Acta Oecologica 59 (2014) 35–45

Contents lists available at ScienceDirect

Acta Oecologica

journal homepage: www.elsevier.com/locate/actoec

Original article

Influence of tree cover on herbaceous layer development and carbon and water fluxes in a Portuguese cork-oak woodland

Maren Dubbert [a,*,1], Alexander Mosena [b,1], Arndt Piayda [c], Matthias Cuntz [c], Alexandra Cristina Correia [d], Joao Santos Pereira [d], Christiane Werner [a]

[a] Agroecosystem Research, BayCeer, University of Bayreuth, Universitätsstraße 30, 95447 Bayreuth, Germany
[b] Experimental and Systems Biology, University of Bielefeld, Universitätsstrasse 25, 33615 Bielefeld, Germany
[c] UFZ – Computational Hydrosystems, Helmholtz Centre for Environmental Research, Permoserstraße 15, 04318 Leipzig, Germany
[d] Instituto Superior de Agronomia, Tecnical University of Lisbon, Tapada da Ajuda, Lisbon, Portugal

ARTICLE INFO

Article history:
Received 25 September 2013
Accepted 20 May 2014
Available online 13 June 2014

Keywords:
Plant interactions
Mediterranean
Understory
Water fluxes
Carbon fluxes
Competition
Facilitation

ABSTRACT

Facilitation and competition between different vegetation layers may have a large impact on small-scale vegetation development. We propose that this should not only influence overall herbaceous layer yield but also species distribution and understory longevity, and hence the ecosystems carbon uptake capacity especially during spring. We analyzed the effects of trees on microclimate and soil properties (water and nitrate content) as well as the development of an herbaceous community layer regarding species composition, aboveground biomass and net water and carbon fluxes in a cork-oak woodland in Portugal, between April and November 2011.

The presence of trees caused a significant reduction in photosynthetic active radiation of 35 mol m^{-2} d^{-1} and in soil temperature of 5 °C from April to October. At the same time differences in species composition between experimental plots located in open areas and directly below trees could be observed: species composition and abundance of functional groups became increasingly different between locations from mid April onwards. During late spring drought adapted native forbs had significantly higher cover and biomass in the open area while cover and biomass of grasses and nitrogen fixing forbs was highest under the trees. Further, evapotranspiration and net carbon exchange decreased significantly stronger under the tree crowns compared to the open during late spring and the die back of herbaceous plants occurred earlier and faster under trees. This was most likely caused by interspecific competition for water between trees and herbaceous plants, despite the more favorable microclimate conditions under the trees during the onset of summer drought.

1. Introduction

Mediterranean oak woodlands are savannah type, pastoral agroforestry ecosystems (called 'Montado' in Portugal) which cover large areas of the Mediterranean basin. They are highly diverse and considered a habitat of high conservation value (Perez-Ramos et al., 2008). The 'Montado' is a multi-layered ecosystem consisting of a widely spaced tree cover composed of *Quercus suber* L., *Quercus ilex* or a combination of these, and an understory layer comprised of shrub formations and/or grasslands, fallows or cereal crops (Diaz et al., 1997; Perez-Ramos et al., 2008). In the 'Montado' ecosystem, the life cycle of herbaceous plants, which typically consist of annual C_3 plants, is terminated by the beginning of the dry season. Commonly the vegetative cycle starts in autumn after the first rains and lasts until the onset of the drought season (Aires et al., 2008), with the main growth phase in spring between March and late May (Jongen et al., 2011, 2013a; Otieno et al., 2011). However, changes in seasonal rainfall can alter this pattern (Figueroa and Davy, 1991; Miranda et al., 2002). Furthermore, factors such as extent of rainfall and the duration of the summer drought period may influence resource availability and affect plant species composition and productivity (Schwinning and Ehleringer, 2001).

