

Carbon and water exchange in semiarid ecosystems in SE Spain

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ABSTRACT

The changing climate is affecting biological and physical processes occurring in the biosphere, including the biogeochemical cycles of water and carbon. The response of ecosystem carbon exchange to changes in temperature and the water balance is still very uncertain, a fact that highlights the need for research in order to understand the role of the biosphere in the future global carbon budget. South east Spain is on the borderline between the tropical and mid-latitude climate zones, with climates ranging from sub-humid to arid, and the majority representing the driest area in Europe. Initial predictions on climate change for this region point to decreases in total precipitation and the number of precipitation events, meaning a decrease in water availability underlining the vulnerability of the region to desertification. This region, due to these special climatic conditions, has been the subject of experimental carbon and water field research in recent years. This paper defines the state of the art of carbon and water balance measurement and modelling studies in this region, analyses the different processes involved in aggregate exchanges (vegetation and soil; net ecosystem carbon balance—evapotranspiration, photosynthesis—transpiration, soil respiration—evaporation), and identifies needs for future research.

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1. Introduction

The response of the ecosystem carbon balance to changes in temperature and the water balance is still very uncertain, and yet essential to understanding the role of the biosphere in the future global carbon budget (Moore et al., 2008). Because carbon and water cycles are strongly linked, mainly through photosynthesis and respiration, changes in the water balance will produce changes in the carbon cycle determining the CO₂ source/sink

behaviour of ecosystems. Initial climate forecasts for the Mediterranean point to a decrease in net precipitation and number of events, and an increase in intensity (Christensen et al., 2007). This would diminish water availability in already water-limited Mediterranean ecosystems sensitive to desertification, especially semiarid regions such as SE Spain. In these semiarid ecosystems, the link between the carbon and water cycles is expected to tighten as the growing period shortens due to drought (Baldocchi, 2008; Janssens et al., 2005).

SE Spain is on the borderline between tropical and mid-latitude climate zones, with climates ranging from sub-humid to arid, and the majority representing the driest area in Europe. Due to the scarce precipitation, socio-economic activities must rely strongly on ground water resources (Pulido-Bosch et al., 2000). In-depth knowledge of the water balance is thus critical for sustainable water management in this region. The water balance can be summarised as the difference between water inputs, mainly precipitation (P) but also dew and atmospheric water adsorption by soil, and water loss processes such as runoff (R_{off}), infiltration (I) and

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evapotranspiration (ET), which affect the aquifer recharge rate (R). Moreover, this equilibrium between water gains and losses determines the soil water content (SWC), a crucial resource in water-limited ecosystems responsible for vegetation scarcity which in turn determines the SWC heterogeneous spatial distribution characteristic of these ecosystems (Rodríguez-Iturbe et al., 1999). As precipitation, runoff, infiltration and recharge are analysed elsewhere in this special issue, our attention in relation to the water balance will be on ET, dew and atmospheric water adsorption by soil in SE Spain.

Water and carbon exchanges between ecosystems and the atmosphere are interrelated, each regulated by processes occurring in both soil and vegetation. To understand how the carbon flux in semiarid ecosystems changes with varying water availability, the relationship between the net ecosystem exchange and ET must be analysed in different seasons. According to studies done in different ecosystems (Law et al., 2002; Luyssaert et al., 2007), this relationship is expected to be important in water-limited ecosystems with highly seasonal precipitation. Therefore, the relationship between transpiration and photosynthesis according to SWC has also been studied in semiarid SE Spain, in order to understand how vegetation growth and resilience will be affected by changes in water availability.

Advances in micrometeorological theory and technology (Aubinet et al., 2000) provide appropriate means of measuring ecosystem-scale fluxes over a spectrum of time-scales ranging from hours to years (Baldocchi et al., 2001). The eddy covariance (EC) technique (Swinbank, 1951) provides a direct measurement of energy and mass (such as CO₂ and water vapour) exchange across the biosphere–atmosphere interface (Baldocchi, 2003; Dabberdt et al., 1993; Valentini et al., 2000) and makes long-term integration possible (Wofsy et al., 1993). Combined with inverse modelling, remote sensing and meteorological information, the information acquired by this technique can be used to estimate reliable regional (and ultimately global) carbon and water cycling (Dolman et al., 2006; Mahadevan et al., 2008). The EC technique has proliferated (Aubinet et al., 2000; Baldocchi et al., 2001), with hundreds of towers/nodes for annual ecosystem CO₂ exchange estimation. In this research, terrestrial CO₂ flux is usually interpreted as a biological flux (Houghton, 2002; Valentini et al., 2000). Net ecosystem exchange (NEE, the difference between gross primary production and heterotrophic ecosystem respiration) determinations are combined with meteorological information in semiempirical hyperbolic models to determine the contribution of uptake (gross photosynthesis) and loss (ecosystem respiration) (e.g. Kowalski et al., 2004; Lasslop et al., 2010; Reichstein et al., 2005). In the last decade, several micrometeorological towers using the EC technique have been installed in semiarid SE Spain.

Hence, in SE Spain, due to its special climate conditions and substrate, carbon and water in all of these mentioned related processes have been the subject of experimental field research in recent years. The aims of this paper are to: i) define the state of the art of carbon and water balance measurement and modelling studies in this region, ii) analyse the different strata (vegetation and soil) and processes involved at different levels (NEE-ET, photosynthesis-transpiration, soil respiration–evaporation), and iii) identify needs for future research.

2. Ecosystem carbon dioxide and water exchange

Although the “flux community” has widened knowledge of the carbon cycle, nascent research has focused mainly on forest and cropland ecosystems, and continental-scale integrations have thus far neglected the functional behaviour of sparse shrubland ecosystems in Mediterranean climates (Schulze et al., 2009).

However, currently this community is expanding to examine the relevance of semiarid lands in the carbon cycle, as highlighted by a recent special issue of the Fluxnet newsletter (FluxLetter Vol. 2 No. 4 - January, 2010).

The micrometeorological towers using the eddy covariance (EC) technique installed to measure NEE and ET in shrubland ecosystems in SE Spain have provided relevant data about CO₂ exchange in such ecosystems. They are characterised by asynchronous annual patterns of sunlight and precipitation, and particularly strong summer droughts (Serrano-Ortiz et al., 2007). Recent measurements from the “El Llano de los Juanes” flux site carbonate ecosystem reveal a possible contribution of abiotic processes to the NEE related to subsurface storage and later release of CO₂ via ventilation processes (Serrano-Ortiz et al., 2010a). “El Llano de los Juanes” is a Mediterranean shrubland plateau at 1600 m altitude located in the Sierra de Gádor (Almería, south east Spain; 36°55′41.7″N 2°45′1.7″W) characterised by a sub-humid montane Mediterranean climate. Such abiotic exchanges can temporarily (during summer drought) dominate the ecosystem CO₂ exchange (Kowalski et al., 2008). Empirical, hyperbolic models based on biological processes fail to describe such CO₂ exchange, and require alternative means of filling data gaps for long-term integration. Despite such difficulties, the mean annual NEE from May 2004 to December 2007 was estimated to vary from –63 (uptake) to 29 g C m⁻² (release), averaging -2 ± 23 g C m⁻² (a nearly neutral carbon sink) (Serrano-Ortiz et al., 2009). However, a recent study shows that heterogeneity of the subterranean pore space (preferential ventilation zones) could violate the micrometeorological “fetch” criterion, such that the measured NEE may not be representative of a wider area (Were et al., 2010). The origin of stored subsurface CO₂, which can exceed concentrations of 50,000 ppm in Mediterranean areas (Vadillo et al., 2007) and the drivers of its exchange with the surface are still unknown.

Additional micrometeorological towers using the EC technique have been installed in semiarid SE Spain at different altitudes and in different land-use types, and preliminary results show differing behaviour. Fig. 1 presents an example of the differing CO₂ exchange patterns for ecosystems in this region during an early summer week in 2008, and a synopsis of more general results from these ecosystems follows.

An alpine Mediterranean shrubland site located in the Sierra Nevada mountain range (2300 m a.s.l.; 37°05′N 2°57′W) was found to be a carbon source of ca. 50 g C m⁻² year⁻¹ during both 2007 and 2008 (Reverter et al., 2010). In addition, two semiarid carbonate shrubland sites near sea level and within a few km of the coast in Cabo de Gata Natural Park (Almería; 36°56′26″N 2°1′58.8″W) showed sizeable CO₂ emissions reaching ca. 8 μmol m⁻² s⁻¹ during dry periods (Serrano-Ortiz et al., 2010b). Preliminary analyses suggest contribution of subsurface ventilation. Finally, an average of more than 100 000 ha of Spanish forest burn annually (MIMAM, 2007), converting ecosystems into carbon sources for months to even years (Amiro et al., 2003; Bond-Lamberty et al., 2007); therefore, there is great interest in quantifying fire's contribution to global CO₂ emissions (Beringer et al., 2003; Conard and Ivanova, 1997) and the effect of different post-fire wood managements. In this context, two towers operating in a Mediterranean pine forest that burned in a wildfire in 2005, with different post-fire management of the burnt trees are shown in Fig. 1 as preliminary results (Sierra Nevada Natural park; Castro et al., 2011). During the displayed period, daytime CO₂ emissions of ca. 1 μmol m⁻² s⁻¹ were measured where all trees had been cut down and the trunks and branches removed (salvage logging, common post-fire silvicultural management; Castro et al., 2011), while the non-intervention treatment (dead forest left standing) showed a daytime CO₂ uptake of ca. 3 μmol m⁻² s⁻¹ (Fig. 1d). However, to assess the

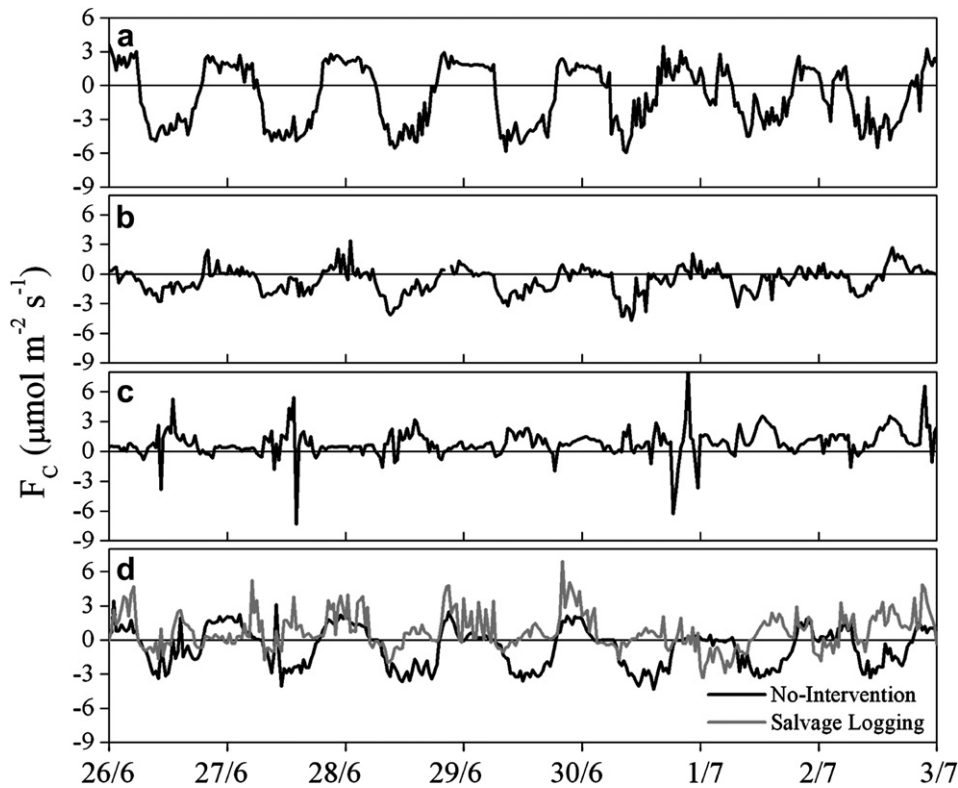


Fig. 1. Patterns of CO₂ exchange (F_c) from 26th June to 3rd July 2008 in different ecosystems located in Southeast Spain. a) Laguna Seca (Sierra Nevada), b) Llano de los Juanes (Sierra de Gádor), c) Balsa Blanca (Cabo de Gata) and d) two ecosystems with different post-fire management of burnt trees.

impact of salvage logging management on the carbon cycle, several years of CO₂ exchange estimations are needed.

