

UNIVERSIDADE DE ÉVORA

Produção primária, ciclo de nutrientes e trocas gasosas em duas espécies halófitas, *Atriplex portulacoides* L. e *Limoniastrum monopetalum* L., no Sapal de Castro Marim - importância no funcionamento base para o ecossistema

Dissertação para a obtenção do grau de Mestre em Biologia da Conservação

Autor: João Pedro Correia das Neves

Orientador: Prof. Dr. Luíz Carlos Gazarini

Esta dissertação não inclui as críticas e sugestões feitas pelo júri

Évora, 21 de Fevereiro de 2006

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*For it so falls out...
That what we have we prize not to the worth
Whiles we enjoy it; but being lacked and lost,
Why, then we wreck the value, then we find the virtue,
that possession would not show us whiles it was ours.*

Shakespeare

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Resumo

Os ecossistemas costeiros albergam uma grande biodiversidade e são um dos ecossistemas mais ameaçados do planeta. A importância das comunidades vegetais para a conservação destes ecossistemas ganha cada vez mais destaque, à medida que a informação a elas associada aumenta.

Este trabalho teve como objectivo aprofundar o conhecimento da produtividade primária, ciclo de nutrientes e trocas gasosas em duas das espécies mais representativas do Sapal de Castro Marim, *Atriplex portulacoides* L. e *Limoniastrum monopetalum* L., contribuindo para um maior e melhor conhecimento do funcionamento base deste ecossistema.

Ambas as espécies apresentaram elevados valores de taxas fotossintéticas, particularmente nos períodos com condições ambientais mais favoráveis, o que reflecte marcadas características adaptativas ao meio ambiente. Observaram-se diferenças entre *A. portulacoides* e *L. monopetalum*, no respeitante à capacidade de sequestro do carbono atmosférico, quer através das trocas gasosas, quer na consequente produtividade. Os valores obtidos para *L. monopetalum* foram superiores aos da maioria das espécies halófitas.

No geral, a capacidade evidenciada por estas espécies, como sumidouros de carbono, através das elevadas taxas de produtividade primária e *turnover*, conferem-lhes um importante papel na estrutura e funcionamento deste e dos ecossistemas adjacentes, constituindo factores chave para a conservação efectiva do sapal.

Primary production, nutrient cycle and gas exchange in two halophyte species, *Atriplex portulacoides* L. and *Limoniastrum monopetalum* L., in Castro Marim Salt Marsh –
Their importance for the ecosystem basic functioning

Summary

Coastal ecosystems or Wetlands sustain a great deal of biodiversity and are among the most threatened ecosystems on the planet. The importance of plant communities to the conservation of such ecosystems is growing, as the knowledge associated to them increases.

The main goal of this work was to increase knowledge on two of the most representative plant species of Castro Marim salt marsh, *Atriplex portulacoides* L. e *Limoniastrum monopetalum* L. Aerial productivity, nutrient cycles, and gas exchange were assessed over one-year, in order to understand and highlight some of the basic functioning mechanisms of this ecosystem.

Both species exhibited high photosynthetic rates, particularly in favourable climate conditions, what reflects marked adaptive characteristics to the environment. Some differences were observed between *A. portulacoides* and *L. monopetalum*, in what concerns their aptitude as carbon sinks, either through their gas exchange variation patterns, or consequent their productivity. The productivity of *L. monopetalum* was higher than for most halophyte species.

In general, the aptitude of these species as carbon sinks, due to their high productivity, turnover rates, and gas exchange potential, enhances their importance, in this so productive ecosystem, and increases the needed awareness about salt marshes conservation.

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Introdução

*We have not inherited the world from our forefathers.
We have borrowed it from our children.*
Provébio Índio

Ecosistemas costeiros

Os ecossistemas costeiros são sistemas complexos que formam uma interface entre os habitats terrestre e aquático. São considerados zonas de transição, contendo características particulares definidas por escalas temporais e espaciais, e pela intensidade das interações entre ecossistemas (Holland 1988). A estabilidade destes ecossistemas reflecte o equilíbrio necessário entre inúmeros factores, quer ecológicos quer ambientais sendo, no entanto, bastante sensíveis a quaisquer alterações neles verificadas.

Dentre os ecossistemas costeiros, destacam-se os sapais, que se desenvolvem em zonas intertidais, hidrodinamicamente protegidas, onde a matéria orgânica e compostos inorgânicos se acumulam, integrando a constituição de um solo particularmente fértil (Mann 2000). Os locais mais habituais para a formação e presença de sapais são os estuários costeiros de topografia mais ou menos plana, onde os sedimentos do rio se depositam. A colonização destes locais, relativamente protegidos por espécies vegetais, provoca um decréscimo na hidrodinâmica tidal e um aumento do depósito de material sedimentar, principalmente originário das águas do rio. A distribuição vegetal acompanha o acréscimo de material depositado, permitindo, ao longo de grandes períodos, a acumulação em profundidade de consideráveis quantidades de sedimentos aluviais e detritos vegetais, integrando a constituição do solo.

A vegetação destes ecossistemas é predominantemente halófitas, possuindo capacidades fisiológicas entre os ambientes terrestre e aquático. As espécies que a constituem evitam a erosão costeira, aprisionam sedimentos aluviais e algumas delas permitem a depuração de material contaminante através da sua capacidade fitorremediadora (Frid & Evans 1995).

Uma das características de um sapal desenvolvido é a presença de meandros e canais de drenagem perfeitamente formados (Adam 1990). Estes estabelecem uma verdadeira rede inter-comunicante, que permite a entrada e saída da água de maré. Uma vez que o nível da maré oscila consoante os ciclos lunares, a maré poderá inundar por completo os sapais, ou atingir somente os níveis do sapal baixo.

De acordo com a teoria geo-hidrológica elaborada por Dame *et al.* (1992), à medida que o nível da água do mar se elevou, ao longo de milhares de anos, relativamente ao nível da plataforma terrestre adjacente, a água salgada avançou cada vez mais para o interior dos estuários. Desta forma, os sapais mais costeiros serão os

mais velhos e maduros, possuindo uma camada mais profunda de sedimentos e um padrão de canais de drenagem mais complexo e eficiente. Os sapais mais próximos da entrada dos estuários serão, por seu lado, os mais imaturos (Mann 2000).

Estado actual de conservação dos ecossistemas costeiros

Os ecossistemas costeiros ou zonas húmidas figuram actualmente entre os ecossistemas mais ameaçados do planeta (Lefeuvre *et al.* 2003, Ramsar 2002), encontrando-se sob medidas de protecção internacionais instituídas pela Convenção de Ramsar, através do Tratado para a Conservação das Zonas Húmidas (ratificado em 1971 por 180 países nos quais Portugal se insere), pela Convenção de Berna, Convenção de Bonna ou Rede Natura 2000.

De acordo com a Convenção de Ramsar, estima-se que a Europa Ocidental possua cerca de 290 000 km² de Zonas húmidas, dos quais 3 000 km² são áreas de sapal (Ramsar 2002).

Várias são as projecções em relação à futura sustentabilidade destas áreas, considerando os inúmeros factores que estão a contribuir para o seu rápido desaparecimento. Em 1993, nas Baías de Chesapeake e Delaware, EUA, apenas 28 a 55% dos sapais estuarinos continuavam não-degradados (Kearney *et al.* 2002). Orson *et al.* (1998) estimou que até ao ano de 2000, no estado de Connecticut, EUA, 45% das áreas de sapal teriam desaparecido, 41% estariam em processo de destruição e apenas 14% estariam conservadas. Na Baía de S. Francisco, cerca de 79% das áreas de sapal desapareceram, comparativamente às áreas verificadas há 200 anos (Valiela *et al.* 2004). Perdas semelhantes ocorreram em praticamente todas as áreas de grande pressão antrópica, na América do Norte.

O desaparecimento destes ecossistemas não é, no entanto um problema restrito aos EUA. Nicholls *et al.* (1999) prevêem que por volta do ano 2080, cerca de 70% dos ecossistemas costeiros terão desaparecido à escala global, devido à influência humana e à subida do nível da água do mar. Estimam que na Europa poderão desaparecer entre 31 a 100% dos sapais da costa Mediterrânica e cerca de 17% dos sapais da costa Atlântica.

O desaparecimento dos ecossistemas costeiros deve-se essencialmente a uma variedade de actividades humanas, mormente as relacionadas com a ocupação das suas áreas. Sejam quais forem as finalidades das áreas ocupadas, prevalece a pressão económica, relativamente aos argumentos conservacionistas.

As espécies que colonizam e habitam áreas de sapal e outras zonas húmidas são consideradas excelentes meios para avaliação da intensidade e importância de alterações a várias escalas, de local a global, devido às suas capacidades fisiológicas particulares (Hansen *et al.* 1988). Esta constatação colocou, recentemente, estes ecossistemas num dos focos de atenção conservacionista, levando a um crescente interesse nos estudos relacionados com a sua funcionalidade básica e com o seu papel nas trocas específicas entre ecossistemas adjacentes.

Sinal do reconhecimento da sua importância é o financiamento que tem vindo a ser atribuído pela União Europeia a diversos projectos que, por um lado, salientam o interesse ecológico dos sapais (Lefeuvre *et al.* 1994, Bouchard *et al.* 1998, Bouchard & Lefeuvre 2000, Lefeuvre *et al.* 2000, Curcó *et al.* 2002, Pont *et al.* 2002) e, por outro lado, reforçam a necessidade do estabelecimento de medidas, cada vez mais objectivas, no sentido da conservação e sustentabilidade destes ecossistemas.

Benefícios dos ecossistemas costeiros e em particular dos sapais

Os ecossistemas costeiros constituem valiosos recursos ecológicos e económicos, proporcionando diversas mais-valias, quer a nível local, quer regional. Desta forma, seguem-se alguns exemplos que salientam várias funcionalidades inerentes a estes ecossistemas:

✓ *Exportação de materiais energéticos para a cadeia trófica*

A hipótese proposta por Eugene Odum, formulada primeiramente em 1964 (Odum 1980), de que os sapais são essencialmente exportadores de elementos minerais e materiais orgânicos para as águas adjacentes (*outwelling*), tem sido confirmada através vários estudos (Winter *et al.* 1996, Wei-Jun Cai *et al.* 2000, Costa *et al.* 2001).

A grande maioria dos ecossistemas de sapal representa uma importante fonte de componentes energéticos, como componentes de azoto reduzidos e matéria orgânica particulada, ou em solução, para as águas mais profundas (Adam 1990, Valiela *et al.* 2004). Estas exportações são de extrema importância para a subsistência metabólica dos ecossistemas receptores.

A elevada produtividade dos habitats costeiros constitui a base energética para a produção dos recursos ictiológicos mundiais (Adam 1990; Alongi 1998, Thom *et al.*

2001). Por exemplo, a quantificação da exportação de matéria orgânica num sapal da Georgia, EUA, seria suficiente para suportar a energia requerida para as elevadas taxas metabólicas do ecossistema marinho contíguo (Hopkinson 1985). O reconhecimento da função dos sapais na disponibilização de componentes altamente energéticos, capazes de suportar populações em ecossistemas adjacentes, tem vindo a ser um dos argumentos base para a sua conservação.

✓ *Berçários de espécies, incluindo stocks de valor comercial*

Devido à sua topografia e grande biodiversidade vegetal, os sapais disponibilizam um enorme conjunto de nichos ecológicos e alimento para inúmeras espécies animais. Muitas espécies de interesse comercial e ecológico utilizam também os ecossistemas de sapal como berçários (Ramsar 2002, Mumby *et al.* 2004).

Turner (1992) salientou a importância destes ecossistemas, ao reportar que os stocks de crustáceos capturados ao largo do Golfo do México eram proporcionais à área imediatamente adjacente aos ecossistemas costeiros, principalmente de sapal. Também Brady & Flather (1994) observaram que, ao longo do séc. XX, a captura de crustáceos na área do Louisiana, EUA, decresceu, associando esta perda ao contínuo desaparecimento e degradação de zonas de sapal contíguas. Estas reduções têm vindo a ser associadas à regressão dos sapais, dado o seu papel como berçários para crustáceos juvenis, assim como na exportação de nutrientes e matéria orgânica para os ecossistemas adjacentes.

✓ *Habitat para espécies filtradoras com valor comercial*

Muitas espécies animais habitam áreas de sapal devido às características deste ecossistema, como águas calmas, protegidas e com uma grande disponibilidade de alimento. Grandes densidades de fitoplâncton e outras partículas em suspensão constituem alimento para uma grande quantidade de espécies filtradoras e consequentemente para outros consumidores secundários (Valiela *et al.* 2004).

✓ *Intercepção de contaminantes*

Os sapais podem funcionar como interceptores de contaminantes de origem antrópica, como metais pesados ou hidrocarbonetos (Reddy *et al.* 2002). No geral, contaminantes como metais pesados apresentam poucos efeitos nas espécies vegetais.

Neste sentido, a simples presença destes ecossistemas previne a contaminação das águas costeiras (Valiela *et al.* 1976, Adam 1990).

✓ *Estabilização do sedimento nas linhas de costa*

O forte enraizamento das espécies vegetais em áreas de sapal, devido às suas necessidades ecológicas (ancoragem, necessidade hídrica), confere uma maior estabilidade à costa. Pela sua simples presença, estas espécies consolidam o solo e minimizam a erosão (McLean & Tsyban 2001).

✓ *Refúgio para espécies migradoras*

Uma grande e diversa panóplia de espécies de avifauna depende da existência de zonas húmidas adequadas, com áreas de descanso e alimentação entre migrações, assim como áreas de invernada. De um modo geral, a preservação destes ecossistemas é essencial para o ciclo de vida destas espécies (Ramsar 2002).

✓ *Intercepção de nutrientes terrestres*

Pela sua localização, os ecossistemas costeiros interceptam determinados materiais transportados dos ecossistemas terrestres para os aquáticos. Os sapais tendem a reter nitratos, em vez de os exportar, composto limitante para o crescimento da maioria das espécies costeiras, incluindo algas. Muitos dos nitratos ficam retidos nos sapais devido às elevadas taxas de desnitrificação e imobilização. Esta característica poderá ser interpretada como um importante mecanismo de protecção ecológico para os ecossistemas adjacentes. Assim, a posição geográfica dos sapais, como intermediários entre a terra e o mar, permite uma filtragem essencial à manutenção da dinâmica ecológica entre ecossistemas (Alongi 1998).

Os ecossistemas costeiros e o ciclo do carbono

Devido à elevada produtividade primária, concentração de nutrientes e cobertura da superfície terrestre, os ambientes costeiros são uma importante componente do ciclo global de carbono. No seu conjunto, as zonas húmidas representam 15% dos reservatórios de carbono na biosfera (Patterson 1999).

