DROUGHT EFFECTS ON MULTI-SCALE WATER USE AND ECOSYSTEM CARBON EXCHANGE IN A DESERT ECOSYSTEM

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	キーワード (Ja):
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	作成者: Gu, Daxing
	メールアドレス:
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THESIS

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Daxing GU

Graduate School of
Science and Technology, Educational
Division

Environment and Energy Systems

Shizuoka University

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マルチスケールでの砂漠生態系における水利用及び生態系炭素交換に対する干ばつの影響

顧 大形

静 岡 大 学

大学院自然科学系教育部

環境･エネルギーシステム専攻

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ABSTRACT

Drought is an important factor markedly influencing biotic and abiotic processes and then have considerable effects on ecosystem key material and energy processes, such as water and carbon cycles over a wide region on the earth terrestrial surface. In arid and semi-arid lands, drought effects on ecosystem are more obvious even decisive. In the current study, drought effects on crucial water and carbon processes of typical desert ecosystem are examined at various scales based mainly on four-year field measurement via sap flow and gas exchange flux techniques. The studied ecosystem is dominated by a desert shrub, *Haloxylon ammodendron* and locates on the southern edge of Gurbantünggüt desert in Northwest China and Central Asia.

Transpiration per leaf area and stomatal conductance for water vapor at leaf, branch and whole plant scales and their response to air drought (atmosphere vapor pressure deficit, VPD) and other climate factors are compared in chapter 2. Daytime average transpiration and stomatal conductance at leaf scale were higher than that at branch and whole plant scales. High level of transpiration at leaf and branch scales appeared proximately at midday time while that of whole plant scale appeared at morning time, inducing reduced transpiration in 79% of daytime. Transpiration at the three scales showed similar response to photosynthesis photon flux density (PPFD), increasing with enhanced PPFD at low light condition and nearly saturating under high-level PPFD. Similarly, transpiration at three scales linearly increased with increasing VPD. Under high VPD, however, leaf- and branch-scale transpiration nearly saturated while that of whole plant-scale declined with increasing VPD. For stomatal conductance, its sensitivity to VPD (m/G_{sref}) decreased continually from 0.52 at whole plant scale to 0.35 at leaf scale. This showed that whole-plant average stomata was more sensitive to air drought and had more conservative water use strategy protecting whole plant water homeostasis compared with that at leaf and branch scales. The different magnitude of transpiration, stomatal conductance and their response to air drought could be only explained by canopy patchiness, which could reduce whole plant water loss and allow partial assimilation by part of the canopy under drought, which was considered as one of the key mechanisms to balance water loss and carbon acquisition at whole plant scale. Results obtained here enriched the database of multi-scale water use strategy of plants in xeric ecosystems and contributed to a better understanding of plant water use strategies in these ecosystems.

Canopy-scale transpiration and stomatal conductance for water vapor and their response to air drought (VPD) and soil drought (volumetric soil water content, SWC) are examined in chapter 3 during the second half of growing season, when annual prolonged drought occurs. The main data for this analysis is sap flow up-scaled canopy transpiration and derived canopy stomatal conductance from August to early October during 2013-2016. When SWC was less than 3%, canopy transpiration linearly increased with increasing PPFD and VPD in each year and the sensitivity of canopy transpiration to VPD (defined as the slope of linear regression between them, K) increased linearly with increasing SWC. At the same time, stomatal sensitivity to VPD (m/G_{sref}) decreased linearly from 0.52 to 0.35 with increasing annual average SWC, inducing a transfer from a more anisohydric to a more isohydric stomatal behavior with increasing soil drought. When SWC decreased less than 3%, canopy transpiration had no response to SWC, while the sensitivity to VPD of canopy transpiration and canopy stomatal conductance were higher and lower than that in the driest year when SWC larger than 3%, respectively. This results pointed out that 3% was the soil drought threshold for normal survival of *H. ammodendron*, below which this plant lost the ability in stomatal regulation on water loss and suffered the high risk of mortality. The flexibility of stomatal behavior to soil drought was one key strategy facilitating the survival of *H. ammodendron* in such an extreme dry environment and making a balance between maximizing carbon production when soil moisture was attractable and keeping hydraulic security when soil moisture was more limited. These results improved our knowledge on plant adaptive mechanism to extreme, prolonged droughts and are helpful to make more accurate evaluation of vulnerability of arid ecosystems under future climate change.