The micrometeorological towers using the EC technique have also been used in SE Spain to measure and model the water balance through measurements of ET. In arid and semiarid environments, where ET is critical to the water balance, it can represent up to 90% of annual P. However, some areas can act as soil water sources when $P > ET$, or as sinks when $P < ET$ (Domingo et al., 2001). Environmental characterisation of these areas as either source or sink is fundamental for determining adequate management policies (Cantón et al., 2010). Evapotranspiration models enable ecosystem-scale estimation, and have been used widely in semiarid SE Spain (Brenner and Incoll, 1997; Domingo et al., 1999, 2001; Ramírez et al., 2007a; Villagarcía et al., 2007, 2010; Were et al., 2007, 2008). Brenner and Incoll (1997) developed a physically-based evapotranspiration model (Clumped Model-CM) for sparse vegetation. This model has been successfully applied in stands of three species typical of SE Spain (*Retama sphaerocarpa* L. (Boiss), *Anthyllis cytisoides* L., and *Stipa tenacissima* L.) and compared to Bowen ratio measurements, eddy covariance, and (sapflow) heat balance methods (Domingo et al., 1999; Villagarcía et al., 2010; Were et al., 2008).

Domingo et al. (2001) demonstrated that by combining CM with data for I and R_{off} , sites may be classified as sources or sinks. For example, they found that the valley floor of the Rambla Honda experimental site (Tabernas, Almería 37°8'N, 2°22'W, 630 m a.s.l.), where the roots of the predominant shrub *R. sphaerocarpa* L. (Boiss) can reach ground water 30 m deep (Haase et al., 1996), acts as a long-term soil water sink ($ET \gg P$). Neither run-on from surrounding slopes, nor infiltration of local rainfall appear to be sufficient to explain the water deficit observed, and they concluded that infiltration of channel flow coming from the top of

the catchment during flash floods replenishes the water deficit. Supporting this idea, Archer et al. (2002) and Domingo et al. (1998) demonstrated that, on the surrounding hill slopes, the typical funnel shape of some plant species (such as *A. cytisoides*) (García, 2006) facilitated preferential flow towards the shallow root system of the shrub, but afterwards, in summer, all this water that did not reach the water table was locally transpired and evaporated. The role of transpiration is also highlighted in wetland areas of SE Spain, where water managers must take the high transpiration rates of riparian zones into account (Moro et al., 2004).

South east Spain exhibits a wide variety of ecosystems from alpine Mediterranean to semiarid coastal ecosystems that should be analysed from these perspectives and major efforts are ongoing to characterise ET and associated processes in aquifer recharge areas (Sierra de Gádor-Almería; Ventós catchment-Alicante) and coastal carbonate areas (Cabo de Gata, Almería).

As already indicated in the Introduction, in order to project the effects of climate change on the functioning of ecosystems it is important to understand the interrelationship of the carbon and water cycles (e.g., Janssens et al., 2005; Law et al., 2002). In the SE of Spain, where climate change is predicted to have strong effects, with higher temperatures and lower precipitations, this issue is of high importance. Although, some first steps have been taken to study water use efficiency in steppe ecosystems (Ramírez et al., 2008b), several ongoing projects are monitoring the carbon and water balances over a range of ecosystems, from mountainous areas to coastal steppes. These projects will generate results that will help to better understand how the water balance affects the carbon balance of these ecosystems, and, therefore, how the expected reduction in water availability will affect the vegetation growth and resilience in these ecosystems.

3. Component water and CO₂ processes and scaling

3.1. Soil respiration

In semiarid ecosystems, SWC is the fundamental driver of biological activity and soil respiration (Almagro et al., 2009; Conant et al., 2000; Jia et al., 2006; Liu et al., 2009). The dry and warm climate of SE Spain determines that the seasonal dynamics of soil respiration are mainly controlled by water availability, and only occasionally by temperature. Results from Rey et al. (2011) (Fig. 2) show such dynamics in Cabo de Gata Natural Park where precipitation is hardly 200 mm.

Although SWC has been recognised as an important factor incorporated in respiration models (Rey et al., 2002), its role as a determinant in semiarid ecosystems may be more complicated (Schwinning et al., 2004). Drylands are characterised by erratic, random rainfall events that interact with the functioning of autotrophic and heterotrophic soil respiration processes, and cause pulses of CO₂ to the atmosphere (Jarvis et al., 2007; Rey et al., 2002, 2005) that contribute significantly to the total amount of carbon respired (Huxman et al., 2004). Two major processes may contribute to the rapid increase in soil emissions following rainfall. First, the large amounts of CO₂ accumulated in pore spaces during dry periods are physically displaced and released (Emmerich, 2003; Huxman et al., 2004; Inglima et al., 2009; Serrano-Ortiz et al., 2010a), and second, decomposition of readily available carbon accumulated during the previous dry period are rapidly activated (Kieft et al., 1997).

Another distinctive characteristic of arid and semiarid ecosystems such as those in SE Spain is the high spatial variability and patchy distribution of resources (Schlesinger and Pilmanis, 1998), which must be reflected in fluxes via soil respiration. Small rainfall events and dew may potentially trigger microbial respiration in canopy interspaces, whereas larger rainfall events are required to stimulate root and microbial activity under plants (Luo and Zhou, 2006). Rey et al. (2011) found no significant differences in soil respiration between canopy and intercanopy spaces during one year in a semiarid steppe in SE Spain (Cabo de Gata, Almería) (Fig. 2), although significant differences were observed in soil properties and soil carbon content. Therefore, the interaction between water availability and ecosystem structure is another critical aspect that needs to be considered. In semiarid ecosystems, inorganic carbon can exceed organic carbon by up to tenfold (Schlesinger, 1982). Current estimates of inorganic accumulation rates in arid and semiarid soils range from 0.5 to 5 g C m⁻² yr⁻¹ (Marion et al., 2008). Diaz-Hernandez et al. (2003) estimated that in an intramontane sedimentary basin in SE Spain (an important landscape for the evaluation of soil carbon stored in semiarid regions) the organic carbon content was 7.8 kg m⁻² (down to 2–3.5 m depending on soil depth), whereas inorganic carbon was as high as 134.4 kg m⁻². Recent studies have indicated that the turnover time of inorganic carbon may be much shorter than previously thought (Monger and Gallegos, 2000), and thus, this fraction may play an important role in the ecosystem carbon balance (Kowalski et al., 2008). Part of soil CO₂ emissions may be the result of the weathering of soil inorganic carbon in the form of carbonates, whereas CO₂ accumulation occurs as a result of carbonate precipitation (Serrano-Ortiz et al., 2010a). Furthermore, arid and semiarid ecosystems are prone to soil degradation, which may be aggravated by land use and climate change (UNEP, 1997). The impact of land degradation on soil respiration is therefore likely to lead to considerable changes in the carbon balance of semiarid ecosystems (Rey et al., 2011).

Some studies on soil respiration carried out in SE Spain illustrate some of these processes. Almagro et al. (2009) investigated the dynamics of soil respiration under different land uses in Murcia Province where mean annual precipitation is around 400 mm and mean annual temperature around 15 °C. Mean annual soil respiration rates beneath canopies were 2.35, 1.87 and 2.18 μmol CO₂ m⁻² s⁻¹ in forest, abandoned agricultural and rainfed olive orchards, respectively. Whereas temperature was the main driving variable of soil respiration during the autumn and winter, SWC was the limiting factor for late spring and summer. In a drier area (200 mm and 18 °C) Rey et al. (2011) found that SWC was the main driver of soil respiration for most of the year, particularly below a threshold of 13% (volumetric SWC), and even during those few winter months with soil moisture above this, the effect of temperature was mediated by soil moisture. Annual mean soil respiration was 1.01 and 0.77 μmol CO₂ m⁻² s⁻¹ for natural and degraded sites, respectively. Both studies analysed the spatial variability of soil respiration, measuring rates under plants versus canopy interspaces, and found somewhat contrasting results. Whereas Rey et al. (2011), as mentioned above, did not find any significant differences between ground cover types in either ecosystem (natural and degraded sites), Almagro et al. (2009) found significant differences in the olive grove and forest sites, but no differences in the abandoned field. Similarly, Maestre and Cortina (2003) in a nearby area in the Province of Alicante (380 mm yr⁻¹, and 16 °C), found that SWC was the main factor controlling temporal dynamics of soil respiration. In contrast, they reported significant differences between rates measured under alpha grass tussocks and in bare ground. However, they reported results only during the growing season (spring), and differences were

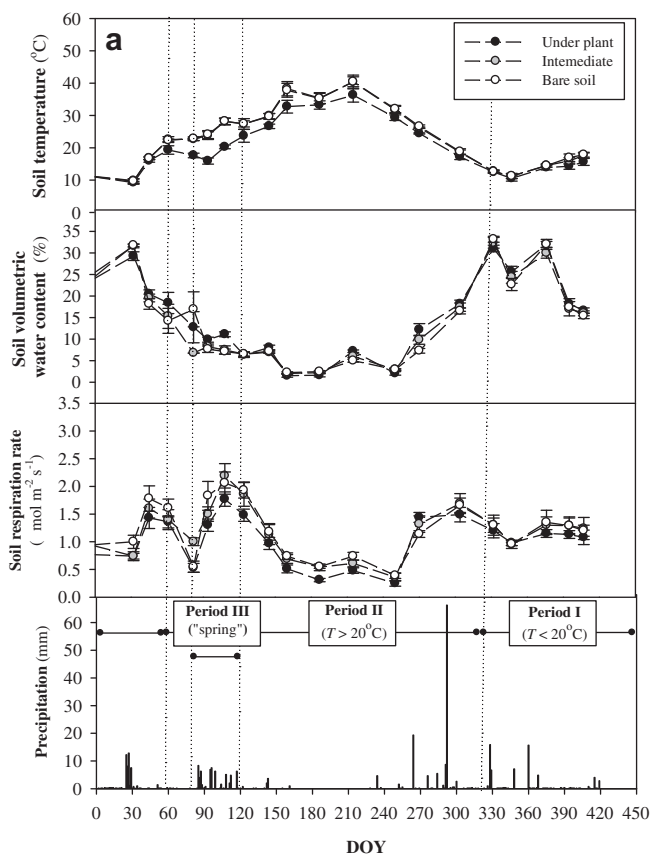


Fig. 2. Precipitation and soil respiration dynamics, soil water content and soil temperature in three surface positions in a semiarid steppe (*Stipa tenacissima* L.) ecosystem in Balsa Blanca (Cabo de Gata) (Rey et al., 2011).

pronounced mostly after rainfall events, which is in agreement with the results reported by Rey et al. (2011).

