a	74±3 a	3±0 a	34±1 a	24±3 a	58±3 a
CPOP	4±0 c	14±1 c	14±1 c	28±1 c	0±0 b	10±1 c	6±1 b	16±1 b
CPSI	4±0 c	22±1 b	46±3 a	68±3 a	1±0 b	22±1 b	30±2 a	52±2 a

Values are mean±SE (n=9). Significant differences (P<0.05) between species are indicated by different letters.
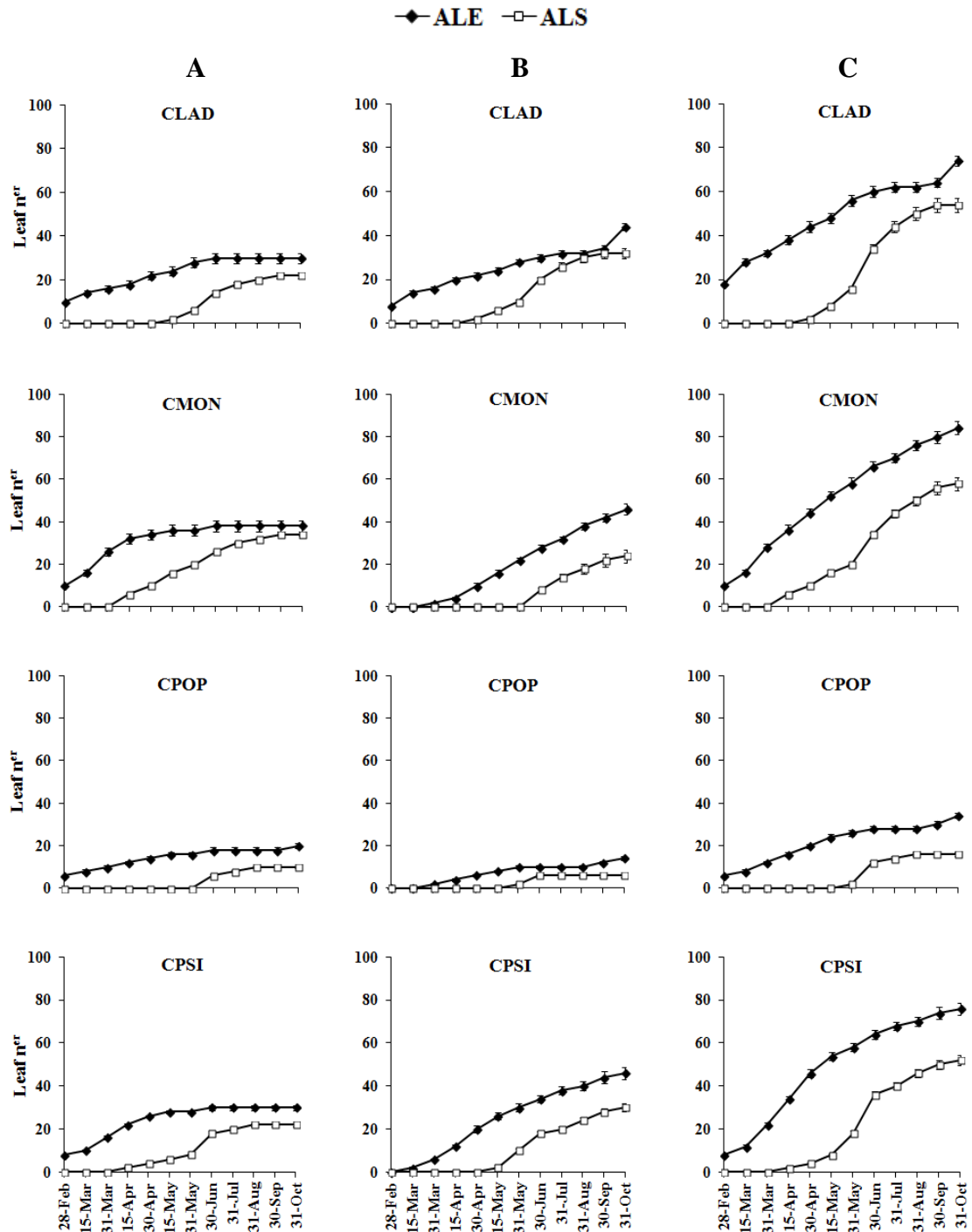
Figure 4. Accumulated leaf emergence (ALE) and accumulated leaf shedding (ALS) on dolichoblast (**A**), brachyblast (**B**), and the whole shoot (**C**) of *Cistus ladanifer* (CLAD), *C. monspeliensis* (CMON), *C. populifolius* (CPOP), and *C. psilosepalus* (CPSI), from March to October 2012. Means±SE are represented (n=9).

Soil water content

In the overall, soil water content was higher in April and October and lower in June and September for both 0–10 cm (Figure 5A) and 10–20 cm (Figure 5B) soil depths. It

should however be underlined that, excepting for values recorded for the 10–20 cm depth in October, soil water content was significantly higher (*P*<0.05) in both depths beneath CPOP than beneath the other three species, including in the drought period. In contrast, a trend to lower water content was observed in soil under CLAD canopies, in both soil depths, throughout the whole study period. Significant differences were not found beneath CMON and CPSI. It should also be emphasized that, unlike under CLAD, CMON, and CPSI, water content in the 10–20 cm soil depth under CPOP did not suffer a pronounced decrease during the dry season and, on the other hand, did not recover immediately after the first autumn rains.
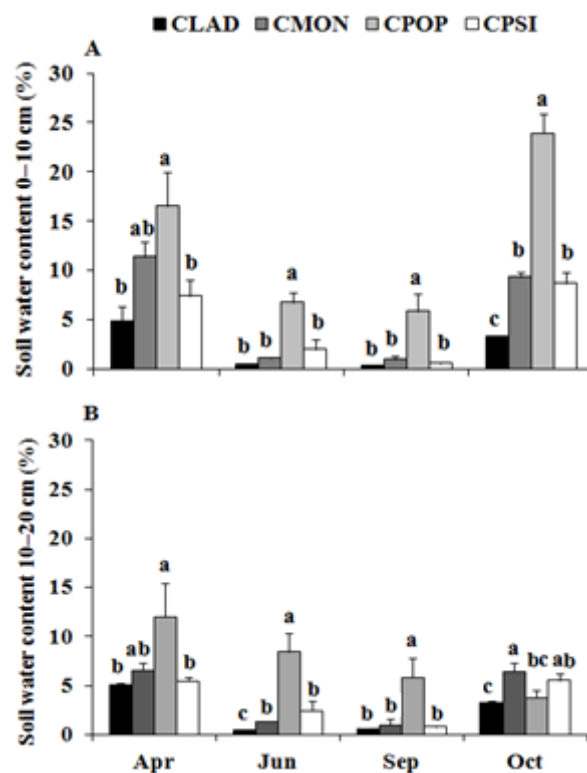
**Figure 5.** Soil water content (%) at 0–10 cm **(A)** and 10–20 cm **(B)** soil depths beneath shrub canopies of *Cistus ladanifer* (CLAD), *C. monspeliensis* (CMON), *C. populifolius* (CPOP), and *C. psilosepalus* (CPSI). Values are mean±SE (n=3). Means for the same date and depth followed by different letters are significantly different (P<0.05).

Leaf water potential

Predawn leaf water potential (Ψ_{IPD}) (Figure 6A) in all *Cistus* species remained high and approximately constant during spring (April to middle of June), between -0.4 MPa and -0.7 MPa related with the rainy season (Figure 6C). As rain is scarce, Ψ_{IPD} started to decline and reached lower values in mid and late summer. Ψ_{IPD} in CPSI was lower in