O conhecimento das fontes, sumidouros e dinâmica do carbono dentro destes ecossistemas é extremamente relevante para o balanço global do carbono e para os efeitos associados, como o aumento da concentração de CO₂ atmosférico e o aquecimento global.

Os produtores primários, como o fitoplâncton, microalgas bentônicas, mangais, sapais e prados de ervas costeiras, constituem a principal componente biótica no sequestro do carbono atmosférico (Adam 1990).

Segundo Valiela (1995), a área coberta, a nível mundial, por pântanos e sapais é de apenas 2×10^6 km², o que, correspondendo a 0,004% da área mundial, representa 3,5% da produtividade primária mundial. Estes ecossistemas, incluindo zonas de *upwelling* (fenómeno de elevação de massas de águas frias originárias do fundo do oceano, ricas em nutrientes, para a superfície), correspondem a cerca de 7% da fixação global de carbono.

A elevada produtividade anual verificada nestes ecossistemas, significa que o *turnover* (P:B, quociente entre produção e biomassa) e a exportação são relativamente importantes na escala global. A relação P:B pode variar entre 1 e cerca de 300, o que indica que a biomassa desses ecossistemas pode ser reciclada até 300 vezes num ano (Thom *et al.* 2001).

Os destinos do carbono fixado são frequentemente: o sequestro por incorporação no solo; a reciclagem dentro dos sistemas, através do consumo por herbívoros ou decompositores; a exportação para sistemas adjacentes; e a libertação para a atmosfera, como aerossóis (Adam 1990, Thom *et al.* 2001).

Estimativas da taxa de deposição/imobilização de carbono nos ecossistemas costeiros variam consideravelmente, sendo que em ambientes de sapal situam-se entre 0,2 e 1 cm de carbono por ano (Thom *et al.* 2001). A ocorrência de fenómenos naturais pontuais, como sismos ou colapso do solo e conseqüente sobreposição por sedimentos oceânicos permite a inclusão de material vegetal morto no solo, constituindo esta uma importante forma de imobilização de carbono (Adam 1990, Thom *et al.* 2001).

Mecanismos de regulação ecológica

O estudo detalhado dos ecossistemas costeiros tem contribuído para um mais profundo e fundamentado conhecimento dos mesmos e de outros a estes associados. Neste contexto, a atribuição de uma maior importância ao controlo destes ecossistemas

consiste em definir, como elementos-chave para o seu funcionamento, os organismos pertencentes à base funcional, produtores primários – mecanismos *bottom-up* – ou os organismos pertencentes ao topo da cadeia trófica – mecanismos *top-down*.

A taxa de crescimento do fitoplâncton costeiro está largamente associada à disponibilidade de nutrientes, particularmente de azoto (Downing *et al.* 1999, Howarth *et al.* 2000). Como resultado do seu incremento, aumenta a abundância dos consumidores secundários e, por conseguinte, altera-se a dinâmica trófica. Cumulativamente, a dinâmica das taxas de crescimento do fitoplâncton está dependente da periodicidade da reciclagem dos nutrientes pelo estuário adjacente, da sua hidrodinâmica e das condições particulares à escala local (Mann 2000). Este exemplo, ainda que simplificado, demonstra a interligação existente entre os diferentes níveis tróficos e a necessidade de conhecer a dinâmica existente entre eles, de forma a compreender os funcionalismos básicos de um ecossistema.

Semelhantes efeitos têm sido verificados na dinâmica trófica de ecossistemas de sapal e mangal. Foram observados aumentos substanciais nas concentrações de material vegetal particulado, com elevado valor nutritivo que, por sua vez, estimulou a taxa de crescimento dos animais filtradores (Evgenidou & Valiela 2002). Em sapais de New England, EUA, adições experimentais de N resultaram no aumento da produção de biomassa vegetal e da densidade de pequenos ruminantes em 4 vezes (Vince *et al.* 1981), e em aumentos na taxa de crescimento de afídeos em 20% (Levine *et al.* 1998). Em mangais na Florida, EUA, o aumento experimental de nutrientes originou um crescimento generalizado na vegetação, aumentando conseqüentemente o número de herbívoros (Onuf *et al.* 1977). É portanto fácil de perceber que, nestes ecossistemas, os consumidores primários e secundários dependem directamente da produtividade primária.

No geral, os efeitos da regulação *bottom-up* estão associados a uma cadeia estruturada de conseqüências: o aumento de nutrientes reflecte-se em acréscimos de biomassa vegetal, que cria vários efeitos nos níveis tróficos superiores, através da sua abundância e composição, isto é, através da disponibilidade e qualidade de alimento, ou ainda através da indução de alterações na qualidade das características físicas e químicas do meio ambiente (Valiela *et al.* 2000).

Relação capacidade fotossintética / produtividade primária

O metabolismo do carbono no interior das plantas passa pela sua captura, através do processo fotossintético, podendo ser libertado pela respiração ou armazenado como componente estrutural da sua biomassa. Este processo de armazenamento leva ao crescimento e sustentabilidade do organismo e pode ser aferido através da sua produtividade primária. O conhecimento destes processos de captura e armazenamento fornece importantes informações sobre a capacidade que determinada espécie vegetal apresenta no sequestro e armazenamento de carbono e, em última análise, a sua contribuição para o ciclo do carbono num determinado ecossistema.

Os ecossistemas de sapal são, ao longo do ano, frequentemente sujeitos a radiações elevadas e temperaturas altas, condicionando a capacidade fotossintética das espécies existentes e, conseqüentemente, a sua produtividade (Larcher 1995). A competição, salinidade, grau de encharcamento e/ou disponibilidade de nutrientes são factores acrescidos de extrema importância para a regulação da produtividade destas comunidades vegetais (Pennings & Callaway 1992, Munns 2002).

Espécies nativas de habitats de sapal desenvolveram diferentes estratégias de adaptação ao défice hídrico e ao excesso de salinidade, demonstrando também uma grande variabilidade quer na fenologia, na distribuição do sistema radical ou na capacidade intrínseca para ultrapassar factores de stresse.

Frequentemente, ocorrem alterações estruturais e químicas nas plantas, como o aumento das concentrações de aminoácidos e açúcares, de forma a minimizar danos resultantes das condições ambientais. Estas alterações poderão ser designadas de aclimação e resultam numa maior capacidade de sobrevivência, quando as condições abióticas são adversas. As plantas poderão, também, demonstrar diferentes níveis de tolerância a stresses particulares, sem aclimação. Algumas espécies conseguem tolerar, intrinsecamente, altas temperaturas ou desidratação melhor que outras, devido ao seu património genético, sem terem que sofrer alterações estruturais e químicas (Adam 1990).

Importância da vegetação costeira para a conservação do sapal

A discussão acerca da importância relativa dos mecanismos que controlam as cadeias tróficas e a dinâmica dos ecossistemas costeiros é, sem dúvida, uma indicação

do interesse, cada vez mais generalizado, da comunidade científica no conhecimento básico do seu funcionamento. Contudo, e apesar do crescente trabalho realizado neste contexto, grande parte destes ecossistemas está gradualmente a desaparecer ou a sofrer alterações drásticas, tornando-se o seu estudo cada vez mais pertinente.

Neste sentido, estudos de base relacionados com a produtividade primária e a capacidade fotossintética de determinadas espécies vegetais, poderão dar boas indicações quer do estado de conservação do ecossistema em que se incluem, quer da sua importância para o funcionamento do ecossistema (Pont *et al.* 2002).

Neste contexto, pretende-se com este trabalho contribuir, de uma forma geral, para um maior e melhor conhecimento do funcionamento base dos sapais, e em particular, aprofundar o conhecimento da produtividade primária, ciclo de nutrientes e trocas gasosas ao longo de um ano, em duas das espécies halófitas mais representativas da vegetação, *Atriplex portulacoides* L. e *Limoniastrum monopetalum* L., do Sapal de Castro Marim.

O presente trabalho é, assim, constituído por duas partes, apresentadas sob a forma de artigo científico:

“Primary production and nutrient content in two saltmarsh species, *Atriplex portulacoides* L. and *Limoniastrum monopetalum* L., in Southern Portugal”: onde se procede ao estudo da produtividade primária e dos ciclos de nutrientes, através de métodos destrutivos de recolha de biomassa aérea e radical e por análise dos respectivos conteúdos em nutrientes, em diferentes épocas, durante o período de um ano. Este conhecimento permite estimar a potencialidade de cada espécie como sumidouro de carbono, assim como perceber a variação sazonal do investimento em biomassa e acumulação de nutrientes, característicos de cada uma;

“Gas exchange in the salt marsh species *Atriplex portulacoides* L. and *Limoniastrum monopetalum* L. in Southern Portugal”: onde se aborda o padrão de variação sazonal das trocas gasosas e relações hídricas, relacionando as formas como cada espécie se adapta às condições ambientais características de cada estação e a sua capacidade de sequestro de carbono atmosférico, para investimento em biomassa.

Para além da Introdução e dos artigos, apresentam-se algumas Considerações Finais, nas quais se integram os resultados das duas componentes estudadas. Sendo o Sapal de Castro Marim parte integrante da Reserva Natural do Sapal de Castro Marim e Vila Real de Santo António, abrigando inúmeras espécies, florísticas e faunísticas, com

estatuto de protecção e conservação, o conhecimento do seu funcionamento é fundamental para a adopção de medidas de conservação adequadas.

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Caracterização da área de estudo

The value of biodiversity is more than the sum of its parts.

Byran Norton

A Reserva Natural do Sapal de Castro Marim e Vila Real de Santo António compreende uma área de 21 km², da qual cerca de 12,3 km² correspondem a áreas de zonas húmidas, incluindo sapais (Lousã 1986, Xavier 1998). Localiza-se no extremo Sudeste de Portugal Continental, no estuário do Rio Guadiana, estendendo-se pelos concelhos de Castro Marim e Vila real de Santo António. As suas coordenadas geográficas são: 37° 12' de latitude Norte e 7° 26' de longitude Oeste (ICN 2001).

Estatutos de protecção

Esta foi a primeira Reserva Natural a ser criada em Portugal, através do Decreto n.º 162/75 de 27 de Março, com os objectivos de assegurar a conservação dos sistemas naturais e das espécies da flora e da fauna, promover e divulgar os valores naturais, socio-económicos e paisagísticos, e promover o desenvolvimento sustentável da área (ICN 2001).

Para além do estatuto de Reserva Natural, criada pelo Decreto n.º 162/75 de 27 de Março e regulamentada pela Portaria n.º 337/78 de 24 de Junho (rectificada pelas Portarias n.º 647/78 de 11 de Julho e n.º 490/90 de 30 de Junho), foram atribuídos a esta área diversos estatutos de conservação internacionais em virtude da importância dos seus valores naturais.

A nível comunitário, a área foi designada Zona de Protecção Especial ao abrigo da Directiva Aves (código PTZPE0018; Decreto-Lei n.º 384-B/99, de 23 de Setembro) e está incluída na Lista Nacional de Sítios ao abrigo da Directiva Habitats (Ria Formosa/Castro Marim, código PTCO0013; Resolução de Conselho de Ministros n.º 142/97, de 28 de Agosto). No âmbito dos compromissos assumidos pelo Estado Português perante a Convenção sobre Zonas Húmidas foi designada como Zona Húmida de Importância Internacional em 1996. Esta área foi também designada na lista de Áreas Importantes para as Aves (IBA) e foi incluída na Rede de Biótopos CORINE (ICN 2001).

Características físicas

O clima da região é do tipo mediterrânico, caracterizado por uma estação seca e quente que coincide com o Verão (Costa *et al.* 1998). A temperatura média anual do ar é

de 17,2° C e a precipitação média anual atinge valores inferiores a 500 mm (492,3 mm), ocorrendo os maiores valores nos meses de Outubro a Abril, sendo considerada uma das faixas menos pluviosas de Portugal (dados do Instituto de Meteorologia e Geofísica, para o período 1961-1990).

Fazendo parte integrante do estuário do Rio Guadiana, a Reserva apresenta uma forte influência do regime de marés. Cerca de 26% dos terrenos são inundados na preamar, de uma forma periódica, segundo um ciclo diário e lunar. A área inundada pelas marés abrange essencialmente as zonas de sapal que envolvem o Rio Guadiana e os dois principais esteiros, o da Lezíria e o da Carrasqueira (ICN 2001).

Os solos da Reserva são, na maioria, salino-sódicos (halomórficos). Estes solos têm origem na deposição de materiais aluvionares depositados na bacia de sedimentação do Rio Guadiana. Na contiguidade da zona aluvionar predominam os solos de xistos e grauvaques e os solos calcários (Xavier 1998).

Características ecológicas

Embora a Reserva abranja quatro unidades ecológicas distintas (Zonas húmidas, Áreas florestais, Matos e Zonas agrícolas), apenas se fará a descrição das Zonas húmidas, unidade mais representativa da área e de maior pertinência no âmbito deste trabalho.

Esta unidade ecológica abrange a zona de sapal (primário ou secundarizado), as salinas, o Rio Guadiana e os seus esteiros.

A zona de sapal da Reserva caracteriza-se pela sua vegetação halófito, sujeita a condições extremas de salinidade e encharcamento periódico pela água das marés. O Sapal de Castro Marim apresenta um elevado valor natural, apresentando características dos biótopos de maior produtividade que actualmente se conhecem. Encontra-se junto ao estuário do Rio Guadiana e alberga uma grande diversidade de flora e fauna características (Carvalho 2005).

Os sapais secundarizados derivam de sapais típicos que deixaram de sofrer a influência da maré devido à construção de diques de protecção junto ao Rio Guadiana, para impedir a entrada da água salgada, tornando assim possível o cultivo dos cereais. Os sapais assim alterados são mais pobres em biodiversidade e o seu interesse para a conservação reduzido (ICN 2001).

As salinas de Castro Marim são uma componente de extrema importância sócio-económica dentro da Reserva. Existem diferentes tipos de exploração do sal nesta área: a artesanal, a semi-industrial e a industrial (Xavier 1998).

O Rio Guadiana e esteiros são de particular interesse. As suas margens encontram-se a descoberto na baixa-mar, expondo uma faixa de vasas e de outros sedimentos relativamente extensa. Estas margens são importantes zonas de alimentação de aves (Carvalho 2005).