3.2. Leaf and plant gas exchange

Numerous ecological studies have focused on leaf-scale gas exchange measurements employing chambers (Kruijt et al., 1997). In semiarid SE Spain, leaf measurements of net photosynthesis, transpiration, and stomatal conductance have been widely used for assessing water stress avoidance strategies (*sensu* Levitt, 1980) for some prominent species (Balaguer et al., 2002; Domingo et al., 2003, 2002; Haase et al., 1999; Pugnaire and Haase, 1996; Pugnaire et al., 1996; Ramírez and Bellot, 2009), ontogenetic comparison (Ramírez et al., 2008b), assessing the results of restoration activities (Vilagrosa et al., 2005), among other things.

More recently, the sub-leaf scale has gained importance for examining intrinsic water use efficiency and competition by making use of the isotopic composition of carbon (Ramírez et al., 2009) and landscape function analysis (Maestre and Cortina, 2006).

Leaf-scale results have also been extrapolated to individual-canopy scale in semiarid SE Spain. In a *S. tenacissima* 'alpha' grassland, Haase et al. (1999) calculated daily canopy net photosynthesis by integrating the hourly carbon assimilation measured by an IRGA chamber, and scaling by the foliar area of the assessed tillers. On the other hand, the combination of crown architecture/geometry (e.g., YPlant, Percy and Yang, 1996) and canopy photosynthesis (Beyschlag and Ryel, 2007) models has allowed individual-canopy net photosynthesis to be calculated by taking the heterogeneity of canopy characteristics such as age, physiology, foliar arrangement and microclimatic conditions of the branches using summation and averaging schemes to scale-up (*sensu* Jarvis, 1995). Neglect of the internal heterogeneity of the individual might lead to overestimation of the individual net photosynthesis. For example, extrapolation of daily net photosynthesis in *S. tenacissima* in the wet season by Haase et al. (1999) ranged from 508 to 893 mmol CO₂ m⁻² day⁻¹, whereas the maximum daily net photosynthesis at individual scale calculated by an architectural model (YPlant) was 292 mmol CO₂ m⁻² day⁻¹ (Valladares and Pugnaire, 1999). These authors highlighted the fact that self-shading of leaves limited carbon assimilation to only 40% of potential.

Regarding water fluxes, calculation of the individual-canopy stomatal conductance and transpiration rates at leaf–branch scale has been carried out for the implementation of the above mentioned evapotranspiration models (Clumped Model-CM) in stands of *S. tenacissima*, *R. sphaerocarpa* and *A. cytisoides*. The goal was to estimate transpiration by combining direct sap flow measurements in some branches (Domingo et al., 1999) with empirical modelling of stomatal conductance in terms of photosynthetic photon flux density and vapour pressure deficit (Villagarcía et al., 2010) and leaf temperature measurements to calculate the vapour saturation density (Brenner and Incoll, 1997). Once transpiration and stomatal conductance are estimated, these are extrapolated to the stand level, scaling by the fraction of vegetation cover and leaf area index. On the other hand, using a crown architectural model and following a sequential scaling process (Baldocchi et al., 1991), Ramírez et al. (2006, 2008a) found that leaf senescence and self-shading are crucial to scaling transpiration from leaf to individual in *S. tenacissima*. Ramírez et al. (2008a) assessed the individual transpiration of three tussock size classes in different soil water conditions (from <5 to >25% of volumetric SWC), by calculating empirical functions for each size class that allowed correcting the overestimation from extrapolated leaf measurements. Ramírez et al. (2007a) used these functions to scale transpiration in *S. tenacissima* from individual to stand with satisfactory results compared to stand transpiration calculated by CM.

3.3. Scaling water and CO₂ fluxes: the role of remote sensing

As mentioned above, eddy covariance (EC) is one of the most successful techniques for ecosystem characterisation of water and carbon fluxes. However, EC measurements limit spatial coverage to a footprint of around 1 km² (Kljun et al., 2004), and the only data source providing frequent simultaneous and spatially explicit information correlated with the biophysical properties of the surface and its water and energy status is remote sensing (RS) (Kustas and Norman, 1996).

The particularities of drylands make remote sensing modelling of carbon and water fluxes more challenging than other biomes. For instance, the mosaics of vegetation, dry matter and bright, and dry soils (Okin, 2002) cause nonlinear effects in pixel reflectance that can mask vegetation signals (Asner, 1998; Huete and Jackson, 1987). This patchiness also results in strong soil–vegetation interaction among surface fluxes (Chehbouni et al., 2000; Moran et al., 1994). Dryland ET and photosynthetic rates are generally low, with peak activity following rainfall pulses (D'Odorico and Porporato, 2006). In semiarid SE Spain, with asynchronous wet and warm seasons (Serrano-Ortiz et al., 2007), water fluxes on many days do not exceed the average error of most RS ET models (~0.8 mm day⁻¹, Seguin et al., 1999), and are even lower than fluxes at other semiarid sites where rainy and warm seasons coincide (Gillies et al., 1997). Additionally, capturing pulse activity requires daily overpasses, guaranteed only by sensors such as MODIS or SEVIRI that have coarse spatial resolution (1–3 km).

To improve comparability and scaling of coarse spectral measurements to EC measurements, Gamon et al. (2006) created SpecNet (Spectral Network) which adds standardised field spectral samplings to existing FLUXNET sites. SpecNet currently includes six desert and semiarid sites. In semiarid SE Spain, the EEZA (CSIC) Desertification and Geocology Group has been working on four nested scale-up levels for monitoring ecosystem fluxes with remote sensing using both permanent and portable field sensors (Morillas et al., 2009), Unmanned Aerial Vehicles (UAVs; Berni et al., 2009) in thermal (40 cm) and VNIR (15 cm) ranges, hyperspectral images (Hymap and DAIS) at 4 m and 10 m, and ASTER (30–90 m) and MODIS data (250 m–1 km) (García et al., 2007; García et al., 2008b, 2009).

Scaling carbon fluxes from stand to patch and landscape can be done using a bottom-up approach, but this requires a high degree of parameterisation and complicates regional applications. In addition, feedback processes might cause bulk stomatal response and CO₂ assimilation to be unscalable from leaf to canopy and region (Houborg et al., 2009). Top-down approaches use simple scaling rules, but require some degree of empiricism at some point (Houborg et al., 2009). The Light Use Efficiency (LUE) model (Monteith, 1972) is widely used to estimate Gross Primary Productivity (GPP) in process-based models such as NASA–CASA (Potter et al., 2003) and also in other remote sensing applications (Hilker et al., 2008). Vegetation Indices (VI) are used to estimate fPAR (fraction of absorbed PAR). Since in drylands, water availability is the main constraint for maximum biological efficiency (Brogaard et al., 2005), remote sensing water-deficit indicators would be useful in improving current LUE estimates (Carlson et al., 1995; Sandholt et al., 2002). These indicators have been tested in semiarid SE Spain using ASTER (García et al., 2007) and MODIS data (García et al., 2008a, 2009), and can be directly incorporated into LUE modelling.

In semiarid SE Spain, Morillas et al. (2009) showed the relationship of the locally field measured PRI (Photochemical Reflectance Index) and thermal stress indices with leaf conductance and transpiration for *S. tenacissima* in Cabo de Gata Natural Park. We used the same dataset to explore correlations with carbon flux (F_c) and LUE (Table 1), and found that pigment content indices (chlorophyll and carotenoids) and canopy water content indices

estimated F_c better than PRI or NDVI. Water stress indicators showed negative correlations with F_c at midday when water stress tends to be maximum, and LUE was significantly correlated with those indices highly correlated with F_c . These results emphasise the importance of using different spectral regions, including thermal and narrow-band to characterise the functioning of semiarid vegetation (Ustin et al., 2009). It remains to be seen whether the performance of these indices is similar at the ecosystem level using imagery and EC measurements.

Regarding the scaling of water fluxes there are some comprehensive reviews describing models ranging from empirical to semiempirical and using physical or numerical approaches (see Courault et al., 2005; Kustas and Norman, 1996). The most popular RS algorithms for estimating water fluxes in semiarid areas calculate ET as a residual of the surface energy balance equation. In semiarid SE Spain, the Simplified Relationship (Seguin and Itier, 1983), that estimates daily sensible heat flux using a classic surface-resistance approach using midday measurements of surface and air temperatures, provided better results despite of considering an homogeneous aerodynamic resistance across the shrublands than the Carlson et al. (1995) approach, where aerodynamic resistances were modelled spatially as a function of vegetation greenness, and which seems to be better suited to dense vegetation cover areas (García et al., 2007). In other semiarid areas, such as Arizona, dual source models explicitly modelling vegetation and soil fluxes separately and also their interactions, showed better results than single source models treating the mixture of soil and vegetation as a whole (Norman et al., 1995). However dual source modelling requires disaggregation of pixel temperature into vegetation and soil which is solved by iterations or else requires measurements of surface temperature from different view angles.

One of the first contextual models estimating ET in semiarid natural vegetation was the WDI (Water Deficit Index) by Moran et al. (1994). Later versions of the WDI such as the TVDI (Temperature Vegetation Dryness Index; Sandholt et al., 2002) or the Jiang and Islam (2001) model have been successfully applied in semiarid regions such as Senegal (Stisen et al., 2008) and semiarid SE Spain (García et al., 2008b). RS data has also been incorporated in the Penman–Monteith equation to characterise surface conductance (Cleugh et al., 2005; Leuning et al., 2008). However, in SE Spain, their performance has been found to be poor, requiring modelling of SWC temporal dynamics (Morillas et al., 2011).