July (-2.3 MPa), for CLAD and CMON in August (-4.6 and -5.0 MPa, respectively) and for CPOP in September (-4.2 MPa). There was a statistically significant difference (P<0.05) in Ψ_{IPD} particularly marked in July, August and September, where Ψ_{IPD} was higher in CPSI than in CPOP, CLAD and CMON. After autumn rains, Ψ_{IPD} recovered to spring values in all species. The mid-day leaf water potential (Ψ_{IMD}) followed the same patterns as Ψ_{IPD}. Thus, Ψ_{IMD} was lower during the drought period. For CPSI, Ψ_{IMD} was -2.7 MPa in July and in August for CPOP, CLAD and CMON were -4.4, -4.8 and -5.8 MPa, respectively (Figure 6B). CPSI had a mid-day leaf water potential (Ψ_{IMD}) statistically higher (P<0.05) than the other three species. Delta leaf water potential ($\Delta\Psi$) (Table 2) was generally higher in all species in rainy season and warm days and was reduced during drought period. At end of summer (September) $\Delta\Psi$ was higher in CPSI than in other species (although not significant).
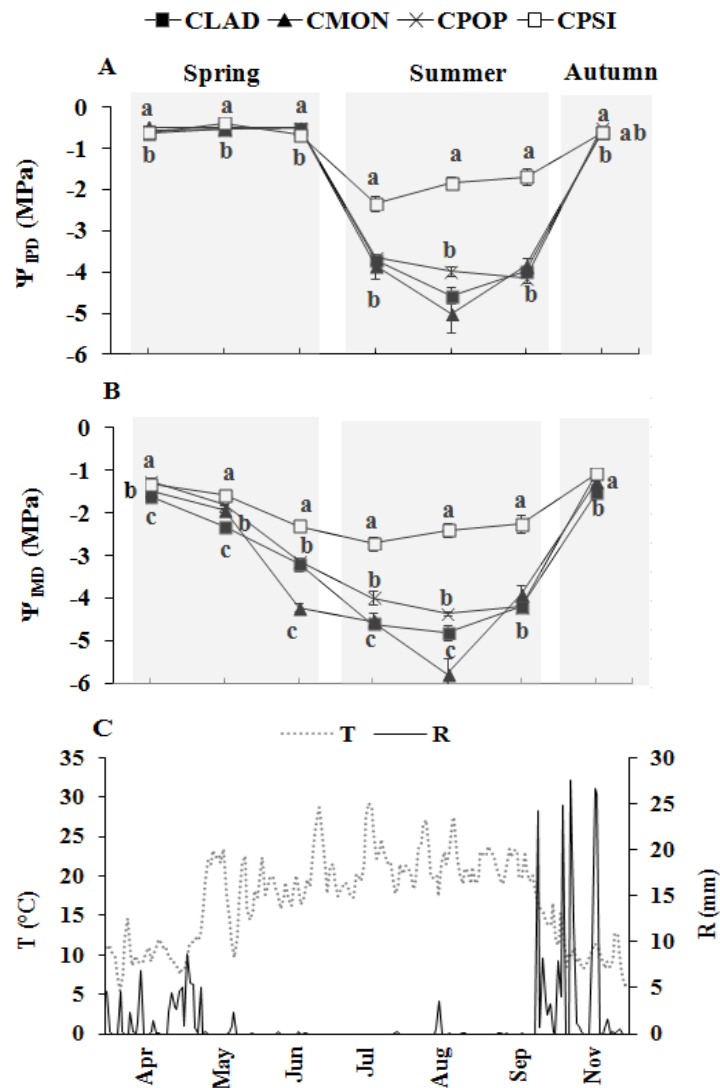
Figure 6. (A) Predawn leaf water potential (Ψ_{IPD}); **(B)** mid-day leaf water potential (Ψ_{IMD}) of *Cistus ladanifer* (CLAD), *C. monspeliensis* (CMON), *C. populifolius* (CPOP), and *C. psilosepalus* (CPSI), from April to November 2012; **(C)** daily air temperatures (T) and rainfall (R) for the same period. Values are mean±SE (n=12). Significant differences (P<0.05) between species are indicated by different letters.

Table 2. Delta leaf water potential ($\Delta\Psi$, MPa) of *Cistus ladanifer* (CLAD), *C. monspeliensis* (CMON), *C. populifolius* (CPOP), and *C. psilosepalus* (CPSI), from April to November 2012.

	$\Delta\Psi$ (MPa)						
	April	**May**	**June**	**July**	**August**	**September**	**November**
CLAD	-0.9±0.1 b	-1.8±0.0 c	-2.8±0.2 b	-0.9±0.1 b	-0.3±0.2	-0.2±0.1 ab	-1.0±0.1 b
CMON	-1.0±0.1 b	-1.5±0.0 b	-3.7±0.1 c	-0.5±0.2 a	-0.5±0.3	0.0±0.0 a	-0.6±0.0 a
CPOP	-0.7±0.1 a	-1.2±0.0 a	-2.6±0.1 b	-0.3±0.2 a	-0.4±0.1	0.0±0.0 a	-0.6±0.1 a
CPSI	-0.7±0.0 a	-1.2±0.1 a	-1.6±0.1 a	-0.4±0.1 a	-0.6±0.1	-0.6±0.2 b	-0.5±0.0 a

Values are mean±SE (n=12). Significant differences (P<0.05) between species are indicated by different letters.

Leaf gas exchange and micro-environmental conditions

Stomatal conductance in environmental conditions (*gs*) (Figure 7A) and carbon assimilation rate (*A*) (Figure 7B) in all *Cistus* species were higher in spring, in sunny days in which photosynthetic photon flux (PPFD$_{max}$) was around 1000 µmol photons m^{-2} s^{-1} and vapour pressure deficit (VPD) around 2.5 kPa, and then, both *gs* and *A* decrease in summer drought. In autumn, a recovery in *gs* and *A* occurred but not for the spring values in all species as PPFD and VPD were lower in this season in relation to spring. However, some inter-specific variations in these physiological parameters were observed. Thus, *gs* in spring was significantly higher (P<0.001) in CLAD and CPSI (0.455 and 0.535 mol H$_2$O m^{-2} s^{-1}, respectively) and significantly lower in CMON (0,021 mol H$_2$O m^{-2} s^{-1}) and CPOP (0.088 mol H$_2$O m^{-2} s^{-1}). In summer, there was no significant difference between the four species and *gs* was around 0.0025 mol H$_2$O m^{-2} s^{-1}. In autumn, CPSI (0.272 mol H$_2$O m^{-2} s^{-1}) was significantly higher and CPOP (0.124 mol H$_2$O m^{-2} s^{-1}) was significantly lower than CMON and CLAD (0.166 and 0.203 mol H$_2$O m^{-2} s^{-1}, respectively). Photosynthetic rate (A, Figure 5B) in spring was significantly higher (P<0.001) in CPSI and CLAD (32.15 and 40.68 µmol CO$_2$ m^{-2} s^{-1}, respectively) and significantly lower in CMON (3.41 µmol CO$_2$ m^{-2} s^{-1}) and CPOP (12.68 µmol CO$_2$ m^{-2} s^{-1}). In summer, there were no significant differences between the four species. In autumn CPOP was significantly lower than CMON, CLAD and CPSI. In spring, transpiration rate (Tr) (Figure 7C) was significantly higher (P<0.001) in CLAD and CPSI (5.21 and 7.60 mmol H$_2$O m^{-2} s^{-1}, respectively) and significantly lower in CMON (0.49 mmol H$_2$O m^{-2} s^{-1}) and in CPOP (1.52 mmol H$_2$O m^{-2} s^{-1}). In summer there were no significant differences between the four species. Values in autumn were significantly higher in CLAD and CPSI (2.91 and 3.80 mmol H$_2$O m^{-2} s^{-1}, respectively) than CPOP