Na área da Reserva encontram-se registadas 462 espécies vegetais, das quais se destacam pelo seu estatuto de conservação as espécies *Picris algarbiensis* (endemismo lusitano considerado “vulnerável”), *Limonium diffusum* (espécie “ameaçada”) e *Beta macrocarpa* (espécie também “vulnerável”). Na Directiva Habitats estão incluídas 4 espécies que aqui ocorrem: *Melilotus fallax*, *Halopeplis amplexicaule* e o briófito *Riella helicophylla* (Castro Marim é a única localidade conhecida em Portugal onde ocorre), incluídos no anexo II e *Picris willkommii*, no anexo IV (endemismo ibérico presente apenas nas colinas junto à foz do Guadiana) (ICN 2001, ICN 2006).

Os factores ecológicos que exercem um maior controlo na distribuição vertical da vegetação do Sapal de Castro Marim são a probabilidade e a duração do encharcamento (ou submersão) pela água da maré. Reconhecem-se três tipos fundamentais de sapal: alto, médio e baixo. O sapal baixo situa-se no extremo inferior do sapal, coloniza solos de salinidade mais ou menos constante, permanentemente saturados de água salgada, sendo completamente submergido durante a preia-mar. Aqui encontram-se *Spartina maritima* (morraça), *S. versicolor*, *Arthrocnemum perenne* (gramata), *Artemisia caerulescens* e *Inula crithmoides* (madorneira-bastarda). Nas comunidades mais interiores do sapal baixo e no sapal médio verifica-se um intenso ciclo de inundação e drenagem bidiário. As condições ecológicas do sapal médio são intermédias entre os sapais baixo e alto. As espécies mais representativas do sapal médio são *Atriplex portulacoides* (gramata-branca), *Arthrocnemum glaucum* (gramata) ou *Mesembryanthemum nodiflorum* (erva-de-orvalho). O sapal alto, em regra, só é visitado pelas águas marinhas na preia-mar. Situa-se desde um pouco abaixo do nível de preia-mar morta até, aproximadamente, ao nível de preia-mar viva, sendo, consequentemente, os períodos de submersão curtos e ocasionais. Nestas condições, os sais tendem a concentrar-se por capilaridade à superfície do solo, atingindo teores de salinidade muito altos, tanto maiores quanto menor a probabilidade de encharcamento. As espécies mais adaptadas a estas condições são *Suaeda vera* (valverde-dos-sapais),

Limonium diffusum, *L. ferulaceum* ou *Limoniastrum monopetalum* (sapeira). Após longos períodos de chuva ou chuvadas muito intensas a salinidade do solo do sapal alto pode descer, temporariamente, a valores muito baixos. Ao contrário do que acontece no sapal baixo, as comunidades de sapal alto suportam variações bruscas e grandes variações sazonais na profundidade dos lençóis freáticos (INAG 1999).

No Sapal de Castro Marim, as espécies mais comuns são *Spartina maritima*, *S. versicolor*, *Arthrocnemum perenne*, *A. glaucum*, *Atriplex portulacoides*, *Suaeda vera* e *Limoniastrum monopetalum* (INAG 1999).

Da fauna aquática de invertebrados destacam-se espécies de valor comercial, como os crustáceos *Penaeus kerathurus* (lagostim) e *Artemia franciscana*. Esta última espécie está intimamente relacionada com as salinas, sendo uma das únicas espécies de invertebrados que tolera salinidades muito elevadas. Desta fauna, nas zonas intertidais destacam-se, pela sua abundância, *Nereis diversicolor* (poliqueta) e *Hydrobia ulvae*. Nas lagoas temporárias que se formam nos meses de Inverno encontram-se espécies de elevado interesse, como *Branchipus schafferi*, endemismo local a nível nacional, e *Tanymastix stagnatilis*, que apenas surge em mais um local em Portugal. O facto de ocorrerem nestas lagoas temporárias de água salobra, espécies típicas de meios dulçaquícolas, eleva o valor conservacionista destes biótopos (INAG 1999, ICN 2001).

Estão referenciadas para a área 31 espécies de peixes, a maioria associadas aos meios marinhos e estuarinos. Os esteiros da Lezíria e da Carrasqueira e as zonas de sapal são de elevada importância para a reprodução de algumas espécies de elevado valor económico, como *Sparus aurata* (dourada), *Dicentrarchus labrax* (robalo) e *Diplodus sargus* (sargo). Todas estas espécies, assim como mais 4 das espécies que aqui ocorrem, são consideradas “comercialmente ameaçadas”. A espécie *Rutilus alburnoides* (bordalo) é a única que está incluída no anexo II da Directiva Habitats (INAG 1999, ICN 2001).

Na área encontram-se regularmente 169 espécies de aves, na sua maioria aves aquáticas invernantes e migradoras. Existem ainda registos de mais 17 espécies que ocorreram de forma ocasional (INAG 1999, ICN 2001). É na zona húmida onde aparece um grande número de espécies, predominando as espécies de limícolas (*Charadrii*), os patos (*Anatidae*) e os galeirões. Esta unidade ecológica assume uma importância especial durante as 8 migrações pós-nupciais (meses de Agosto e Setembro fundamentalmente), quando a diversidade e abundância de espécies de aves aquáticas são maiores. Esta zona húmida alberga uma proporção elevada de algumas espécies que

aqui invernam e é importante como zona de reprodução. Nas zonas de sapal degradado junto ao Rio Guadiana encontra-se ainda *Calandrella rufescens* (calhandrinha-das-marismas), população única no país. Nas áreas mais secas nidificam *Tetrax tetrax* (sisão) e *Melanocorypha calandra* (calhandra-real). Para além destas, reproduzem-se na Reserva mais 65 espécies de aves (INAG 1999, ICN 2001).

Relativamente aos estatutos de conservação, das espécies que ocorrem na Reserva, 15 são consideradas “raras” a nível nacional – destacando-se, pela sua abundância na área *Phoenicopterus ruber* (flamingo-comum), *Tadorna tadorna* (tadorna), *Philomachus pugnax* (combatente), *Gallinago gallinago* (narceja), *Sterna caspia* (garajau-grande) e *Sylvia conspicillata* (toutinegra-tomilheira) — e 12 têm o estatuto de “vulnerável” — destacando-se *Ciconia ciconia* (cegonha-branca), *Platalea leucorodia* (colhereiro), *Circus aeruginosus* (águia-sapeira), *Glareola pratincola* (perdiz-do-mar), *Recurvirostra avosetta* (alfaiate) e *Sterna albifrons* (andorinha do-mar-anã) (INAG 1999, ICN 2001).

Estão referenciadas 16 espécies de mamíferos, destacando-se a presença de *Lutra lutra* (lontra), espécie considerada “insuficientemente conhecida” e incluída no Anexo II da Directiva Habitats (INAG 1999, ICN 2001).

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Artigos Científicos

*There is nothing in which the birds differ more from man
than the way in which they can build
and yet leave a landscape as it was before.*

Robert Lynd

Primary production and nutrient content in two saltmarsh species, *Atriplex portulacoides* L. and *Limoniastrum monopetalum* L., in Southern Portugal

J.P. Neves, L.F. Ferreira, M.P. Simões, L.C. Gazarini

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Primary production and nutrient content in two saltmarsh species, *Atriplex portulacoides* L. and *Limoniastrum monopetalum* L., in Southern Portugal

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Abstract: Seasonal patterns of above and belowground biomass, net primary production and nutrient accumulation were assessed in *Atriplex portulacoides* and *Limoniastrum monopetalum* in Castro Marim salt marsh, Portugal. Sampling was conducted in five periods during 2001/2002 (autumn, winter, spring, summer and autumn).

This study indicates that both species show a clear seasonal variation pattern of above and belowground biomass. Mean live biomass was $2516 \text{ g m}^{-2} \text{ yr}^{-1}$ for *L. monopetalum* and $598 \text{ g m}^{-2} \text{ yr}^{-1}$ for *A. portulacoides*. Peak living biomass, in spring for both species, was three times higher in the former, $3502 \text{ g m}^{-2} \text{ yr}^{-1}$, than in the latter, $1077 \text{ g m}^{-2} \text{ yr}^{-1}$. Despite the applied method, productivity was higher in *L. monopetalum* ($2917 \text{ g m}^{-2} \text{ yr}^{-1}$ – Smalley's – and $3635 \text{ g m}^{-2} \text{ yr}^{-1}$ – Weigert and Evans) than in *A. portulacoides* (1002 and $1615 \text{ g m}^{-2} \text{ yr}^{-1}$, respectively). These results are in accordance with the increase of biomass and productivity with the maturity of the salt marsh. Belowground biomass of *L. monopetalum* was 1.7 times higher than that of *A. portulacoides*. In spite of this *A. portulacoides* showed higher root/shoot ratio along the year. This shows that *A. portulacoides* invests more, along the year in belowground biomass than *L. monopetalum*. Leaf area index was similar for both species, showing *A. portulacoides* twice higher specific leaf area, throughout the year.

The highest nutrient contents were found in leaves. Leaf N content was maximum in summer for both species (14.6 mg g^{-1} for *A. portulacoides*, and 15.5 mg g^{-1} for *L. monopetalum*). The variation pattern of stem and root N contents were similar to those of leaves. The annual variation of leaf P was similar for both species, with the lowest values in the summer period (1.1 mg g^{-1} – *A. portulacoides*, and 1.2 mg g^{-1} – *L. monopetalum*). The leaf K contents in *A. portulacoides* were around three times higher

than in *L. monopetalum*. There was a pronounced variation in *L. monopetalum* Ca content throughout the year, while in *A. portulacoides* no clear seasonal variation was observed. Leaf Ca contents in the former were three times higher than in the latter. Both species exhibited a decrease in Mg leaf contents in the summer period. Mn contents were higher in *L. monopetalum* than in *A. portulacoides*, either in leaves (10 times) or in stems (twice). Seasonal patterns of nutrient contents in *A. portulacoides* and *L. monopetalum* suggest that the availability of these resources were not a limiting factor to their seasonal biomass production.

Introduction

Salt marshes are generally considered among the most productive ecosystems in the world, despite their constant stress conditions like water deficit and salinity excess (Adam 1990; Hughes and Paramor 2004).

The biomass and productivity of coastal wetlands are good indicators of the vegetation health enhancing their importance to the functioning of the overall ecosystem (Pont et al. 2002). Factors such as competition, salinity, degree of waterlogging, and nutrient status play an important role in regulating productivity (De Leeuw et al. 1990; Gross et al. 1990; Pennings and Callaway 1992; Pont et al. 2002). Several studies assessing above and belowground biomass, as well as annual net primary production in salt marsh species, have already been made. These studies centred mainly in species of *Spartina* (Gallagher et al. 1980; Schubauer and Hopkinson 1984; Cranford et al. 1989; Gross et al. 1990; Gross et al. 1991), *Juncus* (De Leeuw et al. 1990; Hsieh 1996) or *Salicornia* (Percy and Ulstin 1984; Curcó et al. 2002; Pont et al. 2002), and few concerned their attention in *Atriplex* spp. (Groenendijk 1984; Groenendijk and Vink-Lievaart 1987; Bouchard et al. 1998; Khan et al. 2000) or *Limoniastrum* spp. (Daoud et al. 2001), despite they are characteristic of many salt marshes.

Salt marsh halophytic species differ widely in the extent to which they accumulate ions and their overall degree of salt tolerance (Khan et al. 2000; Munns 2002). Generally, K^+ is accumulated in response to low soil moisture, while Na^+ is accumulated under saline conditions to create and maintain water potential gradients and turgor necessary for water uptake and growth (Flowers et al. 1977; Gorham et al. 1980; Donovan et al. 1997). The uptake and accumulation of sodium interacts with the cation macronutrients, potassium, calcium and magnesium, often lead to relatively low

leaf ratios of this cation nutrient, resulting in foliar deficiencies (Albert and Popp 1977; Gorham et al. 1980; Gul et al. 2000).

The main objectives of this study were to evaluate seasonal variation patterns of above and belowground biomass; to assess and compare net primary production through two evaluation methods; and to determine the seasonal variation of nutrient contents (N, P, K, Ca, Mg and Mn) in two salt marsh species, *A. portulacoides* and *L. monopetalum*, in Castro Marim saltmarsh, Portugal.

Study Site

The study was carried out in a natural reserve, “Reserva Natural do Sapal de Castro Marim e Vila Real de S^o António”, in southeast Portugal (37°13' N; 7°26' W). This reserve covers about 2087 ha, 28% of which are saltmarshes between the Guadiana River and the Atlantic Ocean. The morphology of the reserve is mostly flat with an altitude ranging from 0 to 5 m above the mean level of water.

The area has a Mediterranean climate, characterized by a dry period in summer (Rivas-Martínez 1981), with a mean annual precipitation of 492 mm and a mean temperature of 17.2°C. In the sampling year (autumn 2001/autumn 2002) total precipitation was 593 mm, and the monthly maximum precipitation, 100 mm, was registered in September; maximum and minimum absolute temperatures were, respectively, 35.9°C in July and 5.8°C in December (Instituto Nacional de Meteorologia e Geofísica).

The soil, of alluvium origin, is hallomorphic (Lousã 1986) with high lime and OM proportion.

The vegetation is dominated by *Spartina maritima* (Curtis) Fernald, *S. densiflora* Brong., *Atriplex portulacoides* L., *Arthrocnemum perenne* (Miller) Moss., *A. glaucum* (Delile) Ung-Sternb., *A. fruticosum* (L.) Moq., *Suaeda vera* Forssk. ex Gmelin and *Limoniastrum monopetalum* L.

Material and Methods

Two salt marsh species, *Atriplex portulacoides* L. and *Limoniastrum monopetalum* L., were selected. *A. portulacoides* is an evergreen Chenopodiaceae, ranging 20-50 cm

height, which colonizes the lower and mid marsh, whilst *L. monopetalum*, an evergreen Plumbaginaceae ranging 50-120 cm height, colonizes the upper marsh.

Sampling was conducted in five periods along 2001/2002 (autumn, winter, spring, summer and autumn). In the beginning of the study, 15 similar individuals (considering age and structure) of each species, were selected and labelled. At each sampling date, aboveground biomass from three square columns (50 x 50 cm on a side) per species was harvested. Total collected biomass (alive and dead) from each column was separated into: green leaves, dead leaves, live axes, dead axes and reproductive organs. Plant material was oven-dried for 48 hours, at 80°C, to constant mass and the dry weights of all fractions were obtained. Leaf area was obtained through measurements in leaf subsamples, using a LI-3000A Portable Area Meter.

At the same sampling dates, belowground biomass was harvested through the extraction of three cores (8 cm diameter) per square, to a depth of 15 cm, with a thin-wall, sharpened stainless steel tube. The roots of each core, after separation from the soil material, were dried and weighted like the aboveground collected biomass.

Litter was collected and placed in nylon mesh bags in each site, according to Bock and Gilbert (1957) litterbag method, to assess the decomposition and turnover rates.