One outstanding issue in the use of sun-synchronous satellites is scaling instantaneous estimates of the energy balance components: net radiation (R_n), soil heat flux (G), sensible heat flux (H) and ET to daily estimates (Bisht et al., 2005). A sinusoidal model for semiarid SE Spain scaling R_n from instantaneous to daily estimates based on the daily solar trend performed better than assuming constant scaling factors (Morillas et al., 2008).

In some approaches, the role of RS is just to estimate vegetation cover and incorporate it into water balance modelling. For instance, Boer and Puigdefábregas (2005) developed a spatial ET model working at annual time-scales in the Guadalentín Basin (SE Spain). Their model was run by Contreras et al. (2008) in the dry Mediterranean mountains of Sierra de Gádor for an average rainfall year. As it relies in the hydrological equilibrium hypothesis, stating that vegetation adjusts to maximise its growth while minimising water stress (Nemani and Running, 1989), this approach is strictly limited to long time-scales (annual averages) and perennial vegetation.

3.4. Non-rainfall water inputs

Non-rainfall water inputs include fog, dew formation and atmospheric water adsorption by soil (AWAS). In the absence of fog, dew and AWAS are outstandingly relevant processes that improve the water balance in semiarid and arid ecosystems. Research on dew and AWAS is underway in semiarid SE Spain.

Few studies have assessed the contribution of dew to the water balance in semiarid environments. The direct use of dew by plants or biological soil crusts has also been poorly studied in these areas. Moro et al. (2007, 2009) have explored the suitability of the EC technique, combined with qualitative methods such as wetness sensors, as a tool to measure actual dewfall in semiarid conditions, both in a dry river bed (Rambla Honda, Tabernas, Almería) (Moro et al., 2007), and in a coastal steppe dominated by *S. tenacissima* with bare soil and biological soil crusts (Balsa Blanca, Cabo de Gata, Almería) (Moro et al., 2009). In Rambla Honda, dewfall was calculated as 12% of rainfall for 2003, averaging 0.08 mm day⁻¹. Dewfall was higher in late winter and early spring, when vegetation starts active growth. Dew episodes were recorded on over 50% of the nights throughout the study period, averaging 6.5 h per night. Sparse *R. sphaerocarpa* canopies significantly influenced condensation on the soil surface. The gradient of dew occurrence increased from the centre of the canopy outward to the open, bare soil. Dew duration (hours per night) decreased from the inner position under the *R. sphaerocarpa* canopy (4.1) outward to the open spaces (7.7), with 7.3 at the edge. These results need further validation, but seem to be due to a combination of aerodynamic and longwave radiative characteristics that differ for plants and soil, and can change the energy balances of the individual components in the system (Domingo et al., 2000).

In a preliminary study in Balsa Blanca, dewfall was recorded on 98% of nights during one whole year (2007). This percentage, although surprisingly high, is being confirmed by ongoing dew measurements in the area (Uclés et al., personal communication). Dewfall length varied from 1 to 16 h per day with an average of 6.3 h per day. The average dewfall rate was 0.016 mm h⁻¹, with relatively little variability over the year (Moro et al., 2009). Dewfall episodes were longer in late autumn and winter and decreased in

Table 1
Pearson's correlation coefficient (R) between carbon assimilation variables: F_c in $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ and light use efficiency (LUE) (Licor6400) vs. spectral (GER2400) and thermal indices (Raytek). Measurements were made at midday on *Stipa tenacissima* in Cabo de Gata (Almería, Spain) between June 2008 and February 2009. * and ** indicate significant correlations at $p < 0.05$ and $p < 0.01$ respectively.

Indicator of	Name/formula	Reference	F_c	LUE
Green vegetation cover	Normalized Difference Vegetation Index: $\text{NDVI} = (R_{800} - R_{670}) / (R_{800} + R_{670})$	Tucker and Sellers, 1986	0.65	0.56
Canopy water content	Normalized Difference Water Index $\text{NDWI} = (R_{860} - R_{1240}) / (R_{860} + R_{1240})$	Gao, 1996	0.86*	0.66
Xanthophyll cycle	Photochemical Reflectance Index $\text{PRI} = (R_{570} - R_{531}) / (R_{570} + R_{531})$	Gamon et al., 1992	0.12	0.28
Chlorophyll content	R_{750} / R_{710}	Zarco-Tejada et al., 2003	0.95**	0.88*
Carotenoids content	R_{800} / R_{470}	Blackburn, 1998	0.96**	0.84*
Water stress	$T_{\text{canopy}} - T_{\text{air}}$	Sepulcre-Cantó et al., 2007	-0.9*	-0.83
Water stress	$T_{\text{soil}} - T_{\text{canopy}}$		-0.93*	-0.83

spring. Comparing the contribution of dewfall to the local water balance in Balsa Blanca during a wet (January–May 2007, total P of 120 mm) and a dry period (January–May 2008, total P of 15 mm), Moro et al. (2009) found dewfall totalled 15% of rainfall in 2007 and more than 100% in 2008. Long-term average rainfall in the area is 200 mm. Overall, these results stress the relevance of dewfall as a relatively small but constant source of water for some arid ecosystems, as well as its significant contribution to the local water balance, mainly during dry periods.

Regarding AWAS, Agam and Berliner (2004, 2006) highlighted that it can be even more common than dew formation in some areas. In semiarid Mediterranean environments, Kosmas et al. (1998) calculated that water gain from AWAS was 26.3% of the precipitation during February–August of 1996 in Athens, Greece. Such water gains via AWAS can supply 55.7%–70.7% of the soil evaporative demand (Kosmas et al., 2001). Verhoef et al. (2006) reported and characterised AWAS occurrence in Mediterranean SW Spain (Seville Province) by implementing a mechanistic model. In semiarid environments like in Almería Province, soil water fluctuation (Villagarcía et al., 2004) has been related to AWAS, and in Alicante Province, Ramírez et al. (2007b) found that the AWAS covers the ET demands of a *S. tenacissima* grassland during the water-deficit season. Some studies (Ramírez and Bellot, 2009; Ramírez et al., 2007b, 2008b) have suggested that *S. tenacissima* could make use of water gains from AWAS in interspaces among tussocks. The main evidence (all gathered during summer) to support this hypothesis was that (1) the total AWAS water gain was very similar to the evaporation of soil under tussocks and bare soil calculated by CM, (2) the stomatal conductance of these tussocks was higher (from 21.8 to 43.1 mmol H₂O m⁻² s⁻¹, Ramírez et al., 2007a) in summer than found in other studies (from 0 to 0.08 mmol H₂O m⁻² s⁻¹, Balaguer et al., 2002; Pugnaire and Haase, 1996), and (3) *S. tenacissima* stands decoupled from the surrounding soil, located in places with high rock outcrops, showed greater stress symptoms (lower gas exchange rates and lower maximum photochemical efficiency of photosystem II) than stands in deep soil well connected with the tussocks. This evidence contradicts the paradigm that *S. tenacissima* is not able to make use of water gains from bare soil among tussocks (Puigdefábregas and Sánchez, 1996; Puigdefábregas et al., 1999).

Based on the above, supporting the hypothesis of water consumption from non-rainfall water gains in bare soil surrounding the tussock, Ramírez, Querejeta and Bellot (personal communication) designed a preliminary experiment with *S. tenacissima* using water enriched with a high concentration of Deuterium (it was mixed 20 ml of D₂O solution with 99.9% of D per liter of distilled water) as a tracer in the “El Ventós” experimental area (38°29'N; 0°37'W), Alicante Province, SE Spain. They detected significant isotopical composition of Deuterium (δD) enrichment in leaves (sampled from 9:00 to 10:00 h local time) after a water pulse in bare soil (Table 2), and also slight δD enrichment in leaves in the tussock upslope in water pulses applied 0.5 m downslope from the

tussock. This result confirms the aforementioned hypothesis and also a possible physiological integration mechanism among tillers in the tussock.

4. Needs for future research

Although several experimental field sites are monitored for net ecosystem carbon and water balance, further research is needed to characterise underlying processes and predict the impact of climate change on such balances on the ecosystems in dry and semiarid Mediterranean SE Spain. For such an extensive area, a high proportion of land use is agricultural (e.g., olive groves) in which gas exchange with atmosphere has yet to be measured. Thus, for understanding and monitoring regional carbon and water flows relating to land-use types, observations are needed in such agricultural systems. In addition, many years of continuous water and CO₂ measurements are required in order to characterise the response of different land-use types to desertification processes, post-fire management practices and climate variability. Regarding interpretation of carbon cycling over carbonate sites, it is imperative to supplement micrometeorological studies with other methodologies in order to discriminate between biological and abiotic components of the CO₂ fluxes. Such information could further be used to achieve reliable regional models based on inverse modelling and remote sensing.

Soil respiration is one of the main sources of carbon loss in arid and semiarid ecosystems. Despite the large amount of research in soil respiration over the last decade, semiarid ecosystems are much less studied than other ecosystems (Subke et al., 2006). Consequently, little is known about the temporal and spatial dynamics of soil respiration in these regions. Although some insights and major directions of research are starting to emerge from recent studies, more work on this subject is needed.

Soil water content is a crucial variable controlling both the carbon and water balances at ecosystem scale, especially in arid and semiarid climates. Since SWC is a key variable in the functioning of semiarid ecosystems and due to its high spatial heterogeneity, more research is needed to be able to characterise the soil water balance of more ecosystems in semiarid SE Spain, and to estimate this variable accurately. Important research efforts have been done to calculate SWC from satellite observations of microwave radiation (Dolman and de Jeu, 2010) that in the future could be key to improve the estimation of this variable in semiarid SE Spain.

In view of the importance of non-rainfall water gains in semiarid environments, this phenomenon should be studied in depth, testing different substrates (e.g. soil mixed with stone, gravel or mulch) on water gains from AWAS or dew in Mediterranean semiarid areas. This would also provide an additional source of water for vegetation in the dry summers, thus improving ecological restoration activities in these environments.

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Table 2

Average Deuterium isotope composition (δD, ‰) ± standard error (*n* = 10) in water in *Stipa tenacissima* leaves located on the growing front (downslope, GF) and in the terracette (upslope, T) of the tussock before (11th December, 2007) and after (14th December, 2007) an enriched water pulse from 0.1 to 0.5 m downslope from the individuals assessed. The water pulse was simulated by filling 5 holes (0.02 m diameter and 0.1 m deep) with water enriched with δD (2%). The repeated measures 2-way ANOVA with time as a factor only detected significant differences in Time (*F* = 9.32, *p* = 0.01).