(1.90 mmol H_2O m^{-2} s^{-1}). There were no significant differences between CMON and the other three species. Micro-environmental conditions at leaf level, namely PPFD$_{max}$, in spring and in summer were similar (P>0.001) for CLAD, CMON and CPSI (1200-1525 µmol m^{-2} s^{-1}) but significantly higher than CPOP (694-875 µmol m^{-2} s^{-1}). In autumn, values were significantly higher in CMON and in CPSI (1255 and 1367 µmol m^{-2} s^{-1}, respectively) and significantly lower in CPOP (158 µmol m^{-2} s^{-1}) and in CLAD (753 µmol m^{-2} s^{-}1). Vapour pressure deficit (Figure 8) in spring and in autumn, had no significant differences between the four species. In summer values in CLAD (3.00 kPa) were significantly higher (P<0.001, Table 3) than in CPSI (2.89 kPa) and in CMON (2.69 kPa). CPOP had the lowest values (2.34 kPa). There were no significant differences between CPSI and CMON and the other two species.
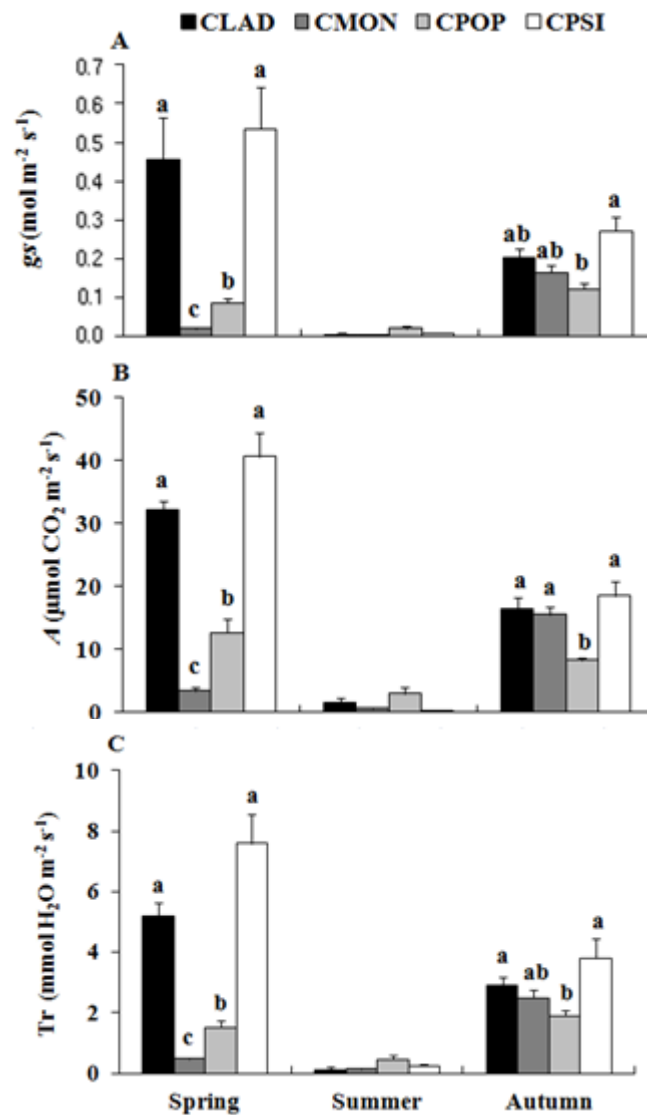
Figure 7. (A) Stomatal conductance (*gs*), **(B)** photosynthetic rate (*A*), **(C)** transpiration rate (Tr) at environment conditions in *Cistus ladanifer* (CLAD), *C. monspeliensis* (CMON), *C. populifolius* (CPOP), and *C. psilosepalus* (CPSI) in spring, summer and autumn 2012. Values are mean±SE (n=24). Significant differences (P<0.05) between species are indicated by different letters.
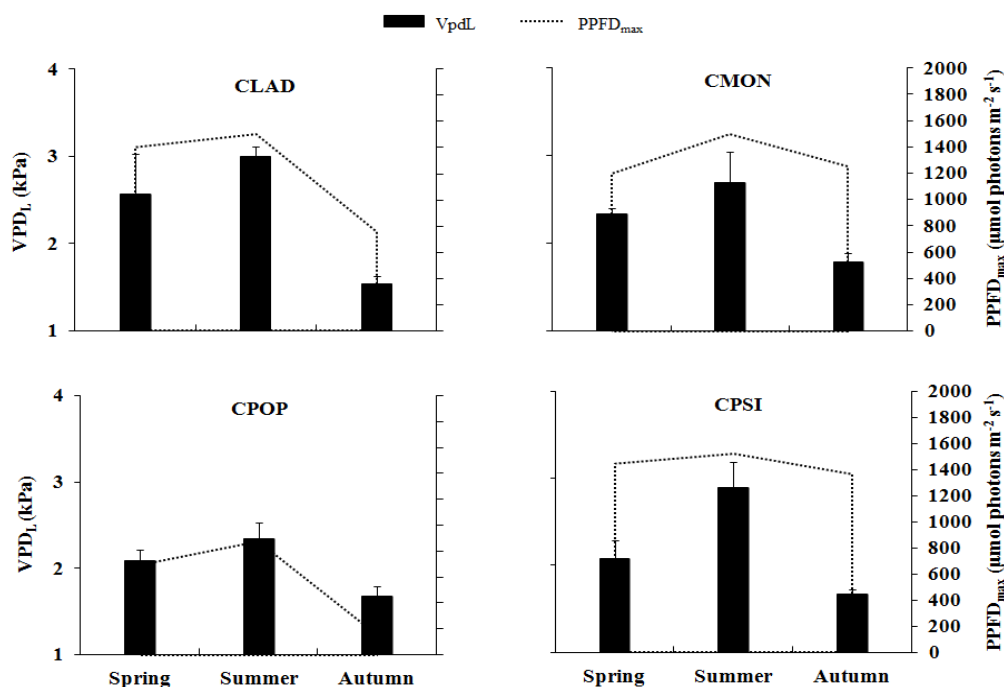
Figure 8. Vapour pressure deficit based on leaf temp (VPD_L) and maximum photosynthetic photon flux density ($PPFD_{max}$) at environment conditions (360 nm) in *Cistus ladanifer* (CLAD), *C. monspeliensis* (CMON), *C. populifolius* (CPOP), and *C. psilosepalus* (CPSI) in spring, summer and autumn 2012. Values are mean±SE (n=24).

Table 3. Results of one-way ANOVA analysis for vapour pressure deficit based on leaf temp (VPD_L, kPa) and maximum photosynthetic photon flux density ($PPFD_{max}$, µmol photons m^{-2} s^{-1}) of *Cistus ladanifer* (CLAD), *C. monspeliensis* (CMON), *C. populifolius* (CPOP) and *C. psilosepalus* (CPSI), in spring, summer and autumn 2012.

	VPD_L (kPa)			$PPFD_{max}$ (µmol photons m^{-2} s^{-1})		
	Spring	**Summer**	**Autumn**	**Spring**	**Summer**	**Autumn**
CLAD	a	a	a	a	a	b
CMON	a	ab	a	a	a	a
CPOP	a	b	a	b	b	c
CPSI	a	ab	a	a	a	a

Significant differences (P<0.05) between species in each date are indicated by different letters (n=24).

Analysis of photosynthetic responses to light

The A_{max} (maximum assimilation rate, estimated from the *A*/PPFD curves in light-saturated and ambient CO_2 concentrations) was lower (P<0.001) in summer than spring and autumn in all *Cistus* species (Figure 9, Table 4). Under optimal environmental conditions (spring and autumn) CLAD and CPSI had higher A_{max} than CMON and CPOP, but similar quantum yield (Φ) and respiration in dark (R_d). However, during summer, A_{max} was low in all species, and lightly lower in CLAD.
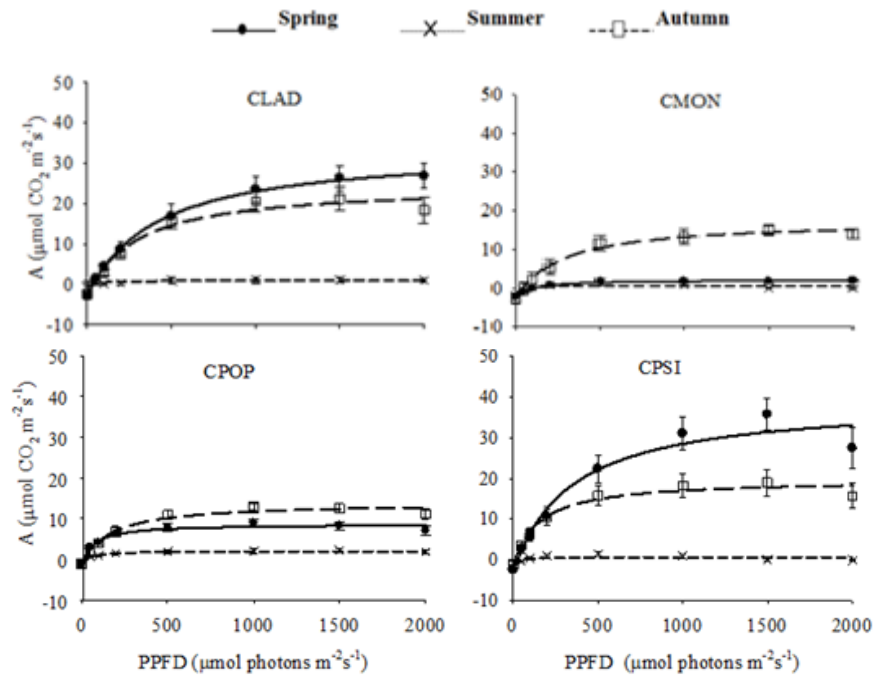
Figure 9. Assimilation rate (A) versus photosynthetic photon flux density (PPFD) curves in *Cistus ladanifer* (CLAD), *C. monspeliensis* (CMON), *C. populifolius* (CPOP), and *C. psilosepalus* (CPSI) in spring, summer and autumn 2012. Bars represent the standard error of the mean (n=24). R^2 higher than 0.80.

Table 4. Quantum yield (Φ, μmol CO_2 m^{-2} s^{-1}/μmol photons m^{-2} s^{-1}), light-saturated photosynthesis (A_{max}, μmol CO_2 m^{-2} s^{-1}) and dark respiration (R_d, μmol CO_2 m^{-2} s^{-1}) in *C. ladanifer* (CLAD), *C. populifolius* (CPOP), *C. monspeliensis* (CMON) *and C. psilosepalus* (CPSI) in spring, summer and autumn 2012.

	Spring	Summer	Autumn
Φ (μmol CO_2 m^{-2} s^{-1}/μmol photons m^{-2} s^{-1})			
CLAD	0.09±0.01 b	0.02±0.01 c	0.10±0.03 b
CMON	0.11±0.01 b	0.03±0.04 c	0.08±0.02 b
CPOP	0.15±0.01 a	0.06±0.01 b	0.10±0.03 b
CPSI	0.13±0.01 a	0.18±0.02 a	0.14±0.02 a
A_{max} (μmol CO_2 m^{-2} s^{-1})			
CLAD	36.55±0.76 b	1.49±0.40 b	27.85±2.17 a
CMON	8.80±0.17 c	3.10±0.89 a	20.59±0.99 b
CPOP	10.18±0.85 c	3.15±0.19 a	15.39±1.13 c
CPSI	42.34±4.50 a	2.99±0.78 a	21.33±1.64 b
R_d (μmol CO_2 m^{-2} s^{-1})			
CLAD	2.87±0.44 b	0.45±0.37 c	3.17±1.62 a
CMON	2.44±0.16 b	2.30±0.80 a	3.14±0.77 a
CPOP	1.56±0.77 c	1.09±0.17 b	1.52±0.98 b
CPSI	3.15±0.34 a	2.33±0.76 a	1.58±1.44 b

Values are mean±SE (n=24). Significant differences (P<0.05) between species are indicate by different letters.