Ash content was obtained in subsamples of above and belowground biomass through OM destruction in a muffle furnace at 450°C, for 6 h. Subsamples of all fractions were ground and analyzed for nutrient (N, P, K, Ca, Mg e Mn) concentrations. N was determined by the modified Kjeldahl method (Bremner and Mulvaney 1982). Ca, Mg, K and P were acid-digested before quantification. Ca, Mg, Mn and K were determined by atomic absorption spectrophotometry. P was estimated by colorimetry followed by UV/V spectrophotometry for quantification according to Murphy and Riley (1962) adapted by Watanabe and Olsen (1965).

Specific leaf area (SLA) was calculated through the ratio between leaf area and leaf dry weight. Leaf area index (LAI) was calculated through the ratio between the total crop leaf area and the crop canopy standing on ground area (2500 cm²).

Aboveground production was estimated for both species using two methods: Smalley method (Groenendijk 1984) and Weigert and Evans method (Weigert and Evans 1964).

Data of all biomass fractions (above and belowground), SLA, LAI, root/shoot ratio (RSR), and relative growth rate (RGR) were analyzed by ANOVA/Kruskal-Wallis

tests ($\alpha=0.05$) and Tukey post-hoc tests, to compare species and sampling periods. SigmaStat for Windows Version 3.1 was used to perform statistical analysis.

Results

Above and belowground biomass

Aboveground biomass was significantly different between species ($P<0.05$), with *L. monopetalum* showing values ($2516 \text{ g m}^{-2} \text{ yr}^{-1}$ in average) approximately four times higher than *A. portulacoides* ($598 \text{ g m}^{-2} \text{ yr}^{-1}$). However, the amounts determined for each species didn't differ significantly ($P<0.05$) throughout the year (Fig. 1). Peak aboveground live biomass was obtained in spring for both species ($1077 \text{ g m}^{-2} \text{ yr}^{-1}$ for *A. portulacoides* and $3502 \text{ g m}^{-2} \text{ yr}^{-1}$ for *L. monopetalum*) (table 1, Fig. 1).

Belowground biomass of *L. monopetalum* (with a mean of $2752 \text{ g m}^{-2} \text{ yr}^{-1}$) was around two times higher than that of *A. portulacoides* ($1601 \text{ g m}^{-2} \text{ yr}^{-1}$) (table 1, Fig. 1). Nevertheless, there were no significant differences ($P<0.05$) either between the values obtained along the year for each species, or between species (excepting in summer and autumn-02). Mean root/shoot ratio (Fig. 2) was significantly different between species ($P<0.001$), with the values obtained for *L. monopetalum* being less than one half of those for *A. portulacoides*. In each species there were no annual significant differences ($P<0.05$) for this ratio.

During the study period, live axes were the main component of total aboveground biomass for both species, amounting to 50% in *A. portulacoides* and 60% in *L. monopetalum*, while the proportions of green leaves were 23% and 12% of the total, respectively. Dead stems accounted for 25% of total aboveground biomass in both species. The maximum proportion of green leaves was obtained in the autumn-01 for both species (31% for *A. portulacoides* and 16% for *L. monopetalum*), while the maximum live axes proportions were determined in the spring (60%) for the former and in the autumn-02 (65%) for the latter (Fig. 1).

LAI values of the two species weren't very different, excepting in autumn-02 (Fig. 3), when the value found for *A. portulacoides* (1.31) almost doubled that of *L. monopetalum* (0.75). Both species showed a significant LAI decrease in summer (0.60). SLA was much lower for *L. monopetalum* (less than one half) than for *A. portulacoides*.

Minimum values were obtained in the summer period, for both species ($54.15 \text{ cm}^2 \text{ g}^{-1}$ for *A. portulacoides* and $19.65 \text{ cm}^2 \text{ g}^{-1}$ for *L. monopetalum*) (Fig. 3).

Significant differences ($P < 0.05$) between species were obtained in aboveground RGR in the autumn/winter and winter/spring periods (table 2). Maximum aboveground RGR was obtained in the winter/spring period for *A. portulacoides* ($7.88 \pm 0.98 \text{ g g}^{-1} \text{ d}^{-1}$) and in autumn/winter for *L. monopetalum* ($5.17 \pm 0.30 \text{ g g}^{-1} \text{ d}^{-1}$). None of the two species showed significant relative growth in the spring/summer period.

Primary productivity

Aboveground primary production was higher for *L. monopetalum* than for *A. portulacoides*, no matter the method applied, either Smalley or Weigert and Evans methods (table 1). According to Smalley's, the value obtained for *L. monopetalum* ($2917 \text{ g m}^{-2} \text{ yr}^{-1}$) was three times higher than for *A. portulacoides* ($1002 \text{ g m}^{-2} \text{ yr}^{-1}$) and after Weigert and Evans method it was around two times higher (3635 and $1615 \text{ g m}^{-2} \text{ yr}^{-1}$, respectively).

The turnover of the aboveground live biomass (primary production/peak live biomass) was lower than 1 for both species, although it was higher for *A. portulacoides* (0.96 yr) than for *L. monopetalum* (0.86 yr) (table 1).

Nutrient contents

The seasonal dynamics of mineral elements, in the different organs of the plants (leaves, stems and roots), are expressed in figs 4 and 5.

Leaf N contents were slightly higher in *L. monopetalum*, than in *A. portulacoides*, except in spring when similar values were obtained, due to a marked decrease in the former. The highest concentrations were obtained in summer for both species (15 mg g^{-1} for *A. portulacoides*, and 16 mg g^{-1} for *L. monopetalum*). Stem N content was also higher for *L. monopetalum* than for *A. portulacoides*, and presented the same seasonal variations patterns as leaves. Root N contents were very similar between species and showed little variation throughout the year.

The highest P concentration was found in leaves of both species, and similarly to N, leaf and stem P contents was higher in *L. monopetalum* than in *A. portulacoides*. The seasonal variation pattern of P in leaves was similar for both species, with the lowest

values in the summer period (1.1 mg g⁻¹ for *A. portulacoides*, and 1.2 mg g⁻¹ for *L. monopetalum*). The lowest contents in *L. monopetalum* stems was also found in summer (1.0 mg g⁻¹), whereas *A. portulacoides* stems showed the maximum concentration (1.0 mg g⁻¹) in the same season. The root P contents were slightly higher in *A. portulacoides* than in *L. monopetalum*, and there was little variation along the year.

Leaf K contents in *A. portulacoides* was around three times higher than in *L. monopetalum*. The maximum was observed in autumn for *A. portulacoides* (25 mg g⁻¹) and in summer for *L. monopetalum* (11 mg g⁻¹). Minimum values (17 mg g⁻¹ and 7 mg g⁻¹, respectively) were obtained in summer and in winter. The variation of stem K concentration was opposite to that of leaves. In *A. portulacoides* the maximum was found in summer (12 mg g⁻¹) while in *L. monopetalum* it was observed in autumn (10 mg g⁻¹). Root K content was similar between species, with no marked oscillation (3 to 5 mg g⁻¹).

Leaf Ca contents in *L. monopetalum* were around three times higher than in *A. portulacoides*. An increase was observed in the former during winter (26 mg g⁻¹), and a pronounced decrease in spring (16 mg g⁻¹), while there was an insignificant variation in the latter (between 7 and 9 mg g⁻¹). Stem Ca contents in *L. monopetalum* were twice higher than in *A. portulacoides* in the rainy seasons, maintaining similar values during the dryer period. The most pronounced difference between root Ca contents was observed in spring, with *L. monopetalum* showing a value twice higher than *A. portulacoides* (15 mg g⁻¹ and 9 mg g⁻¹, respectively).

The most pronounced difference between root Ca contents was observed in spring, with *L. monopetalum* showing a value twice higher than *A. portulacoides* (15 mg g⁻¹ and 9 mg g⁻¹, respectively).

The higher Mg concentrations were found in leaves for both species. However, *L. monopetalum* showed contents twice higher than *A. portulacoides*. In the former, maximum leaf contents were obtained in autumn (20 mg g⁻¹), and minimum in summer (13 mg g⁻¹). In the latter leaf contents were almost the same in every season (7 to 10 mg g⁻¹). Mg contents were much lower in stems than in leaves, and there were no marked oscillations along the year. Like what happened with leaves, *L. monopetalum* had stem contents around two times higher than *A. portulacoides*. Root Mg contents vary between 7 and 9 mg g⁻¹, for both species.

Mn contents were higher in *L. monopetalum* than in *A. portulacoides*, either in leaves (10 times) or in stems (twice). Root Mn contents were similar in both species.

Discussion and Conclusions

Above and belowground biomass

There are few studies regarding the dynamics of above and belowground biomass of *A. portulacoides* (e.g., Groenendijk 1984; Groenendijk and Vink-Lievaart 1987; Bouchard and Lefeuvre 1996; Bouchard et al. 1998; Bouchard and Lefeuvre 2000), and to our knowledge, none has been done for *L. monopetalum*. The present study indicates that both species show a clear pattern for the seasonal variation of above and belowground biomass.

L. monopetalum showed a much higher mean aboveground biomass ($2516 \text{ g m}^{-2} \text{ yr}^{-1}$) than *A. portulacoides* ($598 \text{ g m}^{-2} \text{ yr}^{-1}$) (table 1). Despite the difference, these values are within the range reported for other salt marsh species (Gallagher et al. 1984; Groenendijk 1984; De Leeuw et al. 1990; Gross et al. 1991; Bouchard et al. 1998; Bouchard et al. 2000; Curcó et al. 2002). Besides this, primary productivity and biomass increased along the vertical gradient of the salt marsh, with upper marsh species showing highest values then middle or lower marsh species, as stated by Lefeuvre (1996). Both species began growing in autumn, with *L. monopetalum* reaching its maximum growth rate ($5.17 \text{ mg g}^{-1} \text{ d}^{-1}$) in the autumn/winter period and *A. portulacoides* ($7.88 \text{ mg g}^{-1} \text{ d}^{-1}$) in winter/spring (table 2). Peak aboveground biomass was observed for both species in spring, despite the marked difference in values (table 1). This pattern has often been observed in other species, as *Spartina alterniflora*, *Juncus roemerianus* (Gallagher et al. 1984), *Juncus maritimus*, *Juncus gerardii*, *Artemisia maritima* (De Leeuw et al. 1990), *Elytrigia aetherica* (Bouchard and Lefeuvre 2000), *Arthrocnemum macrostachyum* (Curcó et al. 2002). As aboveground biomass decreased for both species in the spring/summer period (Fig. 1), there was no growth during summer.

The values determined for mean belowground live biomass are within the range obtained for other Mediterranean-type climate salt marsh species (Curcó et al. 2002; Scarton et al. 2002). Like for aboveground biomass, the mean value was higher in *L. monopetalum* ($2752 \text{ g m}^{-2} \text{ yr}^{-1}$) than in *A. portulacoides* ($1601 \text{ g m}^{-2} \text{ yr}^{-1}$), although the difference has been less pronounced. These results show that *A. portulacoides* allocates higher resource amounts in roots than *L. monopetalum*, what is also emphasized by the root/shoot ratio (Fig. 2). This strategy is often observed in salt marsh species which

suffer periodic waterlogging, like *A. portulacoides*, indicating a higher investment in the root system under stressful conditions (Schubauer and Hopkinson 1984; Scarton et al. 1999; Pont et al. 2002; Scarton et al. 2002).

Although LAI was similar for both species, *L. monopetalum* showed a lower SLA. This indicates a better adaptation of this species to the higher salt and water stress, which is more frequent in the upper marsh. The decrease of both LAI and SLA, observed in summer, reflects the decrease of the transpiratory surface (Fig. 1), an adaptive strategy to the particular climatic constraints of this season, as high temperatures, intense radiation and depletion of the soil water availability (Larcher 1995).

Primary productivity

Despite the few work done in these species, the values for above and belowground biomass and net aerial primary production (NAPP) are similar to most values obtained in other studies, concerning salt marsh species in Mediterranean regions (Gallagher et al. 1980; Schubauer and Hopkinson 1984, De Leeuw et al. 1990, Gross et al. 1990, Pont et al. 2002).

Calculating the NAPP through the Smalley's method, the value obtained in this work for *A. portulacoides* ($1002 \text{ g m}^{-2} \text{ yr}^{-1}$) is slightly lower than in other studies (Groenendijk 1984; Bouchard and Lefeuvre 1996; Bouchard et al. 1998; Bouchard et al. 2000), according to which NAPP in this species can reach up to $3600 \text{ g m}^{-2} \text{ yr}^{-1}$. Nevertheless, the value obtained in this work is within the range indicated to European mid marsh species, such as *Arthrocnemum fruticosum*, averaging $1200 \text{ g m}^{-2} \text{ yr}^{-1}$ (Ibañez et al. 1999) and $700 \text{ g m}^{-2} \text{ yr}^{-1}$ (Scarton et al. 2002). Using the same method, *L. monopetalum* showed a much higher productivity ($2917 \text{ g m}^{-2} \text{ yr}^{-1}$). These results indicate that in European salt marshes productivity can be as high as in American salt marshes, which reach up to $3700 \text{ g m}^{-2} \text{ yr}^{-1}$, as observed by Gallagher et al. (1980).

When using Weigert-Evans (W-E) method for estimating productivity, the values obtained in this work for *L. monopetalum* were similar to *Juncus roemerianus* (Gallagher et al. 1980), *Spartina anglica* (Groenendijk 1984) or *S. alterniflora* (Hopkinson et al. 1980). By the same method, *A. portulacoides* showed a lower productivity, similar to *Phragmites australis* (Scarton et al. 2002).

The NAPP of both species calculated through the Smalley's method increased around 60% for *L. monopetalum* and 25% for *A. portulacoides* using the W-E method. These increments are due to the fact that Smalley method is based solely on biomass changes, whilst W-E method also takes the disappearance of the dead material in account. Therefore the latter is expected to be closer to the actual productivity (Linthurst and Reimold 1978; Gallagher et al. 1980; Groenendijk 1984). In spite of this, Linthurst and Reimold (1978) concluded that the Smalley method is the most suitable for salt marshes because of tidal movement of material and also because it allows a more intensive biomass sampling.

The aboveground turnover rate (primary production/peak live biomass) obtained for *A. portulacoides* (0.96 yr^{-1}) was slightly higher than in other studies in Europe for the same species (0.77 yr^{-1} - Bouchard et al. 1998; 0.69 yr^{-1} - Bouchard and Lefeuvre 2000), nevertheless it was similar to other Mediterranean-type climate salt marsh species (Curcó et al. 2002). The turnover of *L. monopetalum* (0.86 yr^{-1}) was similar to other high marsh species (Bouchard et al. 2000), but lower than that of *A. portulacoides*, probably due to the fact that *L. monopetalum* has more lignified components (woody stems). According to Curcó et al (2002), in Mediterranean-type climate salt marshes, maximum aboveground biomass and net primary production occur in the middle marsh, where the frequent stresses (waterlogging and hypersalinity) that affect the vegetation dynamics are more moderated than in the lower and the upper marshes. However, in this study, we have obtained a higher aboveground biomass and net primary production in the upper marsh species (*L. monopetalum*), with high NAPP values, similar to those reported in American salt marshes (Linthurst and Reimold 1978; Gallagher et al. 1980).