	GF	T	0.1m	0.5m
Before	3.1 ± 1.9	5.0 ± 1.2	3.9 ± 1.9	4.3 ± 1.3
After	11.4 ± 2.4	6.7 ± 0.8	7.2 ± 1.1	12.3 ± 2.6

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References

- Agam (Ninari), N., Berliner, P., 2004. Diurnal changes in the bare soil of a coastal desert. *Journal of Hydrometeorology* 5, 922–933.
- Agam, N., Berliner, P.R., 2006. Dew formation and water vapor adsorption in semi-arid environments – a review. *Journal of Arid Environments* 65, 572–590.
- Almagro, M., López, J., Querejeta-Mercader, J.I., Hernández, T., 2009. Temperature dependence of soil CO₂ efflux is strongly modulated by seasonal patterns of moisture availability in a Mediterranean ecosystem. *Soil Biology and Biochemistry* 41, 594–605.
- Amiro, B.D., MacPherson, J.L., Desjardins, R.L., Chen, J.M., Liu, J., 2003. Post-fire carbon dioxide fluxes in the western Canadian boreal forest: evidence from towers, aircraft and remote sensing. *Agricultural and Forest Meteorology* 115, 91–107.
- Archer, N., Hess, T., Quinton, J., 2002. The water balance of two semi-arid shrubs on abandoned land in South-Eastern Spain after cold season rainfall. *Hydrology and Earth System Sciences* 6 (5), 913–926.
- Asner, G.P., 1998. Biophysical and biochemical sources of variability in canopy reflectance. *Remote Sensing of Environment* 64 (3), 234–253.
- Aubinet, M., Grelle, A., Ibrom, A., Rannik, Ü, Moncrieff, J.B., Foken, T., Kowalski, A.S., Martin, P.H., Bernbigier, P., Bernhofer, C., Clement, R., Elbers, J.A., Granier, A., Grünwald, T., Morgenstern, K., Pilegaard, K., Rebmann, C., Snijders, W., Valentini, R., Vesala, T., 2000. Estimates of the annual net carbon and water exchange of forests: the EUROFLUX methodology. *Advances in Ecological Research* 30, 113–173.
- Balaguer, L., Pugnare, F.I., Martínez-Ferri, E., Armas, C., Valladares, F., Manrique, E., 2002. Ecophysiological significance of chlorophyll loss and reduced photochemical efficiency under extreme aridity in *Stipa tenacissima* L. *Plant and Soil* 240, 343–352.
- Baldocchi, D.D., 2003. Assessing the eddy covariance technique for evaluating carbon dioxide exchange rate of ecosystem: past, present and future. *Global Change Biology* 9, 479–492.
- Baldocchi, D.D., 2008. Breathing of the terrestrial biosphere: lessons learned from a global network of carbon dioxide flux measurement systems. *Australian Journal of Botany* 56 (1), 1–26.
- Baldocchi, D.D., Falge, E., Gu, L., Olson, R., Hollinger, D., Running, D., Anthoni, P.M., Bernhofer, C., Davis, K.J., Evans, R., Fuentes, J.D., Goldstein, A.H., Katul, G.G., Law, B.E., Lee, Z., Malhi, Y., Meyers, T.P., Munger, W., Oechel, W., Paw, U.K.T., Pilegaard, K., Schmid, H.P., Valentini, R., Verma, S.B., Vesala, T., Wilson, K.B., Wofsy, S.C., 2001. FLUXNET: a new tool to study the temporal and spatial variability of ecosystem-scale carbon dioxide, water vapor, and energy flux densities. *Bulletin of the American Meteorological Society* 82, 2415–2434.
- Baldocchi, D.D., Luxmoore, R.J., Hatfield, J.L., 1991. Discerning the forest from the trees: an essay on scaling canopy stomatal conductance. *Agricultural and Forest Meteorology* 54, 197–226.
- Beringer, J., Hutley, L.B., Tapper, N.J., Coutts, A., Kerley, A., O'Grady, A.P., 2003. Fire impacts on surface heat, moisture and carbon fluxes from a tropical savanna in Northern Australia. *International Journal of Wildland Fire* 12, 333–340.
- Berni, J.A.J., Zarco-Tejada, P.J., Sepulcre-Cantó, G., Fereres, E., Villalobos, F., 2009. Mapping canopy conductance and CWSI in olive orchards using high resolution thermal remote sensing imagery. *Remote Sensing of Environment* 113 (11), 2380–2388.
- Beyschlag, W., Ryel, R.J., 2007. Canopy photosynthesis modeling. In: Pugnare, F.I., Valladares, F. (Eds.), *Functional Plant Ecology*. CRC Press, Taylor & Francis Group, New York, pp. 627–653.
- Bisht, G., Venturini, V., Islam, S., Jiang, L., 2005. Estimation of the net radiation using MODIS (Moderate Resolution Imaging Spectroradiometer) data for clear sky days. *Remote Sensing of Environment* 97, 52–67.
- Blackburn, G.A., 1998. Spectral indices for estimating photosynthetic pigment concentrations: a test using senescent tree leaves. *International Journal of Remote Sensing* 19 (4), 657–675.
- Boer, M.M., Puigdefábregas, J., 2005. Assessment of dryland condition using spatial anomalies of vegetation index values. *International Journal of Remote Sensing* 26 (18), 4045–4065.
- Bond-Lamberty, B., Peckham, S.D., Ahl, D.E., Gower, S.T., 2007. Fire as the dominant driver of central Canadian Boreal forest carbon balance. *Nature* 450, 89–93.
- Brenner, A.J., Incoll, L.D., 1997. The effect of clumping and stomatal response on evaporation from sparsely vegetated shrublands. *Agricultural and Forest Meteorology* 84 (3–4), 187–205.
- Brogaard, S., Runnström, M., Seaquist, J.W., 2005. Primary production of Inner Mongolia, China, between 1982 and 1999 estimated by a satellite data-driven light use efficiency model. *Global and Planetary Change* 45 (4), 313–332.
- Cantón, Y., Villagarcía, L., Moro, M.J., Serrano-Ortiz, P., Were, A., Alcalá, F.J., Kowalski, A.S., Solé-Benet, A., Lázaro, R., Domingo, F., 2010. Temporal dynamics of soil water balance components in a karst range in southeastern Spain: estimation of potential recharge. *Hydrological Sciences Journal* 55 (5), 1–17.
- Carlson, T.N., Capehart, W.J., Gillies, R.R., 1995. A new look at the simplified method for remote-sensing of daily evapotranspiration. *Remote Sensing of Environment* 54, 161–167.
- Castro, J., Allen, C.D., Molina-Morales, M., Marañón-Jiménez, S., Sánchez-Miranda, A., Zamora, R., 2011. Salvage logging versus the use of burnt wood as a nurse object to promote post-fire tree seedling establishment. *Restoration Ecology* 19 (4), 537–544.
- Chehbouni, A., Watts, C., Kerr, Y.H., Dedieu, G., Rodriguez, J.-C., Santiago, F., Cayrol, P., Boulet, G., Goodrich, D.C., 2000. Methods to aggregate turbulent fluxes over heterogeneous surfaces: application to SALSA data set in Mexico. *Agricultural and Forest Meteorology* 105 (1–3), 133–144.
- Christensen, J.H., Hewitson, B., Busuioac, A., Chen, A., Gao, X., Held, I., Jones, R., Kolli, R.K., Kwon, W.-T., Laprise, R., Rueda, V.M., Mearns, L., Menéndez, C.G., Räisänen, J., Rinke, A., Whetton, A.S.P., 2007. Regional climate projections. Contribution of working group I to the fourth assessment report of the intergovernmental panel on climate change. In: Solomon, S., Qin, D., Manning, M., Chen, Z., Marquis, M., Averyt, K.B., Tignor, M., Miller, H.L. (Eds.), *Climate Change 2007: The Physical Science Basis*. Cambridge University Press, Cambridge, pp. 847–943.
- Cleugh, H.A., Leuning, R., Mu, Q., Running, S.W., 2005. Regional evaporation estimates from flux tower and MODIS satellite data. *Remote Sensing of Environment* 106, 285–304.
- Conard, S.G., Ivanova, G.A., 1997. Wildfire in Russian boreal forests-potential impacts of fire regime characteristics on emissions and global carbon balance estimates. *Environmental Pollution* 98 (3), 305–313.
- Conant, R.T., Klopatek, J.M., Klopatek, C.C., 2000. Environmental factors controlling soil respiration in three semiarid ecosystems. *Soil Science Society American Journal* 64, 383–390.
- Contreras, S., Boer, M.M., Alcalá, F.J., Domingo, F., García, M., Pulido-Bosch, A., Puigdefábregas, J., 2008. An ecohydrological modelling approach for assessing long-term recharge rates in semiarid karstic landscapes. *Journal of Hydrology* 351 (1–2), 42–57.
- Courault, D., Seguin, B., Olioso, A., 2005. Review on estimation of evapotranspiration from remote sensing data: from empirical to numerical modeling approaches. *Irrigation and Drainage Systems* 19 (3–4), 223–249.
- Dabberdt, W.F., Lenschow, D.H., Horst, T.W., Zimmerman, P.R., Oncley, S.P., Delany, A.C., 1993. Atmosphere-surface exchange measurements. *Science* 260, 1472–1481.
- Diaz-Hernandez, J.L., Barahona Fernandez, E., Linares Gonzalez, J., 2003. Organic and inorganic carbon in soils of semiarid regions: a case study from the Guadix-Baza basin (Southeast Spain). *Ecohermia* 114, 65–80.
- D'Odorico, P., Porporato, A., 2006. Geohydrology of arid and semiarid ecosystems: an Introduction. In: D'Odorico, P., Porporato, A. (Eds.), *Dryland Ecohydrology*. Springer, Netherlands, pp. 4–10. doi:10.1007/1-4020-4260-4_15.
- Dolman, A.J., de Jeu, R.A.M., 2010. Evaporation in focus. *Nature Geoscience* 3 (5), 296.
- Dolman, A.J., Noilhan, J., Durand, P., Sarrat, C., Brut, C., Pignat, B., Butet, A., Jarosz, N., Brunet, Y., Loustau, D., Lamaud, E., Tol, L., Ronda, R., Miglietta, F., Gioli, B., Magliulo, V., Esposito, M., Gerbig, C., Körner, S., Glademard, P., Ramonet, M., Ciais, P., Neininger, B., Hutjes, R.W.A., Elbers, J., Matcatangay, R., Schrems, O., Pérez-Landa, G., Sanz, M.J., Scholz, Y., Facon, G., Caschia, E., Beziat, P., 2006. The CARBOEUROPE regional experiment strategy. *American Meteorological Society*, 1367–1379. doi:10.1175/BAMS-87-10-1367. October.
- Domingo, F., Brenner, A.J., Gutiérrez, L., Clark, S.C., Incoll, L.D., Aguilera, C., 2003. Water relations only partly explain the distributions of three perennial plants species in a semi-arid environment. *Biologia Plantarum* 46 (2), 257–262.
- Domingo, F., Gutiérrez, L., Brenner, A.J., Aguilera, C., 2002. Limitation to carbon assimilation of two perennial species in semi-arid south east Spain. *Biologia Plantarum* 45 (2), 213–220.
- Domingo, F., Sánchez, G., Moro, M.J., Brenner, A.J., Puigdefábregas, J., 1998. Measurement and modelling of rainfall interception by three semi-arid canopies. *Agricultural and Forest Meteorology* 91 (3–4), 275–292.
- Domingo, F., Villagarcía, L., Brenner, A.J., Puigdefábregas, J., 1999. Evapotranspiration model for semi-arid shrub-lands tested against data from SE Spain. *Agricultural and Forest Meteorology* 95 (2), 67–84.
- Domingo, F., Villagarcía, L., Brenner, A.J., Puigdefábregas, J., 2000. Measuring and modelling the radiation balance of heterogeneous shrubland. *Plant, Cell and Environment* 23, 27–39.
- Domingo, F., Villagarcía, L., Boer, M., Alados-Arboledas, L., Puigdefábregas, J., 2001. Evaluating the long-term water balance of arid zone stream bed vegetation using evapotranspiration modelling and hillslope runoff measurements. *Journal of Hydrology* 243 (1–2), 17–30.
- Emmerich, W.E., 2003. Carbon dioxide fluxes in a semiarid environment with high carbonate soils. *Agricultural and Forest Meteorology* 116, 91–102.
- Gamon, J.A., Peñuelas, J., Field, C.B., 1992. A narrow-waveband spectral index that tracks diurnal changes in photosynthetic efficiency. *Remote Sensing of Environment* 41 (1), 35–44.
- Gamon, J.A., Rahman, A.F., Dungan, J.L., Schildhauer, M., Huemmrich, K.F., 2006. Spectral Network (SpecNet)—What is it and why do we need it? *Remote Sensing of Environment* 103 (3), 227–235.
- Gao, B.C., 1996. NDWI — a normalized difference water index for remote sensing of vegetation liquid water from space. *Remote Sensing of Environment* 58 (3), 257–266.
- García, E., 2006. Efecto de la estructura de la copa en la partición de lluvia. Ph D thesis. University of Almería, Almería, Spain. pp. 404.
- García, M., Contreras, S., Domingo, F., Puigdefábregas, J., 2009. Mapping land degradation risk: potential of the non-evaporative fraction using Aster and MODIS data. In: Roeder, A., Hill, J. (Eds.), *Recent Advances in Remote Sensing*