Specific leaf area and leaf nitrogen concentration

Seasonal variation of specific leaf area (SLA) (Figure 10) for all species, indicate higher values in spring and autumn and lower values in summer. There were also evident differences between species. Thus, in spring, the leaves of CLAD had a lower SLA (P<0.001) than those of CMON and leaves of CMON had also a lower SLA (P<0.001) than those of CPOP and CPSI. In summer SLA in leaves of CLAD and CMON was significantly lower (P<0.001) and SLA in leaves of CPOP significantly higher than those of CPSI (P<0.001). Values of SLA in autumn were significantly lower (P<0.05) in CLAD than in CMON, SLA in leaves of CMON was significantly lower (P<0.001) than those of CPSI, and values in CPOP were significantly higher (P<0.001) than those in CPSI.

The higher values of leaf nitrogen concentration of green leaves occurred in summer (N, per area) or in autumn (N, per mass) for all study species. (Table 5). CPSI had the highest values of N (per mass) in the three seasons and CLAD the lowest values in spring and summer. CPOP had the lowest values of N (per area) and CLAD the highest.
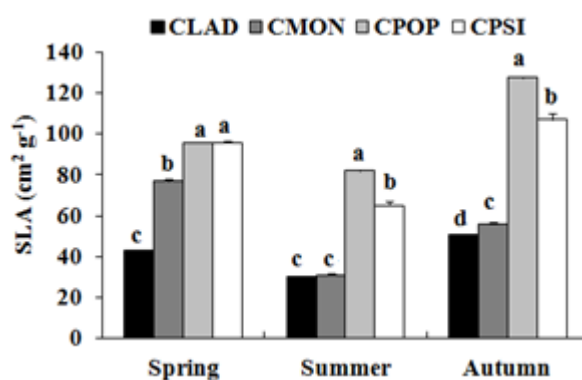
Figure 10. Seasonal variation of the specific leaf area (SLA, cm^2 g^{-1}) of *Cistus ladanifer* (CLAD), *C. monspeliensis* (CMON), *C. populifolius* (CPOP), and *C. psilosepalus* (CPSI). Means±SE are represented (n=40). Significant differences (P<0.05) between species are indicated by different letters.

Table 5. Leaf nitrogen concentration (N, mg g^{-1} and mg cm^{-2}) in *Cistus ladanifer* (CLAD), *C. monspeliensis* (CMON), *C. populifolius* (CPOP) and *C. psilosepalus* (CPSI) in spring, summer and autumn 2012.

	N (mg g^{-1})			N (mg cm^{-2})		
	Spring	Summer	Autumn	Spring	Summer	Autumn
CLAD	8.34	10.47	16.02	0.19	0.35	0.31
CMON	12.43	12.10	13.06	0.16	0.39	0.23
CPOP	11.10	11.40	18.15	0.12	0.14	0.14
CPSI	14.04	13.36	19.95	0.15	0.21	0.19

Litterfall production

The highest leaf litterfall and total litterfall production were observed for CLAD followed by and CPSI (Table 6). The values determined for CMON and CPOP were the lowest and did not differed significantly. The production of other litterfall was also significantly higher for CLAD.

Table 6. Litterfall production (g m^{-2}) of *Cistus ladanifer* (CLAD), *C. monspeliensis* (CMON), *C. populifolius* (CPOP), and *C. psilosepalus* (CPSI), from March to October 2012 (LLF - leaf litterfall; OLF - other litterfall; TLF - total litterfall).

	Litterfall production (g m^{-2})		
	LLF	**OLF**	**TLF**
CLAD	575±49 a	90±12 a	665±59 a
CMON	75±5 c	11±2 c	85±6 c
CPOP	56±7 c	17±3 bc	73±8 c
CPSI	121±15 b	26±4 b	147±18 b

Values are mean±SE (n=9). Significant differences (P<0.05) between species are indicated by different letters.

Maximum leaf litterfall (Figure 11) occurred in June for CLAD, CPSI, and CPOP (50 %, 63 % and 84 % of the total sampling period, respectively) and from mid-March to the end of June for CMON (21 % and 24 %, respectively). Leaf litterfall amount of CLAD was significantly higher than that of the other species for almost the entire study period (Table 7). In contrast, leaf litterfall amount of CPOP was significantly lower in the majority of sampling dates, excepting in June when most leaf litter was produced. Comparing CPSI and CMON, while leaf fall occurred almost only in June for the former, a second maximum was observed in March for the latter.
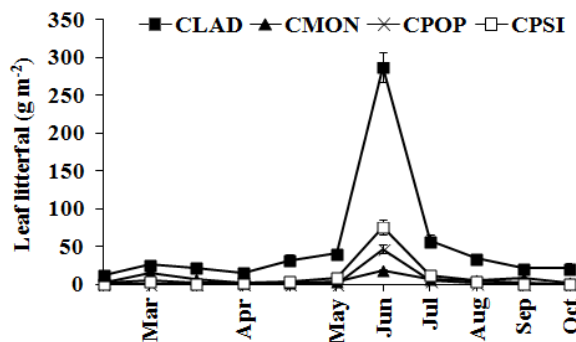
Figure 11. Seasonal variation of leaf litter dry weight (g m^{-2}) of *Cistus ladanifer* (CLAD), *C. monspeliensis* (CMON), *C. populifolius* (CPOP) and *C. psilosepalus* (CPSI), from March to October 2012. Each leaf litter value is the mean and bars represent the standard error of the mean (n=9).

Table 7. Results of one-way ANOVA analysis for seasonal leaf litter production (g m^{-2}) of *Cistus ladanifer* (CLAD), *C. monspeliensis* (CMON), *C. populifolius* (CPOP) and *C. psilosepalus* (CPSI), from March to October 2012.

	15Mar	31Mar	15Abr	30Abr	15Mai	31Mai	30Jun	31Jul	31Ago	30Set	31Out
CLAD	a	a	a	a	a	a	a	a	a	a	a
CMON	b	a	b	b	bc	c	c	bc	b	b	b
CPOP	c	c	d	c	c	d	b	c	c	d	c
CPSI	b	b	c	b	b	b	b	b	b	c	c

Significant differences (P<0.05) between species in each date are indicated by different letters.

Nutrient concentrations in leaf litter

CMON followed by CPSI presented the highest mean weighted N concentration (6.02 and 4.36 mg g^{-1}, respectively) (Table 8), while CPOP and CLAD showed the lowest values (3.63 and 3.34 mg g^{-1}). On the other hand, P and K concentrations were higher in CLAD (0.89 and 3.67 mg g^{-1}) followed by CMON (0.48 and 2.78 mg g^{-1}), CPSI (0.26 and 2.08 mg g^{-1}), and CPOP (0.22 and 2.10 mg g^{-1}). For Ca the highest values were determined in CMON (12.63 mg g^{-1}) and CLAD (11.96 mg g^{-1}) and the lowest in CPOP (9.69 mg g^{-1}) and CPSI (6.43 mg g^{-1}). Concentration of Mg was significantly higher in CPOP (3.43 mg g^{-1}) and lower in CLAD (1.58 mg g^{-1}), while the latter species presented the highest Mn concentration (0.52 mg g^{-1}) and CMON the lowest (0.16 mg g^{-1}).

Table 8. Weighted mean nutrient concentrations in leaf litter of *Cistus ladanifer* (CLAD), *C. monspeliensis* (CMON), *C. populifolius* (CPOP), and *C. psilosepalus* (CPSI), from March to October 2012.

	Nutrient concentrations (mg g^{-1})					
	N	**P**	**K**	**Ca**	**Mg**	**Mn**
CLAD	3.34±0.02 d	0.89±0.02 a	3.67±0.04 a	11.96±0.01 b	1.58±0.01 d	0.52±0.01 a
CMON	6.02±0.05 a	0.48±0.00 b	2.78±0.08 b	12.63±0.02 a	2.03±0.01c	0.16±0.00 d
CPOP	3.63±0.06 c	0.22±0.01 d	2.10±0.02 c	9.69±0.03 c	3.43±0.01 a	0.24±0.00 c
CPSI	4.36±0.03 b	0.26±0.00 c	2.08±0.01 c	6.43±0.02 d	2.26±0.00 b	0.27±0.00 b

Values are mean±SE (n=9). Significant differences (P<0.05) between species are indicated by different letters.