Nutrient contents

In salt saturated soils as salt marshes, Na and Cl concentrations often exceed by one or two orders of magnitude those of most macronutrients and even more in the case of micronutrients, therefore depressing nutrient-ion activities and extreme ratios of Na/Ca, Na/K and Mg/Ca (Qadir and Schubert 2002). As a result, plants become susceptible to high osmotic stress, specific ion toxicity and nutritional disorders. Plant species vary not only in the rate at which they absorb an available nutrient, but also in the manner by which they distribute that element spatially within their components.

The highest N concentrations in the overall living tissue of both species were determined in the dry season, period in which no growth occurred (Figs. 4a and b; table 2). Many halophytes invest a large proportion of N in compatible solutes such as glycinebetaine for cytoplasmic osmoregulation (Gorham and Wyn Jones 1983), and these high N concentrations may be associated with greater salinity tolerance. A general decrease was observed during the growing season, with the minimum in spring, coinciding with the peak biomass. The results were also obtained for other species by Gallagher et al. (1980) and Boyer et al. (2001). According to these authors, the minimum concentration in the end of the growing season suggests a dilution of N as plants accumulate biomass.

The overall P content is closely related to the vital growth processes and with the efficient functioning and utilization of nitrogen. In spite of this, this nutrient decreased in the dry season in biomass components of both species, excepting in *A. portulacoides* stems (Figs. 4c and d). The latter showed a clear summer allocation of this relative immobile nutrient to the stems, as noted for N.

K is specifically needed for protein synthesis and enzyme activation. High concentrations of this mineral in the stroma are considered essential for the maintenance of optimum photosynthetic capacity, and therefore biomass production, under stress conditions (Grattan and Grieve 1999). The overall K contents in the living tissue decreased, for both species, in summer (Figs. 4e and f), probably due to the presence of Na which interferes with the function of K as a cofactor in various reactions (Blumwald 2000; Khan et al. 2000). Since K is not bound to organic compounds in plants but in an ionic form, this mineral is readily leached from plant tissue. However, while *A. portulacoides* occupies the mid marsh, *L. monopetalum* is found in the upper marsh, less subjected to waterlogging in summer. This may explain the decrease observed in leaf K content of the former, whereas in a slight increase was registered in the latter.

One of the main nutritional disorders associated with high salinity soils is impaired uptake of Ca caused by high Na concentration in the soil solution. Ca plays a vital nutritional and physiological role in plant metabolism. It is essential in processes that preserve the structural and functional integrity of plant membranes, stabilizes cell wall structures, regulates ion transport, and controls ion exchange behavior, as well as cell wall enzyme activities (Rengel 1992). As salinity increases along the dry season, high concentrations of Na in the soil reduce the amounts of available Ca and may displace Ca from the cell membrane-bound structure (Cramer et al. 1985). This may

explain the lower contents of this element in the spring and summer period, and the subsequent increase in the autumn, after the first rains (Figs. 5a and b).

Mg plays a key role in the photosynthetic process, being an important constituent of chlorophyll. *L. monopetalum* exhibited higher leaf Mg contents (Figs. 5c and d), what is in accordance with its higher photosynthetic capacity (personal observation) and productivity (table 1).

Similar patterns were obtained for both species of overall Mn contents (Figs. 5e and f). The highest concentrations were found in roots, what is related to the low requirement of this nutrient in photosynthesis (water oxidation), respiration and nitrogen metabolism, which occur mainly in the shoot. In the other hand, being a relatively immobile element, it accumulates in the older components, probably the roots.

The nutrient contents determined in this study are within the range indicated by Larcher (1995) for terrestrial plants. So, the results obtained suggest that the availability of these resources is not a limiting factor to biomass production. This may be due to the ability of *A. portulacoides* and *L. monopetalum* to exclude high mineral levels, through their roots and shoots, as the main mechanism of adaptation to high salinity (Greenway and Munns 1980; Cheeseman 1988; Daoud et al. 2001).

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Table 1 - Mean aboveground live biomass (MALB), peak aboveground live biomass (PALB), mean belowground live biomass (MBLB), annual net primary production (ANPP), in accordance with Smalley (Groenendijk 1984) and Wiegert-Evans (W-E) (Wiegert and Evans 1964) methods, and turnover rates (TO) in *A. portulacoides* and *L. monopetalum*. Values with different letters in a row are significantly different ($P < 0.05$).

	<i>A. portulacoides</i>	<i>L. monopetalum</i>
MALB (g m⁻²)	598 ^a	2516 ^b
PALB (g m⁻²)	1077 ^a	3502 ^b
MBLB (g m⁻²)	1601 ^a	2752 ^b
ANPP (g m⁻² yr⁻¹)		
(Smalley)	1002	2917
(W-E)	1615	3635
TO (yr⁻¹)	0.96	0.86

Table 2 - Seasonal variation of aboveground RGR in *A. portulacoides* and *L. monopetalum* (means \pm SE). Values with different letters in a column are significantly different ($P < 0.05$).

	Autumn/ Winter	Winter/ Spring	Spring/ Summer	Summer/ Autumn
<i>A. portulacoides</i>	2.00 \pm 0.47 ^a	7.88 \pm 0.98 ^a	0.00 ^a	2.95 \pm 1.28 ^a
<i>L. monopetalum</i>	5.17 \pm 0.30 ^b	2.82 \pm 1.31 ^b	0.00 ^a	0.00 ^a

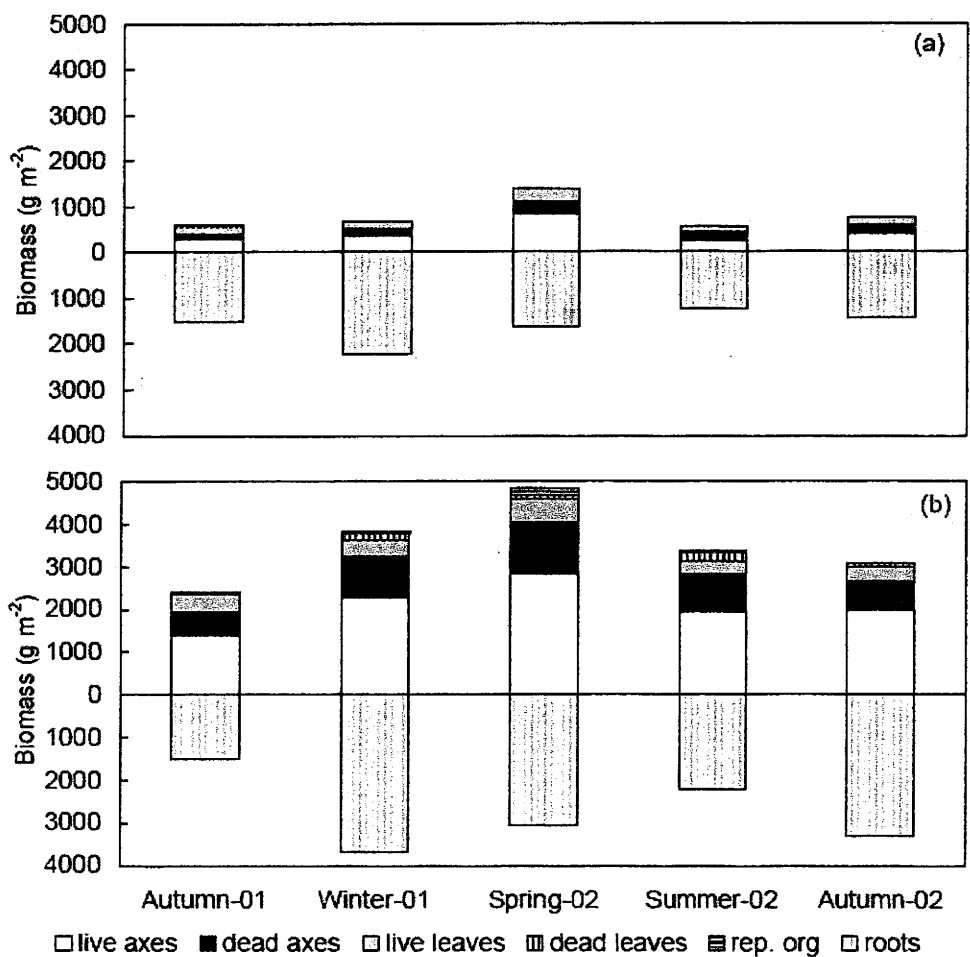


Figure 1 – Seasonal variation of above and belowground biomass in a) *Atriplex portulacoides* and b) *Limoniastrum monopetalum*.

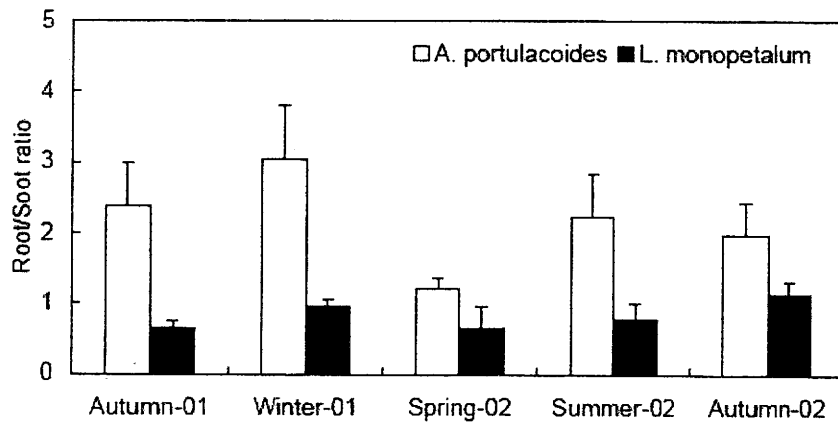


Figure 2 – Seasonal variation of the root/shoot ratio in *Atriplex portulacoides* and *Limoniastrum monopetalum* (means \pm SE).

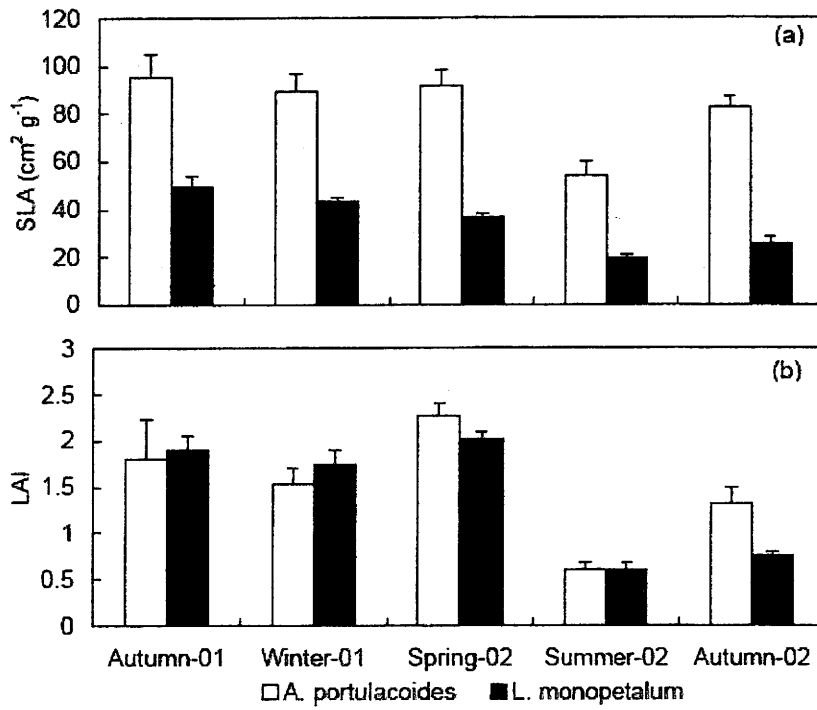


Figure 3 – Seasonal variation of a) specific leaf area (SLA) and b) leaf area index (LAI) in *Atriplex portulacoides* and *Limoniastrum monopetalum* (means \pm SE).

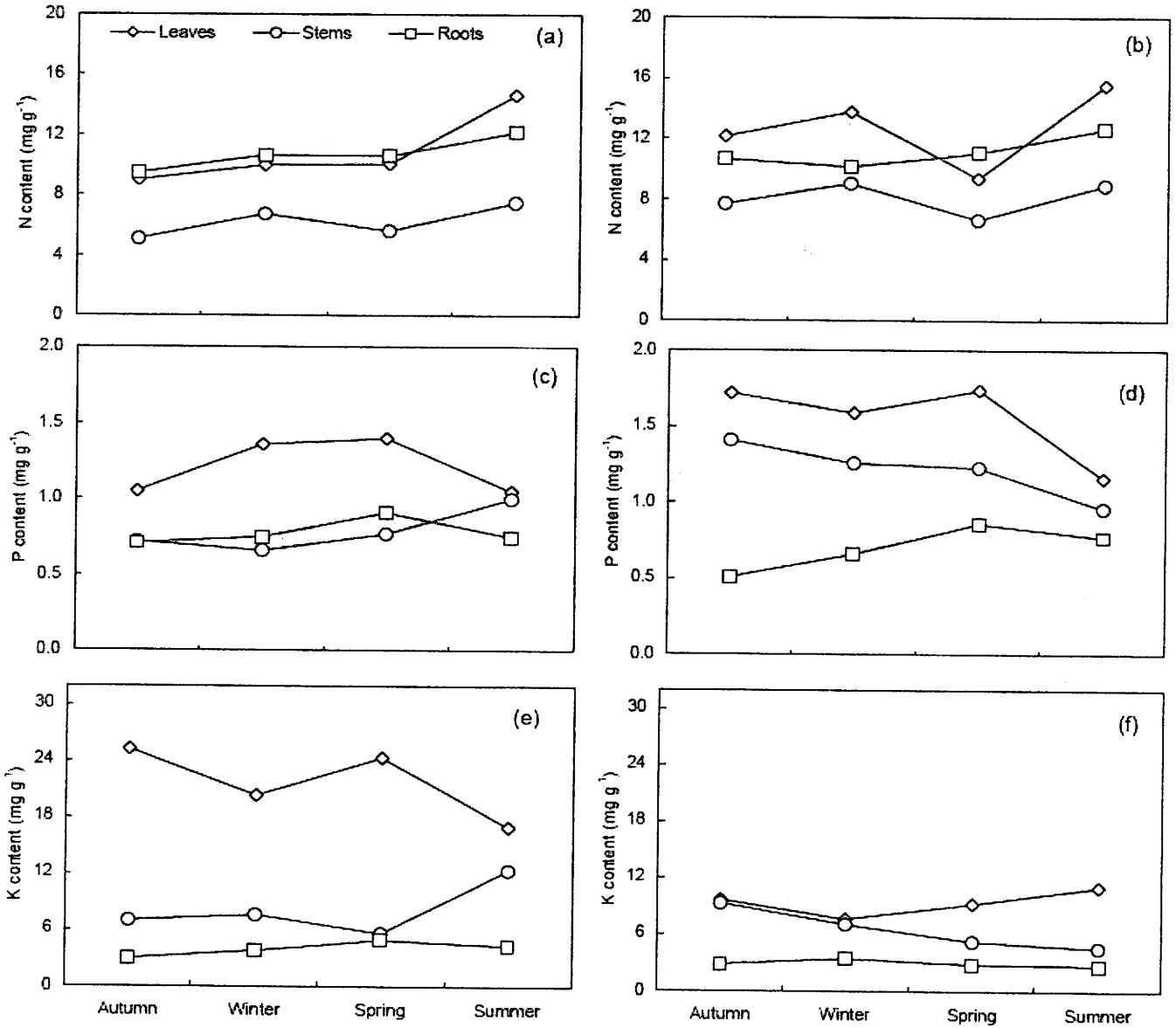


Figure 4 – Seasonal patterns of N, P and K contents in leaves, stems and roots of *Atriplex portulacoides* (a,c,e) and *Limoniastrum monopetalum* (b,d,f).