- and Geoinformation Processing for Land Degradation Assessment. CRC Press (Taylor & Francis), Boca Raton, London, New York, Leiden, pp. 261–280. isbn: 978-0-415-39769-8.
- García, M., Fernández-Abad, F., Villagarcía, L., Palacios-Orueta, A., Puigdefábregas, J., Domingo, F., 2008a. Estimating latent and sensible heat fluxes using the temperature vegetation dryness index (TVDI) and MODIS data. In: IGARSS'08. Proceedings of the International and Remote Sensing Symposium July, 2008, Boston (USA), IEEE, Piscataway (N.J.), pp. 867–870. 3.
- García, M., Oyonarte, C., Villagarcía, L., Contreras, S., Domingo, F., Puigdefábregas, J., 2008b. Monitoring land degradation risk using ASTER data: the non-evaporative fraction as an indicator of ecosystem function. *Remote Sensing of Environment* 112 (9), 3720–3736.
- García, M., Villagarcía, L., Contreras, S., Domingo, F., Puigdefábregas, J., 2007. Comparison of three operative models for estimating the surface water deficit using ASTER reflective and thermal data. *Sensors* 7, 860–883.
- Gillies, R.R., Carlson, T.N., Cui, J., Kustas, W.P., Humes, K.S., 1997. A verification of the 'triangle' method for obtaining surface soil water content energy fluxes from remote measurements of the normalized difference vegetation index (NDVI) and surface radiant temperature. *International Journal of Remote Sensing* 18 (15), 3145–3166.
- Haase, P., Pugnaire, F.I., Fernández, E.M., Puigdefábregas, J., Clark, S.C., Incoll, L.D., 1996. An investigation of rooting depth of the semiarid shrub *Retama sphaerocarpa* (L.) Boiss. by labelling of ground water with a chemical tracer. *Journal of Hydrology* 177, 23–31.
- Haase, P., Pugnaire, F., Clark, S.C., Incoll, L., 1999. Environmental control of canopy dynamics and photosynthetic rate in the evergreen tussock grass *Stipa tenacissima*. *Plant Ecology* 145, 327–339.
- Hilker, T., Coops, N.C., Wulder, M.A., Black, T.A., Guy, R.D., 2008. The use of remote sensing in light use efficiency based models of gross primary production: a review of current status and future requirements. *Science of the Total Environment* 404 (2–3), 411–423.
- Houborg, R., Anderson, M.C., Norman, J.M., Wilson, T., Meyers, T., 2009. Intercomparison of a 'bottom-up' and 'top-down' modeling paradigm for estimating carbon and energy fluxes over a variety of vegetative regimes across the U.S. *Agricultural and Forest Meteorology* 149 (11), 1875–1895.
- Houghton, R.A., 2002. Terrestrial carbon sink. *Biologist* 49 (4), 155–160.
- Huete, A.R., Jackson, R.D., 1987. Suitability of spectral indices for evaluating vegetation characteristics on arid rangelands. *Remote Sensing of Environment* 23 (2), 213–232.
- Huxman, T.E., Snyder, K.A., Tissue, D., Leffler, A.J., Ogle, K., Pockman, W.T., Sandquist, D.R., Potts, D.L., Schwinning, S., 2004. Precipitation pulses and carbon fluxes in semiarid and arid ecosystems. *Oecologia* 141, 254–268.
- Inglisma, I., Alberti, G., Bertolini, T., Vaccari, F.P., Gioli, B., Miglietta, F., Cotrufo, M.F., Peressotti, A., 2009. Precipitation pulses enhance respiration of Mediterranean ecosystems: the balance between organic and inorganic components of increased soil CO₂ efflux. *Global Change Biology* 15, 1289–1301.
- Janssens, I.A., Freibauer, A., Schlamadinger, B., Ceulemans, R., Ciais, P., Dolman, A.J., Heimann, M., Nabuurs, G.-J., Smith, P., Valentini, R., Schulze, E.-D., 2005. The carbon budget of terrestrial ecosystems at country-scale: a European case study. *Biogeosciences* 2 (1), 15–26.
- Jarvis, P.G., 1995. Scaling processes and problems. *Plant Cell and Environment* 18, 1079–1089.
- Jarvis, P.G., Rey, A., Petsikos, C., Wingate, L., Rayment, M., Pereira, J., Banza, J., David, J., Miglietta, F., Borghetti, M., Manca, G., Valentini, R., 2007. Drying and wetting of soils stimulates decomposition and carbon dioxide emission: the "Birch Effect". *Tree Physiology* 27, 929–940.
- Jia, B., Zhou, G., Wang, Y., Wang, F., Wang, X., 2006. Effects of temperature and soil water content on soil respiration of grazed and ungrazed *Leymus chinensis* steppes, Inner Mongolia. *Journal of Arid Environments* 67, 66–76.
- Jiang, L., Islam, S., 2001. Estimation of surface evaporation map over southern Great Plains using remote sensing data. *Water Resources Research* 37, 329–340.
- Kieft, T.L., White, C.S., Loptin, S.A.R., Aguilar, R., Craig, J.A., Skaar, D.A., 1997. Temporal dynamics in soil carbon and nitrogen resources at a grassland shrubland ecotone. *Ecology* 79, 671–683.
- Kljun, N., Calanca, P., Rotach, M.W., Schmid, H.P., 2004. A simple parameterisation for flux footprint predictions. *Boundary-Layer Meteorology* 112 (3), 503–523.
- Kosmas, C., Danalatos, N.G., Poesen, J., van Wesemael, B., 1998. The effect of water vapor adsorption on soil moisture content under Mediterranean climatic conditions. *Agricultural Water Management* 36, 157–168.
- Kosmas, C., Marathianou, M., Gerontidis, St., Detsis, V., Tsara, M., Poesen, J., 2001. Parameters affecting vapor adsorption by the soil under semi-arid climatic conditions. *Agricultural Water Management* 48, 61–78.
- Kowalski, A.S., Loustau, D., Berbigier, P., Manca, G., Tedeschi, V., Borghetti, M., Valentini, R., Pasikolari, Berninger, F., Rannik, Ü, Hari, P., Rayment, M., Mencuccini, M., Moncrieff, J.B., Grace, J., 2004. Paired comparisons of carbon exchange between undisturbed and regenerating stands in four managed forests in Europa. *Global Change Biology* 10, 1–17.
- Kowalski, A.S., Serrano-Ortiz, P., Janssens, I.A., Sánchez-Moral, S., Cuezva, S., Domingo, F., Alados-Arboledas, L., 2008. Can flux tower research neglect geochemical CO₂ exchange? *Agricultural and Forest Meteorology* 148 (6–7), 1045–1054.
- Kruijt, B., Onger, S., Jarvis, P.G., 1997. Scaling of PAR absorption, photosynthesis and transpiration from leaves to canopy. In: Van Gardinen, P.R., Foody, G.M., Curran, P.J. (Eds.), *Scaling Up: From the Cell to Landscape*. Society for Experimental Biology Seminar Series, vol. 63. Cambridge University Press, Cambridge, pp. 79–104.
- Kustas, W.P., Norman, J.M., 1996. Use of remote sensing for evapotranspiration monitoring over land surfaces. *Hydrological Sciences Journal-Journal des Sciences Hydrologiques* 41, 495–516.
- Lasslop, G., Reichstein, M., Papale, D., Richardson, A.D., Almut, A., Barr, A., Stoy, P., Wohlfahrt, G., 2010. Separation of net ecosystem exchange into assimilation and respiration using a light response curve approach: critical issues and global evaluation. *Global Change Biology* 16, 187–208.
- Law, B.E., Falge, E., Gu, L., Baldocchi, D.D., Bakwin, P., Berbigier, P., Davis, K., Dolman, A.J., Falk, M., Fuentes, J.D., Goldstein, A., Granier, A., Grelle, A., Hollinger, D., Janssens, I.A., Jarvis, P., Jensen, N.O., Katul, G., Mahli, Y., Matteucci, G., Meyers, T., Monson, R., Munger, W., Oechel, W., Olson, R., Pilegaard, K., Paw, U.K.T., Thorgeirsson, H., Valentini, R., Verma, S., Vesala, T., Wilson, K., Wofsy, S., 2002. Environmental controls over carbon dioxide and water vapor exchange of terrestrial vegetation. *Agricultural and Forest Meteorology* 113 (1–4), 97–120.
- Levitt, J., 1980. Responses of plant to environmental stresses. Academic Press, New York.
- Leuning, R., Zhang, Y.Q., Rajaud, A., Cleugh, H., Tu, K., 2008. A simple surface conductance model to estimate regional evaporation using MODIS leaf area index and the Penman–Monteith equation. *Water Resources Research* 44 (10), W10419.
- Liu, W., Zhang, Z., Wan, S., 2009. Predominant role of water in regulating soil and microbial respiration and their responses to climate change in a semiarid grassland. *Global Change Biology* 15, 184–195.
- Luo, Y., Zhou, X., 2006. Soil respiration and the environment. Academic Press/Elsevier, San Diego, CA.
- Luyssaert, S., Inglima, I., Jung, M., Richardson, A.D., Reichstein, M., Papale, D., Piao, S.L., Schulze, E.D., Wingate, L., Matteucci, G., Aragao, L., Aubinet, M., Beer, C., Bernhofer, C., Black, K.G., Bonal, D., Bonnefond, J.M., Chambers, J., Ciais, P., Cook, B.D., Davis, K.J., Dolman, A.J., Gielen, B., Goulden, M., Grace, J., Granier, A., Grelle, A., Griffis, T., Grünwald, T., Guidolotti, G., Hanson, P.J., Harding, R., Hollinger, D.Y., Hutyrá, L.R., Kolar, P., Kruijt, B., Kutsch, W., Lagergren, F., Laurila, T., Law, B.E., Le Maire, G., Lindroth, A., Loustau, D., Malhi, Y., Mateus, J., Migliavacca, M., Misson, L., Montagnani, L., Moncrieff, J., Moors, E., Munger, J.W., Nikinmaa, E., Ollinger, S.V., Pita, G., Rebmann, C., Roupsard, O., Saigusa, N., Sanz, M.J., Seufert, G., Sierra, C., Smith, M.L., Tang, J., Valentini, R., Vesala, T., Janssens, I.A., 2007. CO₂ balance of boreal, temperate, and tropical forests derived from a global database. *Global Change Biology* 13 (12), 2509–2537.
- Maestre, F.T., Cortina, J., 2003. Small-scale spatial variation in soil CO₂ efflux in a Mediterranean semiarid steppe. *Applied Soil Ecology* 23, 199–209.
- Maestre, F.T., Cortina, J., 2006. Ecosystem structure and soil-surface condition drive the variability in the foliar δ¹³C and δ¹⁵N of *Stipa tenacissima* in semiarid Mediterranean steppes. *Ecological Restoration* 21, 44–53.
- Mahadevan, P., Wofsy, S.C., Matross, D.M., Xiao, X., Dunn, A.L., Lin, J.C., Gerbig, C., Munger, J.W., Chow, V.Y., Gottlieb, E.W., 2008. A satellite-based biosphere parameterization for net ecosystem CO₂ exchange: Vegetation Photosynthesis and Respiration Model (VPRM). *Global Biogeochemical Cycles* 22, GB2005. doi:10.1029/2006GB002735.
- Marion, G.M., Verburgh, P.S.J., McDonald, E.V., Arnone, J.A., 2008. Modeling salt movement through a Mojave Desert soil. *Journal of Arid Environments* 72, 1009–1030.
- MIMAM, 2007. Datos estadísticos de coyuntura medioambiental 2000–2004. Ministerio de Medio Ambiente. http://www.mma.es/portal/secciones/info_estadistica_ambiental/estadisticas_info/informes_coyuntura/sintesis_datos/index.htm.
- Monger, H.C., Gallegos, R.A., 2000. Biotic and abiotic processes and rates of pedogenic carbonate accumulation in the southwestern United States—relationship to atmospheric CO₂ sequestration. In: Lal, R., Kimble, J.M., Eswararn, H., Stewart, B.A. (Eds.), *Global Climatic Change and Pedogenic Carbonates*. CRC Press, Boca Raton, FL, pp. 273–289.
- Monteith, J.L., 1972. Solar radiation and productivity in tropical ecosystems. *Journal of Applied Ecology* 9, 747–766.
- Moore, D.J.P., Hu, J., Sacks, W.J., Schimel, D.S., Monson, R.K., 2008. Estimating transpiration and the sensitivity of carbon uptake to water availability in a subalpine forest using a simple ecosystem process model informed by measured net CO₂ and H₂O fluxes. *Agricultural and Forest Meteorology* 148 (10), 1467–1477.
- Moran, M.S., Kustas, W.P., Vidal, A., Stannard, D.I., Blanford, J.H., Nichols, W.D., 1994. Use of ground-based remotely sensed data for surface energy balance evaluation of a semiarid rangeland. *Water Resources Research* 30 (5), 1339–1350.
- Morillas, L., García, M., Zarco-Tejada, P., Ladrón de Guevara, M., Villagarcía, L., Were, A., Domingo, F., 2009. Derivation of the canopy conductance from surface temperature and spectral indices for estimating evapotranspiration in semiarid vegetation. In: Romero Díaz, A., Belmonte Serrato, F., Alonso Sarria, F., López Bermúdez, F. (Eds.), *Advances in Studies on Desertification*. Servicio Publicaciones Universidad de Murcia EDITUM, Murcia, ISBN 978-84-8371-888-9, pp. 583–586.
- Morillas, L., Ucles, O., Sanchez-Cañete, E.P., García, M., Villagarcía, L., Serrano-Ortiz, P., Solé-Benet, A., Domingo, F., 2011. Improving evapotranspiration estimates in semiarid ecosystems: the role of soil evaporation. 12th European Ecological Federation (EEF) Congress, 25–29 September 2011 Avila, Spain.
- Morillas, L., Were, A., Serrano-Ortiz, P., García, M., Villagarcía, L., Kowalski, A.S., Domingo, F., 2008. Estimación de la radiación neta a escala diaria/diurna a partir de datos instantáneos para la determinación de la evapotranspiración