Chapter 4 introduces the soil drought effects on key processes of water and carbon cycles at ecosystem scale in the studied desert ecosystem. At last, whether ecosystem evaporative fraction (EF) can be used as a proxy of drought to trance soil drought effects on ecosystem assimilation and respiration in desert ecosystem is also tested. Water and carbon dioxide exchange between ecosystem and atmosphere measured through eddy covariance approach during growing season from 2013 to 2016 and derived ecosystem gross primary production (GPP) and respiration (R_{eco}) using ‘top-down’ model are employed for this analysis. Both ecosystem GPP and R_{eco} showed positive linear correlation with SWC, however, the sensitivity of GPP to SWC was 3.8 times higher than that of R_{eco} during the entire growing season. As a result, ecosystem carbon sequestration capacity decreased under soil drought. At intra-annual scale, significant correlation between GPP and SWC was found only in spring while that between R_{eco}

and SWC was found in all growing seasons and the sensitivity increased continually from spring to autumn. Ecosystem water use efficiency of gross carbon uptake (WUE) showed a weak correlation with SWC. Similarly, EF also had weak correlation with SWC and explained only 2% and 5% of variation of GPP and R_{eco}, respectively. Hence, EF was not a good proxy of soil drought and failed to trance the response of GPP and R_{eco} to soil drought, indicating energy partitioning was not tightly coupled with ecosystem carbon exchanges in this desert ecosystem. The seasonal variation of environment and vegetation in structure and phenology under drought was responsible for the special observed results in desert ecosystem under extreme drought.

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CHAPTER 1 GENERAL INTRODUCTION

1.1 Background

Climate change has been an obvious character of natural ecosystems spanning global scale in last one hundred years and is predicted to be continue in future (IPCC 2013). One of the main contribution to climate change is the increase in concentration of radiatively important gases in atmosphere, such as CO_2, CH_4 and N_2O, largely as a result of direct and/or indirect effect of human activities (Hansen and Lacis 1990, Montzka et al. 2011). Changes in important greenhouse gases components of atmosphere alter the global radiation balance and then impact energy partitioning and balance at lower atmosphere, as a result, global surface air temperature and water cycle were affected profoundly (Cox et al. 2000, Huntington 2006).

Although uncertainties still exist, Water cycle was proved by substantial evidences to be enhanced through altered rainfall and evapotranspiration regimes, following which regional and temporal hydrologic budgets was modified. Regional average precipitation increased by 7-12% in the north hemisphere (30°N~85°N), increased by 2% in the southern hemisphere (0°S~55°S), together with a substantial decrease in some regions (Houghton et al. 2001). Similarly, continental runoff of major rivers also showed an increase trend during the 20th century (Probst and Tardy 1987, Labat et al. 2004). An increasing trend of evapotranspiration and decreasing trend of pan-evaporation during post-WW to 1990 based on measured data was also observed (Golubev et al. 2001). Another two studies also concluded that evapotranspiration increased based on continental-scale water balance studies, in which precipitation increased greater than that of runoff during 1950-2000 in America (Milly and Dunne 2001, Walter et al. 2004). However, in another hand, drying trend was suggested to be obvious during the last half century over a majority of Africa, Asia, Australia, Europe, Alaska and Canada based on both Palmer Drought Severity Index (PDSI) and soil moisture (Dai 2011). By assessing global PDSI, a conclution was got that drought might not be caused by increasing heat from global warming but drought was expected to be quicker and more intense when it occur (Trenberth et al. 2014). Global land evapotranspiration was showed to have decline trend recently (1998-2008) and the limitation of soil water in the Southern Hemisphere was the primary driver, according to one analysis conducted based on multiple databases (Jung et al. 2010b). Notwithstanding the tendency of climate change and its effects on hydrological cycle varied depending on location and timing and there are many uncertainties, climate change was expected to lead to changes in the likelihood of occurrence or strength of extreme weather and climate events or both based on various studies. Drought is one of the most probable results along with the development of climate change and extreme weather and climate events.