No correlations were found between seasonal variation of leaf litterfall mass and nutrient concentrations. However, some seasonal patterns were determined in the variation of nutrient concentrations throughout the study period. Concentrations of N in leaf litterfall (Figure 12) decreased during the drought period (June for CMON, CPOP, and CPSI and July for CLAD), coinciding with peak leaf shedding and maximum leaf litterfall. The increase observed in autumn (October) after the first rains was lower for CLAD. Similarly to N, P concentration decreased in the period of dryness, although a delay was observed in CMON (August) as compared to the other species (June). Excepting for CLAD, maximum P values was also determined after the first rains of autumn, when leaf shedding and leaf litterfall were minimums. K concentration increased in the drought period with maximums in May for CPOP, June for CMON, July for CLAD and August for CPSI. Minimum values occurred at the end of the dry season (September for CPOP and October for the other study species. Mg concentration in leaf litterfall was highest in spring and early-summer (March for CPSI, May for CLAD, June for CMON and July for CPOP). The lowest values occurred after the first autumn rains (October). Ca concentration showed maximum and minimums values, respectively, in April and October in CMON, July and March in CPOP, August and October in CLAD and October and April in CPSI. Peak content of Mn concentration was reached during March and June for CLAD, April for CMON, June for CPSI and July for CPOP. The lowest values occurred in August and September for CLAD and CPSI, respectively, and in October for CMON and CPOP. Positives correlations between the seasonal variation of N and P concentrations were determined for CMON (r=0.97, P<0.001), CPOP (r=0.96, P<0.001), and CPSI (r=0.96, P<0.001), but not for CLAD. On the other hand variation of N was negatively correlated with K in CLAD (r=-0.81, P<0.05) and CMON (r=-0.77, P<0.05), and with Ca in CLAD (r=-0.79, P<0.05) and CPOP (r=-0.76, P<0.05).
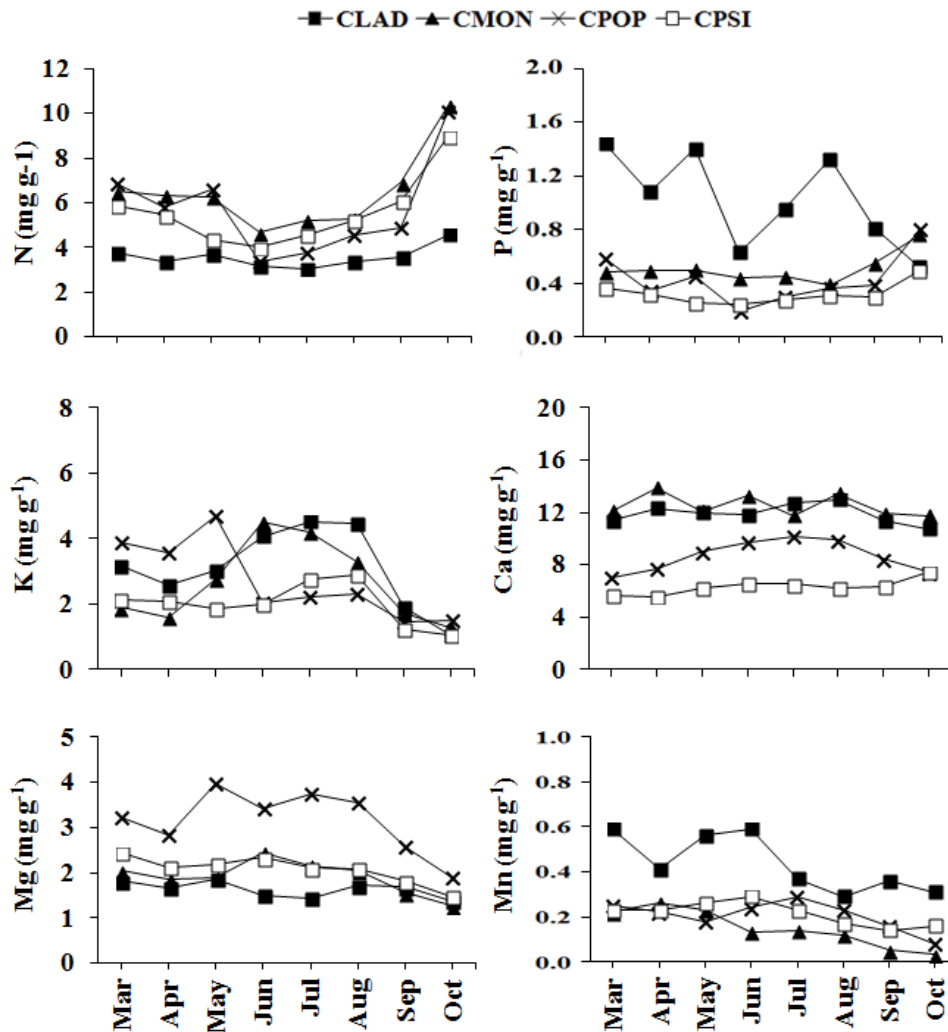
Figure 12. Seasonal variation of N, P, K, Ca, Mg, and Mn concentrations (mg g^{-1}) in leaf litter of *Cistus ladanifer* (CLAD), *C. monspeliensis* (CMON), *C. populifolius* (CPOP), and *C. psilosepalus* (CPSI), from March to October 2012.

Discussion

Phenological patterns

The phenological pattern presented by the four studied *Cistus* species, growing and flowering occurred mainly in spring and arresting most phenological activities in summer, is the characteristic phenological cycle of most Mediterranean shrubs (Gratani & Crescente 1997; Castro-Díez et al. 2005; Simões et al. 2008). The high degree of overlapping between growth flushing and also with flowering and fruiting during spring, the favourable period of the year, suggests that these phenophases are

synchronized by mild temperatures and water availability in spring (Simões et al. 2008). On the other hand, growth arresting during summer seems to be a response to the Mediterranean high temperatures and drought, associated with the decrease observed in leaf water potential for the four species. When leaf water potential is reduced, the osmotic adjustment in leaves occurs more slowly, leading to a reduction or interruption of the extension of cell walls and lower shoot growth (Hsiao & Xu 2000). Although the similar overall phenological patterns, the four studied *Cistus* species differed in their dolichoblast and brachyblast growing calendars. All species arrested dolichoblast growth during summer, but while the suspension continued through the autumn for *C. monspeliensis* and *C. psilosepalus*, *C. ladanifer* and *C. populifolius* reinitiated dolichoblast growth in early-autumn, suggesting that the onset of growth was triggered by the first autumn rains. The response observed in *C. populifolius* is in agreement with the increased soil water content recorded in the 10 cm top soil beneath this species canopies. Since a similar increase was not observed in soil under *C. ladanifer* canopy, we may suggest that some properties of this species may contribute to explain its different growth response. The extended growth of *C. ladanifer* dolichoblast into early-summer, when soil moisture was also very low, corroborates the ability of this species to better cope with drought (Simões et al. 2008). Brachyblast growth, on the other hand, occurred during a smaller and wetter period in *C. populifolius* and all year round in the other three species. It seems thus that while *C. populifolius* balanced the growth period between dolichoblasts and brachyblasts, *C. monspeliensis* and *C. psilosepalus* invested more time in brachyblast growth, and *C. ladanifer* extended the growth period for both shoot types. By protracting the period of vegetative development *C. ladanifer* shrubs can increase the amount of living biomass produced at the end of the growth period, which might be a strategy to face the unfavourable period of the Mediterranean summer (Castro-Díez et al. 2005; Palacio et al. 2006). Development of brachyblasts in summer and dolichoblasts in winter is also reported for other *Cistus* species (Floret et al. 1989).

The higher amount of leaves produced by *C. monspeliensis*, in both dolichoblasts and brachyblasts, is probably associated with its smaller leaves and, in contrast, *C. populifolius* that bears the biggest leaves displayed the smallest leaf production in both shoot types. Nevertheless, while leaf emergence was higher in brachyblasts than in dolichoblasts for *C. ladanifer*, *C. monspeliensis*, and *C. psilosepalus* (64 %, 62 % and 68 % of total leaf production, respectively), *C. populifolius* produced the same proportion of leaves in both shoot type (50 %). Moreover, while *C. ladanifer*, *C.*

monspeliensis, and *C. psilosepalus* displayed new leaves all year round, even in periods with virtually no rainfall (July and August), *C. populifolius* arrested leaf production with increasing temperature and insolation and increasing soil water content. By limiting leaf transpiration during drought, *C. populifolius* can increase water use efficiency, an important drought avoidance strategy reported for other *Cistus* species (Aronne & de Micco 2001; Correia et al. 1992; Gratani & Varone 2006).

Peak leaf abscission, which mostly affected previous-year leaves, occurred mainly during late-spring and early-summer for all studied species, as typically observed in many Mediterranean shrubs, including other *Cistus* species (Gratani & Crescente 1997; Palacio et al. 2006; Simões et al. 2008). Spring–summer leaf senescence can be triggered by factors such as growth events or the arrival of summer drought in Mediterranean evergreens (Munné-Bosch & Alegre 2004). At this time, vegetative and reproductive growths were active in all species, suggesting that leaf fall was triggered by resource demands of the growing sinks (Castro-Díez et al. 2005). Nevertheless, the main leaf fall driver should have been the decreased leaf water potential registered for all studied species with the increasing summer temperature, insolation and drought. These results point to a certain leaf dimorphism and are in agreement with other studies in *Cistus* species under Mediterranean climate (Correia et al. 1987; Harley et al. 1987). Additionally, leaf shedding from *C. monspeliensis* and *C. psilosepalus* began earlier and persisted for a longer period of time as compared to the other species, which in accordance with the also early lowering in leaf water potential. Therefore, *C. monspeliensis*, as reported by Sánchez-Blanco et al. (2002), and also *C. psilosepalus* seem to exhibit higher seasonal dimorphism in plant structure, with greater reduction of transpiring leaf area to face summer drought. By showing lower relative change of its structure and phenology throughout the year, *C. ladanifer* seems to have a strategy being closer to isomorphism (Simões et al. 2008). In *C. ladanifer* and *C. monspeliensis*, the photoprotection of its summer leaves is enhanced by labdanum exudates, which reaches peak secretion in summer (Chaves et al. 1993, 1997). The delay in leaf shedding, the shortest duration of this phenophase and the lowest amount of lost leaves observed in *C. populifolius* might be related with the higher water content in soil beneath this species canopies.