- real mediante teledetección en medios semiáridos. In: López-Geta, J.A., Rubio Campos, J.C., Martín-Machuca, M. (Eds.), VII Simposio sobre el agua en Andalucía, Instituto Geológico y Minero de España, Madrid, vol. I, ISBN 978-84-7840-761-3, pp. 219–228.
- Moro, M.J., Domingo, F., López, G., 2004. Seasonal transpiration pattern of *Phragmites australis* in a wetland of semi-arid Spain. *Hydrological Processes* 18 (2), 213–227.
- Moro, M.J., Were, A., Villagarcía, L., Cantón, Y., Domingo, F., 2007. Dew measurement by eddy covariance and wetness sensor in a semi-arid ecosystem of SE Spain. *Journal of Hydrology* 335, 295–302.
- Moro, M.J., Were, A., Morillas, L., Villagarcía, L., Cantón, Y., Lazaro, R., Kowalski, A., Domingo, F., 2009. Dew contribution to the water balance in a semi-arid coastal steppe ecosystem (Cabo de Gata, Spain). In: Romero Díaz, A., Belmonte Serrato, F., Alonso Sarria, F., López Bermúdez, F. (Eds.), *Advances in Studies on Desertification*. Servicio Publicaciones Universidad de Murcia EDITUM, Murcia, ISBN 978-84-8371-888-9, pp. 587–591.
- Nemani, R.R., Running, S.W., 1989. Testing a theoretical climate-soil-leaf area hydrologic equilibrium of forests using satellite data and ecosystem simulation. *Agricultural and Forest Meteorology* 44, 245–260.
- Norman, J.M., Kustas, W.P., Humes, K.S., 1995. Source approach for estimating soil and vegetation energy fluxes in observations of directional radiometric surface temperature. *Agricultural and Forest Meteorology* 77, 263–293.
- Okin, G.S., 2002. Toward a unified view of biophysical land degradation processes in arid and semi-arid lands. In: Reynolds, J.F., Stafford Smith, D.M. (Eds.), *Global Desertification: Do Humans Cause Deserts?* Dahlem University Press, Berlin, pp. 95–109.
- Pearcy, R.W., Yang, W., 1996. A three-dimensional crown architecture model for assessment of light capture and carbon gain by understory plants. *Oecologia* 108, 1–12.
- Potter, C., Klooster, S., Myneni, R., Genovese, V., Tan, P.-N., Kumar, V., 2003. Continental-scale comparisons of terrestrial carbon sinks estimated from satellite data and ecosystem modeling 1982–1998. *Global and Planetary Change* 39 (3–4), 201–213.
- Pugnaire, F.I., Haase, P., 1996. Comparative physiology and growth of two perennial tussock grass species in a semi-arid environment. *Annals of Botany* 77, 81–86.
- Pugnaire, F.I., Haase, P., Incoll, L., Clark, S.C., 1996. Response of tussock grass *Stipa tenacissima* to watering in a semi-arid environment. *Functional Ecology* 10, 265–274.
- Puigdefàbregas, J., Sánchez, G., 1996. Geomorphological implications of vegetation patchiness on semi-arid slopes. In: Anderson, M.G., Brooks, S.M. (Eds.), *Advances in Hillslopes Processes*. John Wiley & Sons Ltd, New York, pp. 1027–1060.
- Puigdefàbregas, J., Sole, A., Guitierrez, L., del Barrio, G., Boer, M., 1999. Scales and processes of water and sediment redistribution in drylands: results from the Rambla Honda field site in Southeast Spain. *Earth-Science Reviews* 48, 39–70.
- Pulido-Bosch, A., Pulido-Leboeuf, P., Molina-Sánchez, L., Vallejos, A., Martín-Rosales, W., 2000. Intensive agriculture, wetlands, quarries and water management. A case study (Campo de Dalías, SE Spain). *Environmental Geology* 40 (1–2), 163–168.
- Ramírez, D.A., Bellot, J., 2009. Linking population density and habitat structure to ecophysiological responses in semi-arid Spanish steppes. *Plant Ecology* 200 (2), 191–204.
- Ramírez, D.A., Bellot, J., Domingo, F., Blasco, A., 2007a. Stand transpiration of *Stipa tenacissima* grassland by sequential scaling and multi-source evapotranspiration modelling. *Journal of Hydrology* 342 (1–2), 124–133.
- Ramírez, D.A., Bellot, J., Domingo, F., Blasco, A., 2007b. Can water responses in *Stipa tenacissima* L. during the summer season be promoted by non-rainfall water gains in soil? *Plant and Soil* 291 (1–2), 67–79.
- Ramírez, D.A., Querejeta, J.I., Bellot, J., 2009. Bulk leaf $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ reflect the intensity of intraspecific competition for water in a semi-arid tussock grassland. *Plant Cell and Environment* 32 (10), 1346–1356.
- Ramírez, D.A., Valladares, F., Blasco, A., Bellot, J., 2006. Assessing transpiration in the tussock grass *Stipa tenacissima* L.: the crucial role of the interplay between morphology and physiology. *Acta Oecologica* 30 (3), 386–398.
- Ramírez, D.A., Valladares, F., Blasco, A., Bellot, J., 2008a. Effects of tussock size and soil water content on whole plant gas exchange in *Stipa tenacissima* L.: extrapolating from the leaf versus modelling crown architecture. *Environmental and Experimental Botany* 62 (3), 376–388.
- Ramírez, D.A., Valladares, F., Domingo, F., Bellot, J., 2008b. Seasonal water-use efficiency and chlorophyll fluorescence response in alpha grass (*Stipa tenacissima* L.) is affected by tussock size. *Photosynthetica* 46 (2), 222–231.
- Reichstein, M., Falge, E., Baldocchi, D., Papale, D., Aubinet, M., Berbigier, P., Bernhofer, C., Buchmann, N., Gilmanov, T., Granier, A., Grünwald, T., Havránková, K., Ilvesniemi, H., Janous, D., Knohl, A., Laurila, T., Lohila, A., Loustau, D., Matteucci, G., Meyers, T., Miglietta, F., Ourcival, J.M., Pumpanen, J., Rambal, S., Rotenberg, E., Sanz, M., Tenhunen, J., Seufert, G., Vaccari, F., Vesala, T., Yakir, D., Valentini, R., 2005. On the separation of net ecosystem exchange into assimilation and ecosystem respiration: review and improved algorithm. *Global Change Biology* 11, 1424–1439.
- Reverter, B.R., Sánchez-Cañete, E.P., Resco, V., Serrano-Ortiz, P., Oyonarte, C., Kowalski, A.S., 2010. Analyzing the major drivers of NEE in a Mediterranean alpine shrubland. *Biogeosciences* 7, 2601–2611.
- Rey, A., Pegoraro, E., Oyonarte, C., Were, A., Escribano, P., Raimundo, J., 2011. Impact of land degradation on soil respiration in a steppe (*Stipa tenacissima* L.) semi-arid ecosystem in the SE of Spain. *Soil, Biology and Biochemistry* 43, 393–403.
- Rey, A., Pegoraro, E., Tedeschi, V., DiParri, I., Jarvis, P.G., Valentini, R., 2002. Seasonal variability in soil respiration and its components in a coppice oak forest in central Italy. *Global Change Biology* 8, 1–18.
- Rey, A., Pepsikos, C., Jarvis, P.G., Grace, J., 2005. The effect of soil temperature and soil moisture on carbon mineralisation rates in a Mediterranean forest soil. *European Journal of Soil Science* 56, 589–599.
- Rodriguez-Iturbe, I., D'Odorico, P., Porporato, A., Ridolfi, L., 1999. On the spatial and temporal links between vegetation, climate, and soil moisture. *Water Resources Research* 35 (12), 3709–3722.
- Sandholt, I., Rasmussen, K., Andersen, J., 2002. A simple interpretation of the surface temperature/vegetation index space for assessment of surface moisture status. *Remote Sensing of Environment* 79 (2), 213–224.
- Schlesinger, W.H., 1982. Carbon storage in the caliche of arid soils: a case study from Arizona. *Soil Science* 133, 247–255.
- Schlesinger, W.H., Pilmanis, A., 1998. Plant cover-soil interactions in deserts. *Biogeochemistry* 42, 169–187.
- Schulze, E.-D., Gash, J.H.C., Freibauer, A., Luysaert, S., Ciais, P., 2009. CarboEurope-IP An Assessment of the European Terrestrial Carbon Balance. Germany.
- Schwinning, S., Sala, O.E., Loik, M.E., Ehleringer, J.R., 2004. Thresholds, memory, and seasonality: understanding pulse dynamics in arid/semi-arid ecosystems. *Oecologia* 141, 191–193.
- Seguin, B., Becker, F., Phulpin, T., Gu, X.F., Guyot, G., Kerr, Y., King, C., Lagouarde, J.P., Otle, C., Stoll, M.P., Tabbagh, A., Vidal, A., 1999. IRSUTE: a minisatellite project for land surface heat flux estimation from field to regional scale. *Remote Sensing of Environment* 68, 357–369.
- Seguin, B., Itier, B., 1983. Using midday surface-temperature to estimate daily evaporation from satellite thermal IR data. *International Journal of Remote Sensing* 4, 371–383.
- Sepulcre-Cantó, G., Zarco-Tejada, P.J., Jiménez-Muñoz, J.C., Sobrino, J.A., Soriano, M.A., Fereres, E., Vega, V., Pastor, M., 2007. Monitoring yield and fruit quality parameters in open-canopy tree crops under water stress. Implications for ASTER. *Remote Sensing of Environment* 107 (3), 455–470.
- Serrano-Ortiz, P., Domingo, F., Cazorla, A., Were, A., Cuezva, S., Villagarcía, L., Alados-Arboledas, L., Kowalski, A.S., 2009. Interannual CO₂ exchange of a sparse Mediterranean shrubland on a carbonaceous substrate. *Journal of Geophysical Research* 114, G04015. doi:10.1029/2009JG000983.
- Serrano-Ortiz, P., Kowalski, A.S., Domingo, F., Rey, A., Pegoraro, E., Villagarcía, L., Alados-Arboledas, L., 2007. Variations in daytime net carbon and water exchange in a montane shrubland ecosystem in southeast Spain. *Photosynthetica* 45 (1), 30–35.
- Serrano-Ortiz, P., Roland, M., Sánchez-Moral, S., Janssens, I.A., Domingo, F., Goddéris, Y., Kowalski, A.S., 2010a. Hidden, abiotic CO₂ flows and gaseous reservoirs in the terrestrial carbon cycle: review and perspectives. *Agricultural and Forest Meteorology* 150, 321–329.
- Serrano-Ortiz, P., Sánchez-Cañete, E.P., Domingo, F., Were, A., Villagarcía, L., Kowalski, A.S., 2010b. CO₂ fluxes in semi-arid sites on carbonate substrates located in southeast Spain. *Fluxletter the Newsletter of FLUXNET 2* (4), 16–18.
- Subke, J.A., Inglima, I., Cotrufo, M.F., 2006. Trends and methodological impacts in soil CO₂ partitioning: a meta-analytical review. *Global Change Biology* 12, 921–943.
- Stisen, S., Sandholt, I., Norgaard, A., Fensholt, R., Jensen, K.H.G., 2008. Combining the triangle method with thermal inertia to estimate regional evapotranspiration – applied to MSG-SEVIRI data in the Senegal River basin. *Remote Sensing of Environment* 112, 1242–1255.
- Swinbank, W.C., 1951. The measurement of vertical transfer of heat and water vapor by eddies in the lower atmosphere. *Journal of Meteorology* 8, 135–145.
- Tucker, C.J., Sellers, P.J., 1986. Satellite remote sensing of primary production. *International Journal of Remote Sensing* 7 (11), 1395–1416.
- UNEP, 1997. *World Atlas of Desertification*, second ed. United Nations Environment Programme, Nairobi, Kenya.
- Ustin, S.L., Gitelson, A.A., Jacquemoud, S., Schaepman, M., Asner, G.P., Gamon, J.A., Zarco-Tejada, P., 2009. Retrieval of foliar information about plant pigment systems from high resolution spectroscopy. *Remote Sensing of Environment* 113 (1), S67–S77.
- Vadillo, I., Soler, A., Benavente, J., Carrasco, F., Liñan, C., 2007. $\delta^{13}\text{C}$ CO₂ as indicator of sources of CO₂ in the unsaturated zone of a carbonated aquifer (Nerja Area, South of Spain). In: 7th International Symposium on Applied Isotope Geochemistry, Stellenbosch, South Africa, pp. 155–156.
- Valentini, R., Matteucci, G., Dolman, A.J., Schulze, E.-D., Rebmann, C., Moors, E.J., Granier, A., Gross, P., Jensen, N.O., Pilegaard, K., Lindroth, A., Grelle, A., Bernhofer, C., Grünwald, T., Aubinet, M., Ceulemans, R., Kowalski, A.S., Vesala, T., Rannik, Ü., Berbigier, P., Loustau, D., Guöndmonson, J., Thorgeirsson, H., Ibrom, A., Morgenstern, K., Clement, R., Moncrieff, J.B., Montagnani, L., Minerbi, S., Jarvis, P.G., 2000. Respiration as the main determinant of carbon balance in European forests. *Nature* 404, 861–865.
- Valladares, F., Pugnaire, F.I., 1999. Tradeoffs between irradiance capture and avoidance in semi-arid environments assessed with a crown architecture model. *Annals of Botany* 83, 459–469.
- Verhoef, A., Diaz-Espejo, A., Knight, J.R., Villagarcía, L., Fernandez, J.E., 2006. Adsorption of water vapor by bare soil in an olive grove in southern Spain. *Journal of Hydrometeorology* 7 (5), 1011–1027.
- Vilagrosa, A., Cortina, J., Rubio, E., Trubat, R., Chirino, E., Gil-Pelegrin, E., Vallejo, V.R.J., 2005. El papel de la ecofisiología en la restauración forestal de ecosistemas mediterráneos. *Investigación Agraria: Sistemas y Recursos Forestales* 14 (3), 446–461.