Drought is a key ecological variable affecting terrestrial ecosystem functions across the word and always determined by the imbalance between water supply (i.e., soil water availability, precipitation) and water demand (i.e., transpiration, evaporation) (Dai 2011). Hence, understanding and assessing the consequences of soil and atmosphere drought on natural ecosystem processes are emerging. Drought effects on plant physiology mainly focused on transpiration (Kume et al. 2007, Hasselquist et al. 2010, Naithani et al. 2012, Grossiord et al. 2014) and photosynthetic capacity (Calvet et al. 2004, Centritto et al. 2011) that correlated with CO_2 and water vapor exchanges, at leaf (Blackman et al. 2009, Swarthout et al. 2009, Doughty et al. 2015), canopy (Crosbie et al. 2007, Gartner et al. 2009, Schafer 2011) and ecosystem scales (Ciais et al. 2005, Dong et al. 2011, van der Molen et al. 2011, Gatti et al. 2014, Rajan et al. 2015, Hoover and Rogers 2016). Abundant studies have showed that drought effect on plant are species (Cunningham 2004, Gartner et al. 2009, Du et al. 2011, Grossiord et al. 2014), age (Gao et al. 2015), environment (Yang et al. 2009, Chen et al. 2014b, Li and Li 2014, Bourne et al. 2015), functional type (Fisher et al. 2007, Franks et al. 2007, Welp et al. 2007, Farooq et al. 2010), and also drought intensity (Hoover and Rogers 2016) and timing (Kumagai and Porporato 2012, Gorai et al. 2015, Jia et al. 2016) dependent. Published literatures on drought effects on plant are mainly concentrate upon humid- and semi humid area and semi-arid ecosystems where drought occurred occasionally or short-time lastingly or non-extremely (Harris et al. 2004, Fisher et al. 2007, Igarashi et al. 2015). However, the related studies on plant response to drought in arid lands are relative rare and lead large uncertainties in accessing feedbacks from arid ecosystems to drought and in projecting ecosystem trend in future under changing climate.

Drylands are commonly defined as regions where characterized with low precipitation and high potential evapotranspiration, or low ratio of total annual precipitation to potential evapotranspiration (0.05-0.65) (Glenn et al. 1993, Lal 2004). These regions are the home for more than 38% of the total population in the word, and account for about 41% of the global terrestrial surface and are estimated likely to expand substantially under the pressure of climate change and population reinforce (Reynolds et al. 2007, Wang et al. 2012). Most drylands distributed in southwestern and central Asia, northern and southwestern Africa, southwestern United States and Mexico, Australia. Due to vast area, drylands store 241 Pg soil organic carbon (SOC) or 15.5% of global total surface SOC pool and contribute appropriate 40% of global net primary productivity (Lal 2004, Wang et al. 2012). However, drylands are predicted to be vulnerable to climate change and drought. it was estimated that appropriate 60% of drylands are either suffering desertification or prone to desertification, causing accumulated carbon loss of 20 to 30 Pg in history (Lal 2004) or about 2% of global terrestrial NPP lost each year (Zika and Erb 2009). Drylands are also regard as having high turnover rates of carbon pools, which in addition imposed its sensitivity to climate change and/or drought (Poulter et al. 2014). Central Asia is one of distribution center of dryland and consist mainly of temperature grassland and desert. With the increase of regional population, land use was significantly changed in Central Asia, which in turn intensify local climate change (Lioubimtseva et al. 2005). Despite differences in the range of change among different scenarios, the majority of models project there is a slight decrease in precipitation rete over most of Central Asia with a stronger decrease in the western and southwestern parts (Lioubimtseva and Henebry 2009).

Vegetation processes are profoundly affected by climate change and give significant feedbacks to climate, which in turn reinforce or weaken impacts of climate change (Joos et al. 2001, Lenihan et al. 2003, Bonan 2008). However, there are still great uncertainties in assessing response of drylands to global climate, resulting mainly from rare of available field data, especially the data on water and carbon processes which tightly controlled by surrounding climate and environment (Lioubimtseva and Henebry 2009).