The contribution of the herbaceous layer to ecosystem fluxes and productivity consequently varies intra-annually and can be remarkably high, especially in spring. Paço et al. (2009) showed

* Corresponding author. Tel.: +49 (0)921552181; fax: +49 (0)921552315.
E-mail addresses: maren-dubbert@gmx.de, maren.dubbert@uni-bayreuth.de (M. Dubbert), amosena@uni-bielefeld.de (A. Mosena), arndt.piayda@ufz.de (A. Piayda), matthias.cuntz@ufz.de (M. Cuntz), alexandrac@isa.utl.pt (A.C. Correia), jspereira@isa.utl.pt (J.S. Pereira), c.werner@uni-bayreuth.de (C. Werner).

[1] Both authors contributed equally to the work.

http://dx.doi.org/10.1016/j.actao.2014.05.007
1146-609X/

that in times of high water availability (October–May/June) herbaceous evapotranspiration is equal to and sometimes exceeds tree transpiration (see also Dubbert et al., 2013). Furthermore, the herbaceous layer can make upto more than 50% of total gross primary productivity (GPP) during spring and thus play a significant role for ecosystem productivity (Unger et al., 2009, 2010). Herbaceous plants also play an important role in the nitrogen budget enhancing soil nitrogen input and retention in the ecosystem (Otieno et al., 2011) and enhancing growth rate and fruit production of the trees (Pulido, et al., 2010).

The high spatial heterogeneity created by the sparse tree cover, affects microclimate and nutrient availability (Huber-Sannwald and Jackson, 2001; Hussain et al., 2009; Moreno, 2008), creating distinct patches where herbaceous plants grow in the open or under the tree crown. In summer and late spring, the combination of water stress with high radiation can lead to plant photoinhibition (Werner and Correia, 1996; Werner et al., 2001, 2002). Trees can potentially mitigate the photosynthetic damage in the herbaceous vegetation providing shade and temporarily moistening the top soil layers by hydraulic lift (Cubera and Moreno, 2007). This process is characterized by water movement upwards through the root systems of plants that have access to deeper soil depths (Caldwell et al., 1998) and may temporarily increase the soil water content in the upper soil layers (e.g. Kurz-Besson et al., 2006). Hydraulic lift might have a facilitating effect for herbaceous plants, but that effect might easily be overwhelmed by competition for water with trees (Ludwig et al., 2004). Soil nutrient content has also been found to be positively affected by trees (e.g. Gallardo et al., 2000; Gallardo, 2003). However, trees might also act as competitors for nutrients, water and light for the understory, since competition for resources in agroforestry systems is a frequent phenomenon (José et al., 2004).

Most studies on tree versus herbaceous interactions in these ecosystems focus on biomass production (Scholes and Archer, 1997) at large spatial scales (landscape level; Casado et al., 2004; Costa et al., 2009; José et al., 2004). An issue that has not been adequately covered yet is how changes might occur in the competitive balance between trees and the herbaceous layer over the course of a year. During times when water is generally not a limiting factor, maybe shade effects of trees crowns have no significant impact on the herbaceous layer. With increasing drought intensity though, facilitation may play a more important role, although also the opposite was found in 'Montado' systems (Bertness and Callaway, 1994; Maestre et al., 2009; Moreno, 2008). According to previous findings in 'Montado' sites with similar annual rainfall than our site (i.e. Moreno, 2008), we hypothesize that the herbaceous layer will overall profit from the reduced light and temperature stress that should occur under the trees. We propose that this should not only influence overall herbaceous layer yield but also species composition and understory longevity, and hence the ecosystems carbon uptake capacity especially during spring. The main aim of this study was to determine possible facilitating and competitive effects of tree cover on herbaceous vegetation (cover and biomass, species composition and water and carbon fluxes) and their impact during distinct periods within the year: the peak growing period (April–May); the transition of wet spring to summer drought (late May–June); peak summer drought (September) and the re-wetting period at the beginning of autumn (October–November).