- Villagarcía, L., Were, A., Cantón, Y., Fernández, F., Moro, M.J., Domene, M.A., Solé-Benet, A., Domingo, F., 2004. Daily soil water content fluctuations in rangelands from semi-arid SE Spain. In: Tropeano, M., Arattano, M., Maraga, F., Pelissero, C. (Eds.), *Progress in Surface and Subsurface Water Studies at the Plot and Small Basin Scale*, ERB Euromediterranean Conference, CNR, ISBN 88-8080-053-1, pp. 72–75. Turin, Italy.
- Villagarcía, L., Were, A., Domingo, F., Garcia, M., Alados-Arbotedas, L., 2007. Estimation of soil boundary-layer resistance in sparse semiarid stands for evapotranspiration modelling. *Journal of Hydrology* 342 (1–2), 173–183.
- Villagarcía, L., Were, A., García, M., Domingo, F., 2010. Sensitivity of a clumped model of evapotranspiration to surface resistance parameterisations: application in a semi-arid environment. *Agricultural and Forest Meteorology* 150 (7–8), 1065–1078.
- Were, A., Villagarcía, L., Domingo, F., Alados-Arboledas, L., Puigdefabregas, J., 2007. Analysis of effective resistance calculation methods and their effect on modelling evapotranspiration in two different patches of vegetation in semi-arid SE Spain. *Hydrology and Earth System Sciences* 11 (5), 1529–1542.
- Were, A., Villagarcía, L., Domingo, F., Moro, M.J., Dolman, A.J., 2008. Aggregating spatial heterogeneity in a bush vegetation patch in semi-arid SE Spain: a multi-layer model versus a single-layer model. *Journal of Hydrology* 349 (1–2), 156–167.
- Were, A., Serrano-Oriz, P., Moreno de Jong, C., Villagarcía, L., Domingo, F., Kowalski, A.S., 2010. Ventilation of subterranean CO₂ and eddy covariance incongruities over carbonate ecosystems. *Biogeosciences* 7, 859–867.
- Wofsy, S.C., Goulden, M.L., Munger, J.W., Fan, S.-M., Bakwin, P.S., Daube, B.C., Bassow, S.L., Bazzaz, F.A., 1993. Net exchange of CO₂ in a mid-latitude forest. *Science* 260, 1314–1317.
- Zarco-Tejada, P.J., Rueda, C.A., Ustin, S.L., 2003. Water content estimation in vegetation with MODIS reflectance data and model inversion methods. *Remote Sensing of Environment* 85 (1), 109–124.