1.2 State of the art

As an important limiting factor on vegetation growth, drought have received abundant attentions in the last few decades (Mishra and Singh 2010). With different study aims and methods, various indices have been developed to monitor and quantify drought magnitude in published literatures, such as soil water content (Gartner et al. 2009, Farooq et al. 2010, Dong et al. 2011, Hartmann et al. 2013, Grossiord et al. 2014), potential evapotranspiration, Palmer Drought Severity Index (Dai 2012, Schwalm et al. 2012), evaporative fraction (Schwalm et al. 2010, Ford et al. 2014) and so on. For the vascular plants covering most of the terrestrial surface, soil is the dominant water source absorbed through root systems. Besides water supply ability in soil, atmosphere vapor demand also significantly affect water imbalance in soil and moisture availability for plant growth (Gu et al. 2006, Eamus et al. 2013). As a result, soil moisture content and atmosphere vapor demand were two of the most direct and common drought proxies used to describe vegetation response to soil or atmosphere drought.

Transpiration is a key physiological process for vegetation to form the power for absorbing water and mineral nutrition and to regulate canopy temperature. Plant transpiration shares the same passageway of stomata as photosynthesis, so it tightly couple with carbon assimilation and has significant effects on ecosystem water and carbon cycles (Cunningham 2004, Nicolás et al. 2008). It was estimated that transpiration account for more than 50%~90% of evapotranspiration, approximate 40% of incident precipitation and half of received solar radiation, playing predominant effect on energy partitioning and balance in terrestrial surface (Jasechko et al. 2013, Schlesinger and Jasechko 2014). Plant transpiration is tightly controlled by climate variables, such as solar radiation, temperature and atmosphere vapor demand which was found closely coupled with stomatal conductance (Oren and Pataki 2001, Mellander et al. 2004, Lopez C et al. 2007, Kumagai et al. 2008, Nicolás et al. 2008, Peters et al. 2010, Clausnitzer et al. 2011, Huang et al. 2011, Brümmer et al. 2012, Naithani et al. 2012, Seversike et al. 2013, Kobayashi et al. 2014, Zheng and Wang 2015, Ji et al. 2016). At leaf scale, portable gas exchange measurement system with leaf chamber have been largely used to measure transpiration rate and its relationships with climate factors (McDonald et al. 2002, Daley and Phillips 2006, Huo and Wang 2007, Will et al. 2013). At branch and tree scale, sap flow was commonly view as transpiration and measured by various thermodynamics approaches, such as stem heat balance (Senock and Ham 1993, Grime et al. 1995, Grime and Sinclair 1999, Čermák et al. 2004), heat dissipation (Lundblad et al. 2001, Do and Rocheteau 2002, James et al. 2002, Bush et al. 2010), heat pulse velocity (Cohen et al. 1981, Olbrich 1991, Barrett et al. 1995, Green et al. 2003). Sakuratani type sensor was designed to measure plant sap flow by sakuratani based on the principle of heat balance (Sakuratani 1981, 1990, Sakuratani et al. 1999). Granier type sensor is a typical of thermal dissipation probe and estimate sap flow through empirical relationship between sap flow rate and temperature difference between two probes installed in plant sapwood (Granier 1987, Granier et al. 1996a, Köstner et al. 1998). Compared with other methods, thermodynamic approach can approach plant transpiration perfectly and worked continually with little effect on plant and surrounding environment (Smith and Allen 1996, Wilson et al. 2001). Benefiting from the method advantage, vegetation transpiration can be monitored in the long term and be scaled up to larger scales based on forest sapwood estimation (Granier et al. 1996a, Vertessy et al. 1997, Zhang et al. 2015). Although climate control effect on plant transpiration have been studied at different scales, the compare studies among multi scales are rare, which was an important issue relating scaling up regime for interaction between vegetation and climate system. For example, many physiology-based models have been built to simulate canopy- or larger-scale water use or stomatal conductance response to climate change based on field data measured at smaller (leaf) scale (Reichstein et al. 2002b).