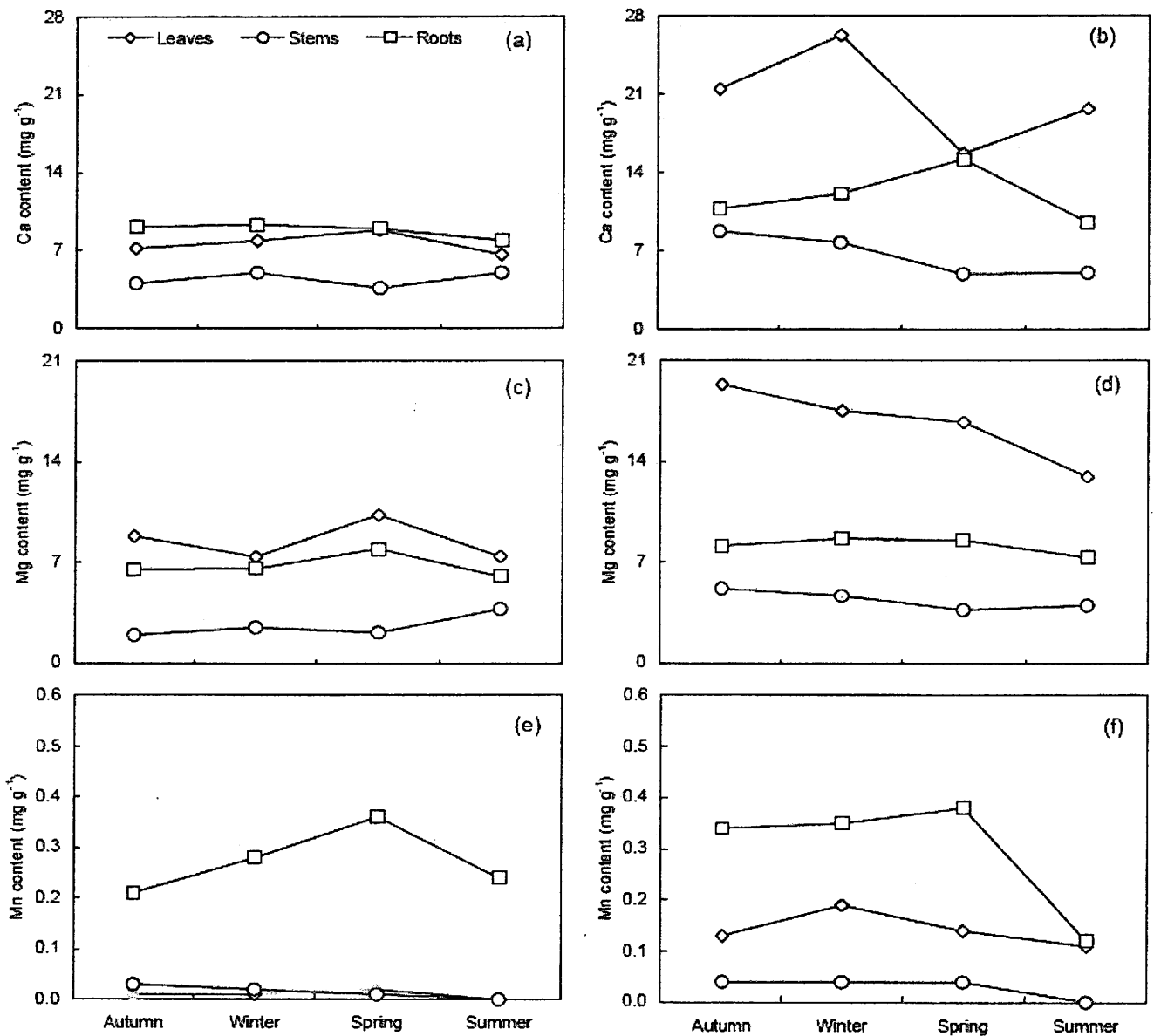


Figure 5 - Seasonal patterns of Ca, Mg and Mn contents in leaves, stems and roots of *Atriplex portulacoides* (a,c,e) and *Limoniastrum monopetalum* (b,d,f).

Gas exchange in the salt marsh species *Atriplex portulacoides* L. and *Limoniastrum monopetalum* L. in Southern Portugal

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Key words: *Atriplex portulacoides* L., *Limoniastrum monopetalum* L., photosynthesis, salt marsh, seasonal patterns, stomatal conductance, water potential

Abstract: Salt marshes are ecosystems subjected to a variety of environmental stresses like high salinity, water deficit, intense radiation or high temperatures. Field measurements were conducted in two halophyte species, *Atriplex portulacoides* L. and *Limoniastrum monopetalum* L., in the Reserva Natural do Sapal de Castro Marim, to compare their physiological response, *i.e.*, water potential (ψ), net photosynthetic rate (A), stomatal conductance (gs) in natural conditions. Both species demonstrated marked variations in ψ throughout the year, with very low values in the summer, the period of more intense salinity, drought and temperature. Deficit water potential ($\Delta\psi = \psi_{\text{midday}} - \psi_{\text{predawn}}$) was lower in summer than in other seasons in *A. portulacoides* but not in *L. monopetalum*. The highest values for A and gs in *L. monopetalum* were observed autumn and for *A. portulacoides* in winter, presenting both lowest values in spring and summer. A_{max} was particularly high for *L. monopetalum* than for *A. portulacoides* in summer and autumn, despite g_{smax} was similar in both species. Diurnal pattern of A and gs were similar in both species, with higher values in the morning, decreasing throughout the day.

Introduction

Salt marsh ecosystems are characterized by a high primary productivity, being one of the most productive biotopes despite their constant stress conditions, like deficit of water and excess of salinity (Adam 1990). Also, these ecosystems are often subject of intense radiation and high temperatures throughout the year, thus constraining their

primary productivity (Larcher 1995). Structural and chemical changes often occur, within the plants, like increased sugar and amino acid content, to minimize damage from changing environment conditions. These changes are called acclimation and result in a higher survival capacity of plants under adverse abiotic conditions. Also, plants can show different ranges of tolerance to particular stresses, without acclimation. Due to their genetic background, some species can intrinsically tolerate higher temperatures or dehydration better than others, without having to suffer structural and chemical changes (Adam 1990). Hence, in order to survive, the vegetation, predominantly halophytic, is well adapted to cope with such conditions and their photosynthetic apparatus is acclimated to a wide variety of environmental stress factors.

Previous research on halophytic species centred the attention mainly on the effects of the salinity on photosynthesis, water relations and growth rates of salt marsh species, in greenhouse (Gul *et al.* 2000, Khan *et al.* 2000, Pearcy & Ulstin 1984) controlled (Nieva *et al.* 1999) and natural conditions (Hacke *et al.* 2000). Therefore, little is documented about photosynthetic response to environmental stresses under natural conditions. Native salt marsh shrubs have developed different strategies of coping with the challenge of drought and excess salinity stress and show a great deal of variability in their phenology, rooting depth and intrinsic capacity to overcome stress factors. In this context, two species were selected for this study which show similar aspects in their morphology and anatomy, typical of salt marsh species, *i.e.*, increase of succulence, thicker leaf cuticle or existence of excretory salt mechanisms (salt secretory trichome in *Atriplex* spp., multicellular salt glands in the Plumbaginaceae family) (Wahid 2003). *Atriplex portulacoides* L. is an evergreen Chenopodiaceae ranging 20-50 cm height, which colonizes the lower and mid marsh. *Limoniastrum monopetalum* L. is an evergreen Plumbaginaceae ranging 50-120 cm height, which colonizes the upper marsh.

The Castro Marim salt marshes offer an interesting system for ecophysiological studies due to the generally high salinity levels in summer and large seasonal changes in salinity and soil hydric content resulting from the lack of summer precipitation. Thus, the aim of this study was to assess seasonal and daily patterns of gas exchange in *A. portulacoides* and *L. monopetalum*, under field conditions, in order to identify the major climatic constraints to photosynthesis in these two salt marsh species that grow within a small distance from each other.

Materials and Methods

The study was carried out in a natural reserve “Reserva Natural do Sapal de Castro Marim e Vila Real de Santo António” in south-east Portugal (lat. 37°13'N; long. 1°40'W). This reserve covers about 2087 ha, of which 28% are saltmarsh, and is located between the Guadiana River and the Atlantic Ocean. The morphology of the reserve is mostly flat with an altitude ranging from 0 to 5 m above the mean sea level. The soil, with alluvial origin, is halomorphic (Louçã 1986) with high percentage of lime, organic matter. The vegetation is composed predominantly by species as *Spartina maritima* (Curtis) Fernald., *S. densiflora* Brong., *Atriplex portulacoides* L., *Arthrocnemum perenne* (Miller) Moss., *A. glaucum* (Delile) Ung-Sternb., *A. fruticosum* (L.) Moq., *Suaeda vera* Forssk. ex Gmelin e *Limoniastrum monopetalum* L. This area has a Mediterranean climate with average yearly rainfall of 492 mm and air temperature of 17.2°C. The climate is characterized by a dry season during summer (Rivas-Martínez 1981). In 2002, the summer was particularly dry, with no precipitation between June and August (fig. 1). The monthly maximum precipitation was in September, 100 mm, and the total precipitation during this year was 593 mm. The maximum absolute temperature was 35.9°C in July and the minimum was 5.8°C in December (Instituto Nacional de Meteorologia e Geofísica).

The study was conducted in a salt marsh area, three meters above the mean sea level, almost never submerged by the tide. The study was carried out in three plants similar in size and age of each species, *Atriplex portulacoides* L. and *Limoniastrum monopetalum* L., two of the most representative species in the area. Leaf water potential, soil humidity and gas exchange were measured in four periods during the year 2002, spring (April), summer (July), autumn (September) and winter (December). Experiments were conducted on clear days, due to the sensibility of the portable photosynthesis system.

Leaf water potential (ψ) at predawn and midday was determined using a pressure chamber (PMS Instruments Co., Oregon, USA) according to Scholander *et al.* (1965). Soil humidity was measured at predawn and midday, using a ThetaKit Delta-T moisture meter, model HH2 (Delta-T Devices Ltd, Cambridge, UK).

Gas exchange measurements were made under natural conditions using a Li-6400 portable photosynthesis system (Li-Cor Inc., Lincoln, USA), in three leaves of each plant, at early morning, midday and late afternoon. Photosynthesis rate (A),

stomatal conductance (g_s), transpiration (E), internal carbon (C_i), vapour pressure deficit (VPD), radiation (PAR) and air temperature (T) values were collected.

Statistical analysis. Descriptive statistics (mean and standard error) were obtained for all data. Measurements of seasonal maximal photosynthetic rate (A_{max}), maximal stomatal conductance ($g_{s_{max}}$), intrinsic water use efficiency ($A_{max}/g_{s_{max}}$), A , g_s , E , apparent carboxylation efficiency (A/C_i), and water potential deficit ($\Delta\psi$) were subjected to Kruskal-Wallis tests ($\alpha=0,05$) and Tukey post-hoc tests, to check differences between species and among measurements. Diurnal measurements of A and g_s , between species at each time of the day, were compared by Mann-Whitney U tests ($\alpha=0,05$). All statistical analyses were performed with SigmaStat for Windows Version 3.1.

Results

Maximum values of predawn leaf water potential (ψ_p) were obtained in spring and winter (Fig. 2). Both species show a clear decrease in ψ_p in summer followed by a slight recovery in autumn, not significant in *L. monopetalum*. Between species, the summer values were significantly different ($P<0.001$), both species showing low values (-6.6 ± 0.1 MPa for *A. portulacoides*, -4.8 ± 0.7 MPa for *L. monopetalum*). The summer values of midday leaf water potential (ψ_{md}) were not significantly different between species (-6.8 ± 0.2 MPa for *A. portulacoides* and -7.0 ± 0.1 MPa for *L. monopetalum*) (Fig. 2).

Seasonal changes in ψ_p , ψ_{md} (Fig. 2) showed similar patterns, for both species. *A. portulacoides* showed minimum deficit water potential ($\Delta\psi$) in summer, while *L. monopetalum* reached the maximum $\Delta\psi$ in this season (Fig. 2, Tab. 1). The April and July values of $\Delta\psi$ were significantly different between species, which show similar values in September and December (Tab. 1).