2. Materials and methods

2.1. Study site

Measurements were conducted between April 6 and November 22, 2011 in an open cork-oak woodland (*Quercus suber* L.) in central Portugal, approximately 100 km north-east of Lisbon (N39°8′17.84″ W8°20′3.76″; Herdade de Machoqueira do Grou). The oak trees are widely spaced (209 individuals ha^{-1}) with a leaf area index of 1.1 and a gap probability of 0.7. The oak trees are managed for cork production, were planted approximately 50 years ago and have a mean maximum crown height of 10 m and diameter at breast height of 25 cm (Piayda et al., unpublished). It is a bi-layered system containing an annual herbaceous layer dominated by native forbs and grasses, with a biomass peak in spring (April–May) and senescence occurring between late May and early June with the onset of summer drought. In autumn 2009 the site was ploughed, limed and then seeded with a legume-rich seed mixture of native species, a common practice in these agro-silvopastoral systems in Portugal to improve productivity and soil fertility (Crespo, 2006). The seed mixture contained: *Trifolium subterraneum* L., *Trifolium michelianum* L., *Trifolium resupinatum* L., *Trifolium vesiculosum* Savi., *Trifolium incarnatum* L., *Trifolium glanduliferum* Boiss., *Biserrula pelecinus* L., *Ornithopus sativus* Brot., *Ornithopus compressus* L. and *Lolium multiflorum* Lam. In total 20 herbaceous species were observed during the measurement period in 2011 (Table 1).

The soil is a Cambisol, its substrate consists of 81% sand, 14% silt and 5% clay. The site is characterized by a Mediterranean climate, with wet spring conditions and hot, dry summers. Long-term mean annual temperature is approximately 15.9 °C and long-term mean annual precipitation is 680 mm (Instituto de Meteorologia, Lisbon).

We established plots in two different locations: one directly under the oak trees crown projected area and another one in an adjacent open area, approximately 5–7 m distant from canopy cover. A total of 10 permanent herbaceous layer plots of 40 × 80 cm were installed with 5 plots in each location. The distance to the cork-oak crown was selected in order to ensure similar soil and environmental conditions between locations and on the other hand eliminate shading or influence of cork-oak roots, which was verified with soil profiles to 100 cm depth.

2.2. Environmental parameters

In the open and the tree plots photosynthetic photon flux density was measured below the oak canopy and above the herbaceous vegetation at approximately 1.5 m height (PPFD, LI-190SB, LI-COR, Lincoln, USA). Rainfall (ARG100 Rain gauge, Campbell Scientific, Logan, UT, USA), air temperature and relative humidity were all measured continuously in the open area (CS-215 Temperature and Relative Humidity Probe, Campbell Scientific, Logan, UT, USA) and means were stored in a datalogger every 30 min (CR10x, Campbell Scientific, Logan, UT, USA). Vapor pressure deficit (VPD, kPA) was calculated from relative humidity and air temperature data.

Soil temperature (custom built Pt-100 elements) and volumetric water content (θ, 10 h, Decagon, Washington, USA) in 5, 15, 30 and 60 cm depth were measured on both plots and stored in a

Table 1
List of herbaceous species growing in the open and tree plots in 2011.

N-fixing forbs	Forbs	Grasses
Ornithopus compressus L.	*Crepis vesicaria* L.	*Briza maxiama* L.
Ornithopus sativus Brot.	*Geranium spec*	*Lolium multiflorum* Lam.
Trifolium glanduliferum Boiss.	*Plantago coronopus* L.	*Vulpia bromoides* Gray
Trifolium michelianum Savi	*Rumex acetosella* L.	*Vulpia geniculata* Link
Trifolium incarnatum L.	*Silene gallica* L.	
Trifolium subterraneum L.	*Spergula arvensis* L.	
Trifolium resupinatum L.	*Tolpis barbata* (L.) Gaertn.	
Trifolium vesiculosum Savi	*Tuberaria guttata* (L.) Fourr.	