Seasonal patterns of water status and photosynthetic capacity

In all studied *Cistus* species, seasonal variations in Ψ_{IPD} and *gs* showed a typical pattern of Mediterranean species, with maximum values in spring followed by a progressive decline during the summer drought and a recovery in response to autumn rains. The progressive reduction in soil water content, SWC, in the drought period, resulted in a decrease in leaf water potential due to an imbalance between water absorbed by the roots and transpired through the leaves, causing a reduction in leaf water potential. Thus, the reduction in *gs*, the first line of defense of the plant to face water deficit soil, restricting water loss through transpiration, affects the input of atmospheric carbon and consequently the carbon assimilation. Although, this seasonal pattern was similar for all four *Cistus* species, different magnitude of variation was observed. During dry season, SWC of soil under *C. populifolius* was higher than under the other three species, which is in accordance with its classification as a submesophyllous species. Shrubs of *C. populifolius* were located under the projection of the tree canopies, and thus they were subject to lower insolation and less soil evaporation. In fact, after de beginning of the dry season, decrease in SWC is slower in areas affected by tree canopies, because soil surface protection by greater amount of organic layers (Nunes et al. 2011). Soil water recovery after the first autumn rains was higher in soil under *C. populifolius* due to enhanced soil porosity and improved soil structure by tree roots, increasing infiltration rates (Schlesinger & Pilmanis 1998; Archer et al. 2002). On other hand, lower SWC under *C. ladanifer*, was probably related to this species location in open areas, where evapotranspiration is higher and soil porosity is lower (Simões et al. 2008).

The pronounced decrease of Ψ_{IPD} obtained during summer for *C. ladanifer*, *C. monspeliensis*, and *C. populifolius* are in accordance with decreased SWC. Among these three species, *C. populifolius* presented higher Ψ_{IPD} values and SWC under these species was also higher. On the other hand, *C. ladanifer* and *C. monspeliensis* had lower values in Ψ_{IPD} during this period. The minimum water potential value in *C. monspeliensis* (about -6 MPa), although very negative is in the range reported by Clemente et al. (2005) for the same species. *C. monspeliensis* shrubs have a safety vascular system with small vessel diameter and high vessel frequency (De Micco et al. 2008) allowing them to support low values of xylem water potential without embolism. The Ψ_{IPD} values observed for *C. psilosepalus* were somewhat unexpected because they

were higher than those of *C. populifolius*, although SWC was lower in the former than in the latter. Taking into account that stomatal conductance, *gs*, did not differ significantly between the four *Cistus* species in drought period, the better water status in summer observed in *C. psilosepalus* could be related to the observed reduction in leaf area during summer. Higher root biomass/leaf area ratio or high hydraulic conductivity may also be associated with this different drought tolerance, as reported for differences between *Cistus albidus* and *Cistus laurifolius* (Martínez-Vilalta et al., 2002). As far as we know there are not any studies in xylem anatomy, hydraulic conductivities or vulnerability to embolism in C. *psilosepalus*. Additionally, at the end of the drought period (September), ΔΨ was generally higher in *C. psilosepalus* than in the other three species.

All study species presented seasonal variation in SLA, as reported for other Mediterranean dimorphics shrubs (Palacio et al. 2006). The decrease in specific leaf area, SLA, during summer drought observed for all *Cistus*, contribute to a more efficient water use by reducing over-temperature effect and limiting leaf area transpiration. *C. monspeliensis* showed a higher dimorphism degree, because SLA variation was much higher (about 2.5 fold) than the other species (1.5-1.7). In this specie, leaf margins fold toward the midrib, reducing the part of leaf lamina exposed to sun. However, after the first autumn rainfall, SLA of the summer standing leaves increase, due to unrolling of leaf margin and the expansion of the leaf lamina (Liberati et al. 2012). In *C. ladanifer* the lower SLA might due to a higher degree of sclerophylly (Mooney & Dunn 1970; Correia et al. 1992; Aronne & de Micco 2001; Castro-Díez et al. 2005; Gratani & Varone 2006). Nevertheless, an inter-specific differentiation in SLA occurred. Higher SLA values for *C. populifolius* can be attributed to the wetter and shadowy conditions of sites usually occupied by this species. All these results suggest a differentiated eco-physiological response in the four co-occurring study *Cistus* species to face drought, which is quite frequent for Mediterranean species (Bahari et al. 1985; Castell et al. 1994; Abrams & Mostoller 1995; Goulden 1996). According to these heterogeneous responses to water deficit, Mediterranean species have been divided into two types of mechanism: avoiders and tolerants (Kramer 1983; Jones 1992). Species that employ a drought-avoidance mechanism prevent damage by early stomatal closure before any change in leaf water status occurs or have a more efficient mechanism in water absorption. Drought-tolerant species exhibit simultaneous decreases in stomatal conductance and water potential (Guehl et al. 1991; Picon et al. 1996). Thus, our data

suggest that while *C. psilosepalus* strategies include avoidance mechanisms, those for *C. ladanifer* and *C. monspeliensis* indicate drought tolerance. Mechanisms of *C. populifolius* seem be in-between avoidance and tolerance. These differences are remarkable since the selected individuals grow within several meters of each other, sharing the same environment.

Photosynthetic rates observed in the four *Cistus* species during spring are in the range reported for other Mediterranean shrubs (Flexas et al 2001; Llorens et al. 2003; Clemente et al. 2005). The reduction in periods of higher radiation and higher temperatures (summer) can be attributed not only to a decrease in *gs* but also to a down-regulation of photosynthetic process as observed by Liberati et al (2012), a common process under these environmental conditions (Angelopoulos et al. 1996; Park & Furukawa 1999; Mohotti & Lawlor 2002). High vapor pressure deficit, VPD, causes a strong reduction in *gs* and consequently in photosynthesis (Marenco et al. 2006). Furthermore, high temperature may reduce the liquid carbon assimilation due to its effect on photochemical processes or in respiration (Ishida et al. 1999; Pons & Welschen 2003). After the first autumn rains, *C. monspeliensis* recovered to pre-summer drought values of *gs*, maximum photosynthetic rate, A_{max}, and photosynthetic rate, *A,* respectively 1154 %, 307 % and 545 % [(autumn values - summer values) * 100 / (spring values - summer values)] due to its capacity to recover from water deficit, as demonstrated by Sánchez-Blanco et al. (2002). *C. populifolius* recovered 155 %, 55 % and 174 % of *gs*, *A* and A_{max} values, respectively. Shrubs of *C. ladanifer* recovered 40 %, 49 % and 75 % of *gs*, *A* and A_{max} values, respectively. *C. psilosepalus* recovered only about 50 % pre-summer drought values, for all considered parameters. The quantum yield (Φ, per unit of leaf area) was lower in *C. ladanifer* and *C. monspeliensis*, than *C. psilosepalus* and *C. populifolius* (if Φ is expressed per unit of leaf biomass this difference is much pronounced, due to lower SLA in the first too species, C *ladanifer* and *C. monspeliensis,* data not show). These results are in agreement with the species locations, since *C. ladanifer* and *C. monspeliensis* are mostly found in sunny places, *C. populifolius* in shadowy places (low PPFD intensity is used in photosynthesis more efficiently), while *C. psilosepalus* is a mesophyllous species. The analysis of the seasonal variation patterns of photosynthetic capacity in *Cistus* species should consider leaf dimorphism and leaf age due to its effects on specific leaf area, mesophyll conductance to CO_2, *gm*, and leaf nitrogen concentration.

The higher nitrogen concentrations per unit leaf mass determined in autumn for all study species can be related to leaf age (Simões et al. 2008), because most leaves were the newly formed winter leaves, and also to a high soil N availability associated with precipitation. The decrease observed in spring/summer leaves can be ascribed to N translocation before leaf abscission, as suggested for *Cistus* species (Simões et al. 2012). Also the highest decrease in *C. ladanifer* leaves is in accordance with the High N translocation reported for this species (81 % of leaf N) reported for this species (Simões et al. 2012). A higher N translocation to the new summer leaves in *C. ladanifer* as compared to the other species is corroborated by the higher leaf N increase from spring to summer observed in the same species. We can thus suggest a more conservative and efficient N use by *C. ladanifer* than by the other study species.

Photosynthetic capacity at PPFD saturation, A_{max} (at area basis) in spring was higher than in autumn for all *Cistus* (excepting for *C. monspeliensis*). However, leaf nitrogen (at area basis) is not positively related since it is lower in spring than autumn. As N decrease with leaf age and SLA increase, measurements in spring were probably in older leaves than in autumn. These results might be unexpected but it is probably because the variation in N (per area) primarily resulted from changes in SLA which generally scaled negatively with A_{max} (at mass basis) due to a positive relation between SLA and *gm* as found for *Olea europea* and *Quercus ilex* (Niinemets et al 2005). If we consider the N concentration by leaf unit area instead of unit leaf mass, variation among species was different. Almost no variation was observed in *C. populifolius* between seasons reflecting the small SLA variation in this species. For the other species the highest concentrations occurred during summer in association with SLA decrease. Comparing A_{max} between species in spring and autumn a pronounced reduction is observed for *C. populifolius* and probably meaning less N leaf investment in Rubisco enzyme and more in chlorophyll (Rubsisco is about 70–80% of leaf nitrogen (Hunt & McNeil 1998)). Moreover, although *C. ladanifer* presented the lowest mean N concentration per unit leaf mass, shrubs of this species showed the highest mean N concentration per unit leaf area, which is related with higher photosynthetic capacity in this species, as reported for other Mediterranean species (Sabaté et al. 1995; Hevia et al. 1999).