Both species showed similar values of $g_{s_{max}}$ in spring and summer, increasing in autumn and winter. For *L. monopetalum*, minimum and maximum A_{max} were obtained in April and September ($9.1 \pm 1.6 \mu\text{molCO}_2\text{m}^{-2}\text{s}^{-1}$ and $26.8 \pm 3.4 \mu\text{molCO}_2\text{m}^{-2}\text{s}^{-1}$, respectively). Minimum and maximum $g_{s_{max}}$ were obtained in July and December ($65.6 \pm 16.0 \text{mmolH}_2\text{Om}^{-2}\text{s}^{-1}$ and $307.3 \pm 53.2 \text{mmolH}_2\text{Om}^{-2}\text{s}^{-1}$, respectively) (Fig. 3a, b). The annual pattern of A_{max} for *A. portulacoides* showed no significant differences among

seasons, although $g_{s_{max}}$ values differed significantly ($P < 0.001$) with minimum values in the summer period ($31.8 \pm 5.0 \text{ mmolH}_2\text{Om}^{-2}\text{s}^{-1}$) and maximum values in December ($237.7 \pm 21.1 \text{ mmolH}_2\text{Om}^{-2}\text{s}^{-1}$). There were significant differences of A_{max} between species in July ($9.4 \pm 1.3 \text{ } \mu\text{molCO}_2\text{m}^{-2}\text{s}^{-1}$ for *A. portulacoides* and $13.8 \pm 1.5 \text{ } \mu\text{molCO}_2\text{m}^{-2}\text{s}^{-1}$ for *L. monopetalum*) and September ($14.3 \pm 2.1 \text{ } \mu\text{molCO}_2\text{m}^{-2}\text{s}^{-1}$ for *A. portulacoides* and $26.8 \pm 3.4 \text{ } \mu\text{molCO}_2\text{m}^{-2}\text{s}^{-1}$ for *L. monopetalum*). *L. monopetalum* showed values of A_{max} in summer and autumn higher than *A. portulacoides*, although $g_{s_{max}}$ values in the same period were similar for both species. Comparing $g_{s_{max}}$ between species, only December showed significant differences, with higher values for *L. monopetalum* (Fig. 3a, b).

The intrinsic water use efficiency ($A_{max}/g_{s_{max}}$) showed significant differences over the seasons ($P < 0.001$), for both species, with the maximum values obtained in the summer ($393.0 \pm 89.3 \text{ } \mu\text{molCO}_2\text{mol}^{-1}\text{H}_2\text{O}$ for *A. portulacoides* and $397.5 \pm 124.2 \text{ } \mu\text{molCO}_2\text{mol}^{-1}\text{H}_2\text{O}$ for *L. monopetalum*). Between species, there were significant differences ($P < 0.001$) in April ($72.2 \pm 10.2 \text{ } \mu\text{molCO}_2\text{mol}^{-1}\text{H}_2\text{O}$ for *A. portulacoides* and $118.9 \pm 25.0 \text{ } \mu\text{molCO}_2\text{mol}^{-1}\text{H}_2\text{O}$ for *L. monopetalum*) and September ($68.7 \pm 10.9 \text{ } \mu\text{molCO}_2\text{mol}^{-1}\text{H}_2\text{O}$ for *A. portulacoides* and $151.8 \pm 36.4 \text{ } \mu\text{molCO}_2\text{mol}^{-1}\text{H}_2\text{O}$ for *L. monopetalum*) (Fig. 3c).

For both species, mean values of A were similar in April and July and differed significantly ($P < 0.001$) from September and December values (Fig. 4).

The mean values of g_s of both species recovered in September ($65.9 \pm 11.9 \text{ } \mu\text{molCO}_2\text{m}^{-2}\text{s}^{-1}$ for *A. portulacoides* and $139.5 \pm 13.5 \text{ } \mu\text{molCO}_2\text{m}^{-2}\text{s}^{-1}$ for *L. monopetalum*), when compared to the values of July ($23.8 \pm 2.8 \text{ } \mu\text{molCO}_2\text{m}^{-2}\text{s}^{-1}$ for *A. portulacoides* and $65.6 \pm 5.2 \text{ } \mu\text{molCO}_2\text{m}^{-2}\text{s}^{-1}$ for *L. monopetalum*). *L. monopetalum* maintained similar values in December ($116.8 \pm 26.4 \text{ } \mu\text{molCO}_2\text{m}^{-2}\text{s}^{-1}$) and *A. portulacoides* increased its values in this period ($142.0 \pm 16.7 \text{ } \mu\text{molCO}_2\text{m}^{-2}\text{s}^{-1}$) (Fig. 4). The transpiration rate (E) of both species showed little variation across the year, with only a slight decrease in July ($0.7 \pm 0.1 \text{ mmolH}_2\text{Om}^{-2}\text{s}^{-1}$ for *A. portulacoides* and $1.4 \pm 0.2 \text{ mmolH}_2\text{Om}^{-2}\text{s}^{-1}$ for *L. monopetalum*) ($P < 0.001$) and a recovery in September. The highest E values for *L. monopetalum* were obtained in September ($3.6 \pm 0.5 \text{ mmolH}_2\text{Om}^{-2}\text{s}^{-1}$) and decreased in December ($2.4 \pm 0.3 \text{ mmolH}_2\text{Om}^{-2}\text{s}^{-1}$). After the autumn recovery ($1.71 \pm 0.2 \text{ mmolH}_2\text{Om}^{-2}\text{s}^{-1}$), *A. portulacoides* maintained similar E

values through winter ($1.9 \pm 0.2 \text{ mmolH}_2\text{Om}^{-2}\text{s}^{-1}$) (Fig 5a). There were differences ($P < 0.001$) in E, between species, in April, July and September, *L. monopetalum* showing higher values. Apparent carboxylation efficiency (A/Ci) showed almost constant values throughout the year, in both species, with the exception of December, in *A. portulacoides*, which showed a slight increase ($P < 0.05$) (Fig. 5b). A/Ci values were very similar, for both species, except in September ($P < 0.05$).

Diurnal variations of A were similar to g_s , with the maximum values obtained mainly in the morning period. The highest values of g_s and A were in general obtained when lower values of vapour pressure deficit and air temperature occurred (Fig.6). The diurnal patterns of g_s and A showed in general lower values, throughout the year, for *A. portulacoides* than for *L. monopetalum*. In July, both species showed very low g_s values all day long.

Discussion

In the present study, seasonal g_s and A measurements showed similar patterns to other salt marsh species and shrubs from the Mediterranean region, which often show a decreasing net photosynthesis pattern in the summer period, due to stomata-controlled gas exchange triggered by soil and atmospheric drought (Flexas *et al.* 2001, Garcia-Plazaola *et al.* 1997, Adam 1990), although these species showed low A values early in spring and maintained these values during summer.

Predawn leaf water potential (ψ_p) values indicated a clear decrease, on both species, in the summer season, in agreement with other studies of halophyte species in controlled conditions, as *Allenrolfea occidentalis* (-4.1 MPa) (Gul *et al.*, 2000), *Arthrocnemum perenne*, *A. fruticosum* (-5.1 e -7 MPa, respectively) (Nieva *et al.*, 1999), and in natural conditions, as *Atriplex canescens*, *A. confertifolia*, *Chrysothamnus viscidiflorus* (-4.5, -4.3 e -3.7 MPa, respectively) (Hacke *et al.*, 2000), *Spartina densiflora* (-4.8 MPa) (Nieva *et al.* 2003).

The difference between species in $\Delta\psi$ obtained in the summer (tab. 1) agreed with g_s values, although *L. monopetalum* showed higher values of g_s than *A. portulacoides* (fig. 4). Hence, these values suggest two different strategies in gas exchange in adaptation to decreasing soil water availability. *A. portulacoides* considerably decreased the stomatal aperture in the periods of most intense water deficit to preserve cellular water content. *L. monopetalum*, although showing some stomatal

closure, maintained relatively high g_s values, allowing the maintenance of A . The summer depletion of the transpiration rate (E) also agreed with the variation of g_s , particularly in *A. portulacoides*, showing lower values in the drought period (Fig. 5a).

During the summer period, both species maintained A spring values, only with a slight decrease for *A. portulacoides*, although not significant. Probably, this maintenance is achieved through an increase in the photosynthetic capacity, compensating some stomatal closure. This adaptation was described in other Mediterranean species (Chaves *et al.*, 2002, Garcia-Plazaola *et al.*, 1997).

During spring, the measurements showed lower values of g_s and A compared to autumn and winter (Fig. 4). The climatic conditions in spring apparently do not justify those values (Fig. 1), hence the reduction might be related with the phenology of the species, since the process of leaf renewal occurs at the end of the summer, beginning of autumn as stated for various salt marsh species (Adam, 1990). Therefore, the spring measurements were made in older leaves, which normally reduce their capacity for carbon assimilation. Another possible factor contributing to these lower values of g_s and A was the increase of the salinity in the soil, during spring and summer, which is known to limit carbon assimilation, as shown in other studies (Gul *et al.* 2000, Nieva *et al.* 1999, Percy & Ulstin 1984). Despite this, summer A values ($4.8 \mu\text{molCO}_2\text{m}^{-2}\text{s}^{-1}$ for *A. portulacoides* and $6.5 \mu\text{molCO}_2\text{m}^{-2}\text{s}^{-1}$ for *L. monopetalum*) were similar to *Scirpus robustus* ($6 \mu\text{molCO}_2\text{m}^{-2}\text{s}^{-1}$) in greenhouse conditions (Percy & Ulstin 1984), and to *Spartina densiflora* ($8 \mu\text{molCO}_2\text{m}^{-2}\text{s}^{-1}$) in natural conditions (Nieva *et al.* 2003). Comparing the mean summer values of g_s (Fig. 4), *L. monopetalum* showed values four times higher than *A. portulacoides* (105.5 and $23.7 \text{mmolH}_2\text{Om}^{-2}\text{s}^{-1}$, respectively), similar to values of *Spartina foliosa* ($100 \text{mmolH}_2\text{Om}^{-2}\text{s}^{-1}$) and two times higher than *Scirpus robustus* ($50 \text{mmolH}_2\text{Om}^{-2}\text{s}^{-1}$) in controlled laboratory conditions (Percy & Ulstin 1984).

During the drought period, both species seemed to maintain A values from spring (Fig. 4). This maintenance is probably achieved by increasing photosynthetic capacity, compensating some stomatal closure. This adaptation is commonly found in several Mediterranean species as reported by Chaves *et al.* (2002) or Garcia-Plazaola *et al.* (1997). From spring to autumn, *A. portulacoides* showed low A/C_i values (Fig. 5b), agreeing with the maintenance of low A values during those periods, although g_s increased in autumn (fig. 4a). *L. monopetalum* maintained A/C_i values along the year,

showing an apparent stomatal regulation of A. In spring and summer, A maintained low values, probably due to the combination of low A/Ci and gs values.

After the summer constrains on photosynthetic activity, A increased in autumn for both species, due to more favourable environmental conditions and consequent stomatal regulation. Both species show the period of leaf formation and accumulation of structural tissue in the autumn and, as young leaves develop, they show a higher photosynthetic rate, stomatal conductance and transpiration, therefore contributing to the increase reported in autumn and winter (Adam 1990).

The A_{max} values in *L. monopetalum* demonstrated a marked increase in September ($26.75 \mu\text{molCO}_2\text{m}^{-2}\text{s}^{-1}$), and *A. portulacoides* showed lower and steady values, with a non-significant slight increase in December. This difference between species is probably related to the ability of each one to use the available water soil content, with *L. monopetalum* showing a faster response, as seen in September, when higher precipitation occurred (Fig. 1).

L. monopetalum also demonstrated higher water-use efficiency in spring and autumn (Fig. 3c), confirming a higher capacity of stomatal response to changes in water availability. *A. portulacoides* maintained constant its water use efficiency throughout the year, only increasing in the drought period, obtaining similar values to *L. monopetalum*. *A. portulacoides* showed a slower stomatal response capacity, even when the soil water content was higher and vapour pressure deficit and temperatures were favourable, as observed in September. This pattern indicates a highly conservative use of water in *A. portulacoides*, a behaviour often showed in various Mediterranean species subject to climatic constrains, highlighting the stomatal dependence on variations of vapour pressure deficit and temperature (Castell & Terradas 1994, Turner *et al.* 1984). Throughout the year, gs and A were generally higher in *L. monopetalum*, independent of the observed pattern, demonstrating a higher photosynthetic capacity of this species.

The diurnal oscillation of A and gs showed a decrease of these values in the periods of more intense radiation, temperature and vapour pressure deficit, particularly in *A. portulacoides* (Fig. 6). This variation agreed with some limitation of gas exchange through stomatal regulation as stated above. The midday values of A and gs were similar to other salt marsh species as described by Gul *et al.* (2000) in *Allenrolfea*

occidentalis ($7.0 \mu\text{molCO}_2\text{m}^{-2}\text{s}^{-1}$) and by Nieva *et al.* (1999) in *Spartina maritima* ($7.6 \mu\text{molCO}_2\text{m}^{-2}\text{s}^{-1}$) and *Spartina densiflora* ($6.2 \mu\text{molCO}_2\text{m}^{-2}\text{s}^{-1}$).

Acknowledgements

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Table 1 – Difference between predawn and midday water potential ($\Delta\psi$) in each season in *Atriplex portulacoides* and *Limoniastrum monopetalum*. (means \pm SE). $\Delta\psi$ was compared between species by Kruskal-Wallis tests (**, $P < 0.001$)

Species	April	July	September	December
<i>Atriplex portulacoides</i>	-2,46 \pm 0,17	-0,23 \pm 0,13	-1,53 \pm 0,15	-0,91 \pm 0,1
<i>Limoniastrum monopetalum</i>	-1,45 \pm 0,12	-2,1 \pm 0,7	-1,58 \pm 0,14	-0,84 \pm 0,06
	**	**	ns	ns

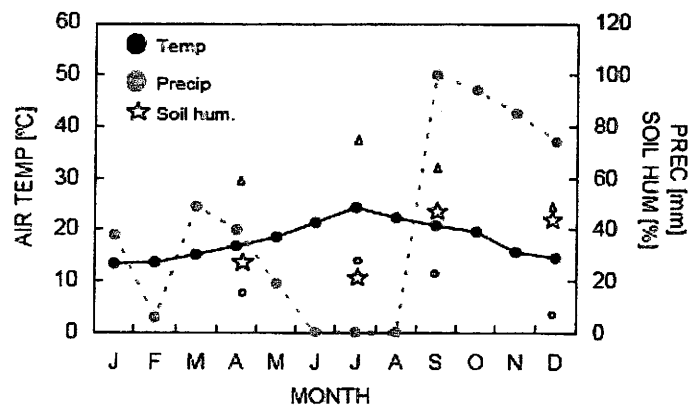


Fig. 1 - Annual variation of monthly mean air temperature, total precipitation and soil humidity in 2002. Maximum (Δ) and minimum (o) temperature values and soil humidity are exposed in April, July, September and December.