Litterfall and nutrient concentrations in leaf litter

In line with the peak leaf abscission observed in shoots labeled for phenological observations, maximum leaf litterfall occurred in late-spring to early summer (June), coinciding with the beginning of the drought period, as observed for other Mediterranean shrubs, including *Cistus* species (Arianoutsou 1989; Moro et al. 1996). By shedding most of their "winter leaves", which were characterized by high SLA, and keeping only a small amount of low SLA "summer leaves" before the summer drought, the study *Cistus* species greatly reduced the total transpiring surface. Leaf litterfall amount of studied shrub species is within the range reported for *Cistus* species (Simões et al. 2009, 2012). Although there were no differences in leaf shedding number between *C. ladanifer*, *C. monspeliensis*, and *C. psilosepalus*, leaf litterfall amount of *C. ladanifer* and *C. psilosepalus* was higher because leaves of the latter species are bigger and heavier than those of the former. Also, SLA of *C. monspeliensis* was relatively low throughout the study period.

The four studied *Cistus* species differed in nutrient concentrations in leaf fall and also in their seasonal variation. The markedly Mediterranean character of *Cistus* shrubs, similarly to oak trees well-adapted to water-deficit situations, have a high internal control of a large number of nutrients, as belonging to the sclerophyllous Mediterranean systems (Escarré et al. 1984). This high control capacity is shown especially for N and P, and also by the occurrence of seasonal variations in the litterfall mineral content (Escarré et al. 1984). The decrease of N and P concentration in leaf litterfall observed in the present study during the drought period is in accordance with other studies for several *Cistus* species (Correia et al. 1992; Milla et al. 2004; Simões et al. 2009, 2012), and also agrees with observations reported for tree species, in Mediterranean areas, with leaf fall peak in early-summer (e.g. *Eucalyptus globulus*, Madeira et al. 1995). This decrease, coinciding with peak leaf shedding and maximum leaf litterfall, suggests reabsorption from senescing leaves (Simões et al. 2008). According to Chapin & Kedrowski (1983), plants with low values of N and P status retranslocate a similar or smaller proportion of leaf N and P prior to leaf abscission than do plants with more favorable nutrients status and during the dry season there are important changes in allocation of N and P to different chemical fractions, associated with changing plant requirements. Our results are in accordance with these authors, since for instance *C. ladanifer*, the species with the lowest N and the highest P concentration, showed only a

slight N variation and, in contrast, a pronounced P variation throughout the year. The higher retention of N during de peak of leaf fall in *C. ladanifer,* revealing a conserving behavior, matches its greater growth rate during the favouring period of the year. This result supports the view of earlier studies (Monk 1966; Cherbuy et al. 2001) that emphasize the role of old leaves as nutrient sources for further growth in evergreen species. High N retention and, in contrast, high P turnover was also observed in other studies on the same species (Simões et al. 2008, 2009). Since P is considered as one of the major limiting factors for many Mediterranean ecosystems (Vallejo et al. 2006), the higher concentration in *C. ladanifer* and the lower in *C. populifolius* might suggest that the former is better adapted to this limitation than the latter. The greater capacity of *C. monspeliensis* and *C. psilosepalus* to reduce its transpiring biomass, might contribute to reduce nutrient retention efficiency (Simões et al. 2008). K concentration increased in the drought period and, in contrast, decreased during the wetter periods since this element is a component easily leachable with rain (Schumacher et al. 2004) resulting in a higher concentration in absence of rainfall. The higher K concentration observed in *C. populifolius* during the rainy March to May period might be attributed to the protection against the rain impact offered by tree canopies, beneath which this species usually inhabits. Ca and Mn concentrations in leaf litterfall of *C. ladanifer*, *C. populifolius*, and *C. psilosepalus* were higher during the dry season, which might be due to the low mobility of these bio-elements, leading to maximum concentrations at senescence (Simões et al. 2008). Therefore, these nutrients do not seem to be retranslocated to younger tissues (König et al. 2002), as observed for tree species in Mediterranean areas (Madeira et al. 1995; Gallardo et al. 1999; Santa Regina 2000). This type of Ca and Mn increase was not observed in *C. monspeliensis*, probably because leaf fall of this species, although more prominent in the dry season was distributed along the year, showing even secondary leaf fall peaks in March and September. A trend to Mn accumulation over time was also observed for other Mediterranean species like *Quercus suber* (Escarré et al. 1984). In the overall, the variation of Mg followed that of K. However, the lowest values of Mg concentration found in *C. ladanifer* and the highest in *C. populifolius* might be associated with the participation of this element in the constitution of chlorophyll a and b (Lima et al. 2010).

Concluding remarks

The simultaneous study of physiological and morpho-phenological responses in co-occurring *Cistus* species have permitted a better understanding of the mechanisms underlying survival in drought conditions. According to previous studies in other Mediterranean species, all studied *Cistus* showed a seasonal pattern of plant growth, water status and photosynthesis with maximum values in spring followed by a progressive decline or interruption during the summer drought and a partial recovery in response to autumn rains. However, different inter-specific leaf traits and water use strategies were observed. *C. monspeliensis and C. ladanifer*, both subheliophyllous species, exhibited a drought-tolerance mechanism and revealed a high ability to cope with drought with the highest values of light-saturated photosynthetic rate after the first rains. Nevertheless, although vegetative growth still occurs in both species at low leaf water potential, *C. monspeliensis* had a more favorable leaf area reduction during drought than *C. ladanifer.* Additionally, by having higher tolerance to critical leaf water potential values, *C. monspeliensis* can protract leaf production and shedding almost all year round and thus this species might have higher survival capacity to face increasing drought. *C. psilosepalus* behaviour is more close to drought avoidance because this species maintains high water status during summer drought and takes great advantage of spring conditions for carbon assimilation, which enhances growth through almost all the year. *C. populifolius* has relatively low photosynthetic rate (at saturating PPFD) and high quantum yield even under favourable soil water conditions (spring and autumn) and vegetative growth very sensitive to drought. Thus, this species seems to be less tolerant to increasing drought.

The different species strategies observed in this study are indicative of the great diversity of mechanisms that allow Mediterranean plants to persist and coexist in water-limited environments. The effects of climate change, with long drought periods and higher insolation, can result in dramatic consequences in *Cistus* persistence and survival. Diversity of *Cistus* could decrease in scenarios of dryness and *C. ladanifer* and in particularly *C. monspeliensis,* among the studied species, will be dominant shrub species. In contrast, *C. populifolius* patches might decline and become residual. Further studies are needed to better understand *C. psilosepalus* mechanisms and strategies. We may also advise additional studies on these *Cistus* species under simulated climate change conditions to corroborate our conclusions.

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3- CONSIDERAÇÕES FINAIS

Como referido a título introdutório, os montados encontram-se seriamente ameaçados pelo pouco cuidado que tem sido dedicado à regeneração natural dos sobreiros e azinheiras. As práticas agrícolas e de pastoreio não são as mais adequadas aos processos de dispersão, estabelecimento de jovens plantas e ao seu desenvolvimento até à fase adulta. Neste ecossistema, com elevado número de árvores adultas, comparativamente à sua taxa de regeneração, a manutenção e gestão dos arbustos são de extrema importância, uma vez proporcionarem um microclima e um substrato vegetal favorável às plântulas que ocorram sob as suas copas, permitindo assim a germinação das bolotas e proteção dos renovos (Pereira et al. 2009). Com as alterações climáticas previstas, para a região Mediterrânica (Miranda et al. 2002), torna-se necessário determinar quais as espécies que melhor se adaptam aos esperados aumentos de temperatura do ar e da seca, de forma a permitir uma gestão sustentada dos montados.

Não obstante as quatro espécies de *Cistus* estudadas tenham evoluído de forma a otimizar a adaptação à variação sazonal da disponibilidade de água e de nutrientes do solo num clima Mediterrânico, os efeitos esperados das alterações climáticas, em termos evolutivos de uma espécie, são de muito curto prazo, podendo resultar em consequências dramáticas na sua distribuição.

O estudo simultâneo das respostas fisiológicas e morfo-fenológicas de espécies de *Cistus* coocorrem, permitiu uma melhor compreensão dos mecanismos subjacentes á sobrevivência em condições de secura. De um modo geral, os resultados obtidos neste trabalho para *C. ladanifer*, *C. monspeliensis*, *C. populifoliu*s e *C. psilosepalus* estão de acordo com a bibliografia referente a outras espécies mediterrânicas, sugerindo que as referidas alterações climáticas podem diminuir a produtividade anual dos arbustos mediterrânicos, embora a sua magnitude varie de espécie para espécie, pois cada uma apresentou diferentes respostas ecofisiológicas no período de verão e na recuperação após as primeiras chuvas de outono.

C. ladanifer, *C. monspeliensis*, *C. populifolius* e *C. psilosepalus* evidenciaram uma variação sazonal no crescimento vegetativo, teor de água no solo, potencial hídrico, taxa de fotossíntese e concentração de nutrientes (N e P), mostrando um típico padrão com valores máximos na primavera seguido de um declínio progressivo durante a seca de

verão e uma recuperação como resposta às primeiras chuvas de outono, variando apenas na sua grandeza. Este padrão sazonal é característico da maioria dos arbustos mediterrânicos (Correia et al. 1992; Angelopoulos et al. 1996; Gratani & Crescente 1997; Park & Furukawa 1999; Mohotti & Lawlor 2002; Milla et al. 2004; Castro-Díez et al. 2005; Simões et al. 2008; Simões et al. 2009; Simões et al. 2012). Os resultados apontaram também para algum dimorfismo foliar, o que está de acordo com estudos efetuados para outras espécies de *Cistus* sob influência do clima mediterrânico (Correia et al. 1987; Harley et al. 1987) e, com uma certa diferenciação inter-específica, o que sugere uma resposta ecofisiológica diferenciada face à seca das quatro espécies de *Cistus* estudadas que coocorrem, o que é bastante frequente em espécies mediterrânicas (Bahari et al. 1985; Castell et al. 1994; Abrams & Mostoller 1995; Goulden 1996; Martínez-Vilalta et al. 2002). Os valores máximos de abscisão foliar ocorreram no final da primavera e início do verão, como tipicamente observado em muitos arbustos mediterrânicos, incluindo outras espécies de *Cistus* (Gratani & Crescente 1997; Palacio et al. 2006; Simões et al. 2008).

C. ladanifer, espécie subheliófila, exibiu um mecanismo de tolerância à seca, apresentando menores variações relativas, ao longo do ano, na sua estrutura e fenologia e, com crescimento contínuo, tal como observado em outras espécies mediterrânicas (Castro-Díez et al. 2005; Palacio et al. 2006; Simões et al. 2008), mesmo com baixos níveis de humidade no solo e reduzidos valores de potencial hídrico durante o verão. Mostrou um comportamento de conservação em termos de nutrientes e parece estar bem adaptado às suas limitações. Os elevados níveis de retenção de azoto e de reciclagem de fósforo foram também observados para a mesma espécie em outros estudos (Simões et al. 2008, 2009). Embora *C. ladanifer* seja a espécie com menor controlo estomático e, após as primeiras chuvas de outono, ter recuperado apenas cerca de 40 % dos valores de condutância estomática e 49 % dos valores da taxa de fotossíntese anteriores ao período de seca, obteve os maiores valores de taxa fotossintética em luz saturante entre as quatro espécies estudadas.

C. monspeliensis, espécie suheliófila, investiu mais tempo no crescimento em braquiblastos do que em macroblastos e exibiu novas folhas praticamente ao longo de todo o ano. Demonstrou um mecanismo de tolerância à seca, obtendo valores bastante baixos em condutância estomática e potencial hídrico foliar, semelhantes aos demostrados por Clemente et al. (2005). Durante o período de seca, a sua estratégia

consistiu também, numa abscisão foliar mais prolongada e numa maior quantidade de abscisão de "folhas inverno", mantendo uma pequena quantidade de "folhas de verão", reduzindo também muito a superfície total transpirante, como também observado por Sánchez-Blanco et al. (2002). Durante a estação quente as margens das suas folhas enrolam em direção à nervura central, reduzindo a parte da lâmina foliar exposta ao sol. Esta capacidade em reduzir a sua biomasssa transpirante pode no entanto ter contribuído para reduzir a eficiência na retenção de nutrientes (Simões et al. 2008). Após as primeiras chuvas de outono as margens das suas folhas desenrolam e a lâmina foliar expande-se (Liberati et al. 2012). Esta espécie, embora tenha obtido valores baixos de eficiência quântica, mostrou uma notável capacidade de recuperação dos valores de condutância estomática, taxa de fotossíntese máxima em luz saturante e taxa de fotossíntese em 1154%, 307 % e 545 % respetivamente, superando os valores anteriores ao período de seca, como evidenciado também por Sánchez-Blanco et al. (2002).

C. populifolius demonstrou uma estratégia simultânea de prevenção e de tolerância à seca. Apresentou um crescimento equilibrado entre macroblastos e braquiblastos, mas com um menor valor de produção foliar, a qual ocorreu por um período menor e mais húmido, mesmo obtendo a maior percentagem de água no solo, assim como algum controlo estomático durante a estação seca, como também reportado para outras espécies de *Cistus* (Aronne & de Micco 2001; Correia et al. 1992; Gratani & Varone 2006). *C. populifolius* exibiu as maiores folhas, com poucas alterações na sua estrutura ao longo do ano e cuja abscisão ocorreu em menor quantidade e também por um curto período. Após as primeiras chuvas de outono, *C. populifolius* obteve valores mais elevados de potencial hídrico foliar que *C. ladanifer* e *C. monspeliensis*, um importante mecanismo de prevenção reportado também para outras espécies de *Cistus* (Aronne & de Micco 2001; Correia et al. 1992; Gratani & Varone 2006), recuperou 155 % e 174 % dos valores de condutância estomática e de taxa de fotossíntese máxima em luz saturante, respetivamente, observados na primavera, obteve valores elevados de eficiência quântica, mas ficou 55 % abaixo dos valores de taxa de fotossíntese anteriores ao período de seca, demonstrando também encontrar-se menos adaptado à limitação de nutrientes do que *C. ladanifer*. *C. populifolius* é uma espécie submesófila, encontrada principalmente em locais frescos e sombrios e, uma vez que a recarga do conteúdo de água do solo em áreas afetadas pela copa de árvores ser mais lenta do que em áreas

abertas, com a diminuição da frequência da precipitação, esta espécie, possivelmente, terá menor capacidade de recuperação após longos períodos de seca.

C. psilosepalus, espécie submesófila, investiu mais tempo no crescimento dos braquiblastos do que nos macroblastos e exibiu novas olhas quase todo o ano. Demonstrou um mecanismo de prevenção aos danos causados pela seca através do fecho precoce dos estomas, antes de qualquer alteração nos níveis de potencial hídrico foliar, obtendo assim os valores mais elevados de potencial hídrico. Observou-se nesta espécie um longo período de abscisão foliar e uma redução acentuada na sua área foliar específica no período de seca, como reportado também para outras espécies mediterrânicas (Palacio et al. 2006), o que pode ter contribuído para reduzir a sua eficiência na retenção de nutrientes. No final do período de seca (setembro), *C. psilosepalus* apresentou melhor controlo estomático do que as restantes espécies estudadas. Após as primeiras chuvas de outono, *C. psilosepalus*, apesar de ter obtido valores elevados de eficiência quântica, apenas recuperou cerca de 50 % dos valores dos parâmetros considerados.

Assim, os resultados obtidos sugerem que, enquanto que a estratégia de *C. psilosepalus* inclui mecanismos de prevenção, as estratégias de *C. ladanifer* e *C. monspeliensis* indicam tolerância à seca. Os mecanismos de *C. populifolius* parecem estar entre a prevenção e a tolerância. Estes resultados estão de acordo com a localização das espécies, uma vez que *C. ladanifer* e *C. monspeliensis* são encontrados essencialmente em locais abertos com incidência direta do sol, *C. populifolius* em locais mais sombrios e *C. psilosepalus* é uma espécie mesófila.

Os efeitos das alterações climáticas previstas, com longos períodos de seca e elevados níveis de insolação, podem resultar numa diminuição da diversidade de *Cistus*. *C. ladanifer* e, particularmente, *C. monspeliensis*, entre as espécies estudadas provavelmente serão espécies arbustivas dominantes e, pelo contrário, manchas de *C. populifolius*, poderão declinar e tornarem-se residuais. Quanto a *C. psilosepalus* são necessários mais estudos para melhor entender as suas estratégias e mecanismos.

Desta forma, as diferentes estratégias observadas neste estudo são indicativas da grande diversidade de mecanismos que permitem às plantas mediterrânicas persistirem e coexistirem em ambientes com limitação ao recurso água. Conclui-se, assim, que espécies que ocorrem sob as mesmas condições de secura e insolação podem não

partilhar de mecanismos comuns para resistir ao stress imposto pelo verão mediterrânico. A heterogeneidade no comportamento ecológico sob stress pode ser de grande importância de forma a descrever a complexidade funcional dos ecossistemas mediterrânicos e permitir ajudar a entender futuras alterações nestes ecossistemas. Entender as estratégias e respostas à seca pode, assim, ser importante para prever as futuras comunidades de espécies em cenários de crescente secura e para o estabelecimento de diretrizes na gestão do montado. É de salientar a plasticidade destas plantas quanto à sua capacidade de adaptação face à distribuição da precipitação ao longo do ano. Daí decorre, portanto, que o estudo acerca das estratégias adaptativas a diferentes condições de secura e insolação deva ser realizado durante o maior número de anos possível e, nomeadamente, estudos adicionais com simulação das alterações climáticas, de forma a corroborar as conclusões aqui obtidas.

Em termos de trabalho futuro, o estudo será complementado com análises à clorofila e os dados de fenologia, folhada e concentração de nutrientes serão completados para todo o ciclo anual das quatro espécies.

Desta forma, espera-se que este trabalho possa ser considerado um importante contributo para futuras medidas na gestão dos montados.

4 - REFERÊNCIAS BIBLIOGRÁFICAS

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