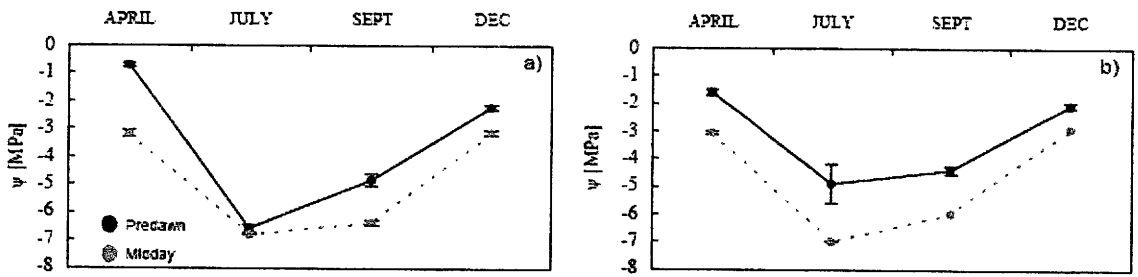


Fig. 2 - Seasonal changes in predawn and midday water potential in a) *Atriplex portulacoides* and b) *Limoniastrum monopetalum* (means \pm SE).

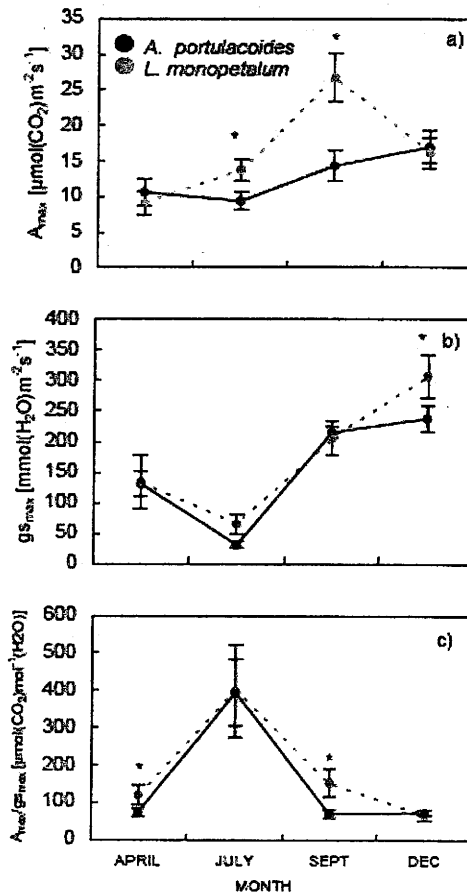


Fig. 3 - Seasonal changes in a) maximal photosynthetic rate (A_{max}), b) maximal stomatal conductance ($g_{s_{max}}$) and c) water use efficiency ($A_{max}/g_{s_{max}}$) (means \pm SE). A_{max} , $g_{s_{max}}$, $A_{max}/g_{s_{max}}$ were compared between species by Kruskal-Wallis tests (*, $P < 0.05$).

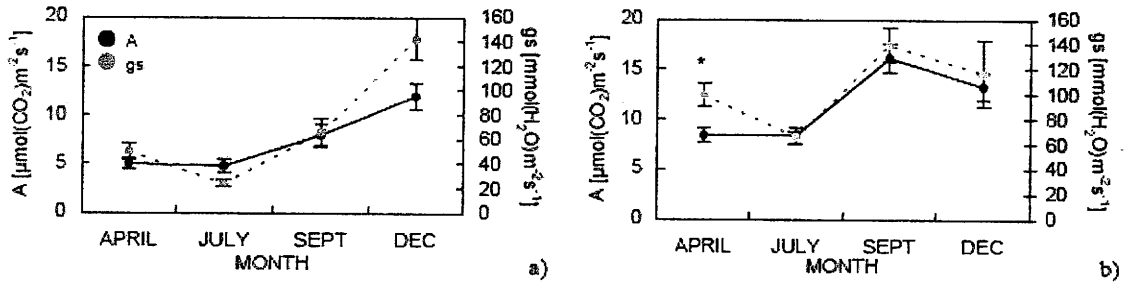


Fig. 4 – Seasonal changes in photosynthetic rate (A, $\mu\text{molCO}_2\text{m}^{-2}\text{s}^{-1}$) and stomatal conductance (gs, $\text{mmolH}_2\text{Om}^{-2}\text{s}^{-1}$) in a) *Atriplex portulacoides* and b) *Limoniastrum monopetalum* (means \pm SE). A and gs were compared between species by Kruskal-Wallis tests (*, $P < 0.05$).

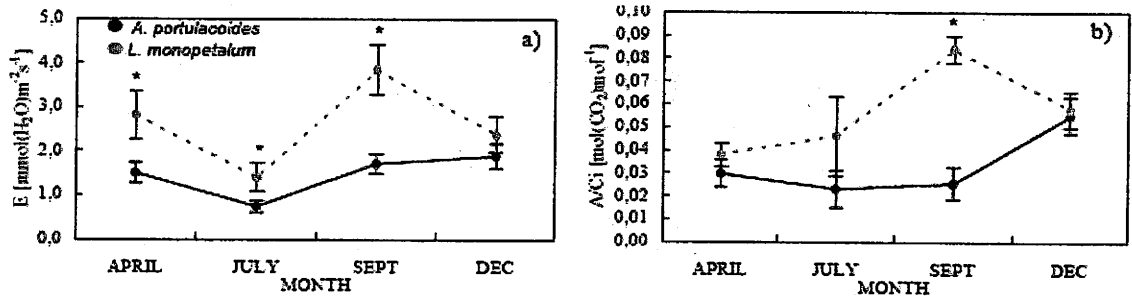


Fig. 5 - Seasonal changes in a) transpiration rate (E , $\text{mmol H}_2\text{O m}^{-2} \text{s}^{-1}$) and b) apparent carboxylation efficiency (A/C_i , $\text{mol CO}_2 \text{m}^{-2} \text{s}^{-1}$) in *Atriplex portulacoides* and *Limoniastrum monopetalum* (means \pm SE). E and A/C_i were compared between species by Kruskal-Wallis tests (*, $P < 0.05$).

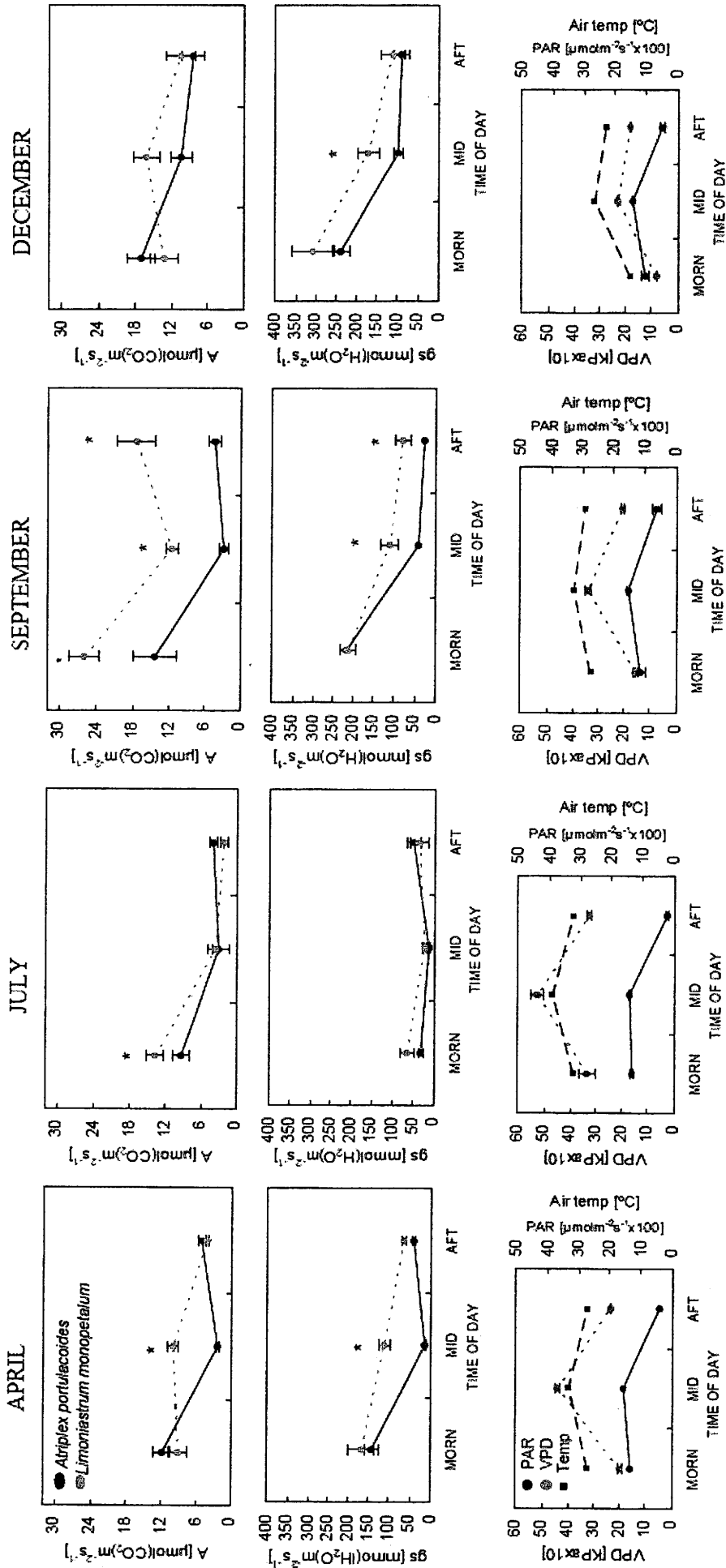


Fig. 6 - Daily changes in diurnal photosynthetic rate (A), stomatal conductance (gs), air temperature, vapour pressure deficit and radiation in *Atriplex portulacoides* and *Limoniastrum monopetalum* (means \pm SE). A and gs were compared between species by Mann U Whitney tests (*, $P < 0.05$). (mo, morning; md, midday; af, afternoon)

Considerações finais

*In the end, we conserve only what we love.
We will love only what we understand.
We will understand only what we are taught.*
Baba Dioum

O crescente progresso no conhecimento, quer da importância relativa das espécies fundamentais para a dinâmica hierárquica das cadeias tróficas, quer a forma como o acréscimo de nutrientes pode afectar a dinâmica trófica ascendente, ou ainda como estes mecanismos poderão interagir influenciando ecossistemas contíguos, são actualmente temas de destaque na investigação ecológica. Adicionalmente, as consequências das modificações nos cursos de água a montante da área do Sapal de Castro Marim, inerentes à gestão da massa de água do Rio Guadiana, são ainda muito pouco conhecidas, sabendo-se de antemão que a alteração dos caudais hidrológicos influencia a dinâmica de qualquer ecossistema costeiro (INAG 1999).

Os estudos conducentes ao conhecimento da funcionalidade básica (relacionados nomeadamente com fisiologia, comportamento e organização na hierarquia trófica) de organismos pertencentes a um determinado nível funcional (população, comunidade ou ecossistema) contribuem de forma basilar para a compreensão e estruturação do contexto ecológico desse nível funcional.

Neste sentido, investigações, como a efectuada neste trabalho, são fundamentais para uma abordagem ecológica integrada e consequente contextualização conservacionista. A existência de estudos a este nível permite a percepção de alterações importantes nas condições individuais ou dinâmicas inter-específicas, como reflexo de distúrbios ou desequilíbrios ecológicos que possam comprometer a sustentabilidade desse ecossistema.

Os estudos anteriores em vegetação de sapal centraram atenções em espécies como *Spartina*, *Juncus* ou *Salicornia* (Percy & Ulstin 1984, Cranford *et al.* 1989, Gross *et al.* 1990, Gross *et al.* 1991, Hsieh 1996, Nieva *et al.* 1999, Curcó *et al.* 2002, Pont *et al.* 2002). No entanto, poucos têm considerado como objecto de estudo espécies de *Atriplex* ou *Limoniastrum* (Groenendijk 1984, Bouchard *et al.* 1998, Khan *et al.* 2000, Daoud *et al.* 2001), embora estes sejam géneros com algumas das espécies mais representativas de sapal, nomeadamente do Sapal de Castro Marim.

Sendo *Atriplex portulacoides* e *Limoniastrum monopetalum* espécies bastante abundantes neste ecossistema e, por isso, com uma importância fundamental no que respeita à sua conservação, torna-se indispensável distinguir o papel funcional de cada uma em particular.

Ambas as espécies apresentaram elevados valores de taxas fotossintéticas, particularmente nos períodos com condições ambientais mais favoráveis, demonstrando também marcadas características adaptativas ao meio ambiente. Os valores obtidos para

a produtividade primária e conteúdo em nutrientes encontraram-se dentro dos valores obtidos para outras espécies de sapal. Observaram-se, no entanto, diferenças notórias entre *Atriplex portulacoides* e *Limoniastrum monopetalum*, no respeitante à capacidade de sequestro do carbono atmosférico, quer através das trocas gasosas, quer na consequente produtividade. A produtividade primária de *L. monopetalum* foi muito elevada, atingindo, tanto pelo método de Weigert-Evans como pelo de Smalley, o triplo dos valores de *A. portulacoides*. Os valores obtidos para *L. monopetalum* são, para além disso, superiores aos referidos na literatura para a maioria das espécies halófitas. *A. portulacoides* apresentou valores de produtividade e padrões nas trocas gasosas similares a outras espécies halófitas de sapais europeus. Confirmou-se, assim, a ideia recente da existência, nos sapais europeus, de espécies tão produtivas como nos norte-americanos, outrora considerados os mais produtivos.

Em concordância com a sua elevada produtividade, a capacidade fotossintética de *L. monopetalum* foi também superior à de *A. portulacoides*, principalmente no início do Outono, em resposta às primeiras chuvas. Verificou-se assim, que a primeira espécie é mais eficaz no sequestro de carbono que a segunda.

As concentrações obtidas para os nutrientes analisados (N, P, K, Ca, Mg e Mn), nos diferentes componentes da biomassa, encontram-se dentro do intervalo estabelecido para as plantas terrestres (Larcher 1995). Não se evidenciou, para além disso, qualquer limitação da produtividade devida a nenhum dos nutrientes analisados.

A capacidade demonstrada por estas espécies como sumidouros de carbono, através das elevadas taxas de produtividade primária e *turnover*, assim como a elevada concentração de nutrientes nos seus componentes, adicionadas à sua abundância no Sapal de Castro Marim constituem factores que lhes conferem grande importância na estrutura do sapal e dos ecossistemas adjacentes.

O Sapal de Castro Marim, como anteriormente descrito, apresenta inúmeras funções ecológicas e económicas, que reforçam a necessidade de se estabelecerem medidas cada vez mais objectivas no sentido da conservação e sustentabilidade deste ecossistema.

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*Any fool can make things bigger,
more complex and more violent.
It takes a touch of genius - and a lot of courage -
to move in the opposite direction*

Albert Einstein

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