Stomata is the main passageway for transpiration and its conductance for water vapor is one crucial plant functional traits describing plant adaptive mechanism to drought. Suffering from soil drought, plant usually tend to turn down their stomatal conductance and decline transpiration rate, but the decrease magnitude and response time to soil drought was species and drought intensity dependent (Mediavilla and Escudero 2004, Zweifel et al. 2009). Some species are drought-resistance and showed little or weak stomatal response to atmosphere vapor demand (VPD) under soil drought (Tardieu and Simonneau 1998, Pou et al. 2012, Rogiers et al. 2012). This stomatal strategy ensure plant to keep photosynthesis under drought or high productivity but it also make plant suffer high vulnerability of xylem air embolism resulted from excessive water loss (Domec and Johnson 2012, Sade et al. 2012). On the contrary, some plant species showed drought-avoidance strategies and had pronounced stomatal close response to VPD under soil drought. For plant with this strategy, one integrate analysis of published literatures showed that stomatal sensitivity to VPD was proportional to the magnitude of stomatal conductance at low VPD, which was consistent with the theoretical relationship between them derived from a hydraulic model which assumes perfect stomatal regulation on water potential (Oren et al. 1999). Compared with the former stomatal behavior, plants equipped with the latter strategy have advantage in keeping hydraulic security but with the cost of low photosynthesis or growth rate under moderate soil drought (Franks et al. 2007, Quero et al. 2011). For example, carbon hunger other than water shortage may induce plant death under longtime mid-level soil water deficit (Hartmann et al. 2013). In order to describe briefly this two different transpirational and stomatal response to drought, anisohydric and isohydric were employed to characterize this two contrasting stomatal behaviors, respectively. However, a natural stand of *Eucalyptus gomphocephala* was found to have relative constant water potential gradient between roots and shoots, measured as the difference between predawn and midday leaf water potential, despite the strong down regulation of stomata on transpiration in an experiment through cycle of varying soil moisture conditions, which was referred to isohydrodynamic (Franks et al. 2007). As a results till now, isohydrdic and ansiohyddric are increasingly regarded as two points of continuum in plant response to drought, other than two sides of dichotomization that one plant species fall in one or the other (Klein 2014, Gu et al. 2015). In recent years, transform between these two strategies has been found for the same species in different studies and for the same individual under different soil drought intensities. Such as, *Vitis vinifera* L. cv. Merlot showed isohydric-like stomatal behavior when soil water potential was low but switched to anisohydric-like stomatal behavior with increasing soil water deficit (Zhang et al. 2012).

Owing to limitation of measuring technology, drought effect on ecosystem gas exchange began much later than that at leaf and individual scales. Traditional methods to estimate ecosystem gas exchange fluxes include chamber (Schulze et al. 1985, Hutchinson and Livingston 2001), stable isotopic (Yakir and Sternberg 2000, Bowling et al. 2001) and sap flow technologies (Williams et al. 2004, Delzon and Loustau 2005, MA et al. 2006). These methods were limited by sampling area and/or changed surrounding physical environment and/or failing to monitor ecosystem gas fluxes continually in long time and/or failing to measure ecosystem CO_2 and H_2O fluxes simultaneously. By assuming no horizontal divergence or convergence, eddy covariance system continually measured the mixing ratio of gases and the three dimensional wind speed at high frequency (usually 10 HZ), and from which gas exchange rate and fluxes across the interface between ecosystem and atmosphere are computed based on micrometeorological theory (Baldocchi 2003, Gu et al. 2012). Advantage in eddy covariance technology remedied the shortage of traditional methods and realized longtime direct measurement with high temporal resolution, less environment effect and large sampling area. The sampling area, named flux footprint, covers an approximate circle with diameter ranging from a hundred meters to several kilometers depending on wind speed and direction, and the device mounting height above canopy surface (Barcza et al. 2009, Aubinet et al. 2012). Now, eddy covariance technology has been widely used for continuous measurement of net CO_2, H_2O, other gases (CH_4, N_2O) and energy (sensible and latent heat) fluxes in many projects on climate change, agricultural, industrial and other fields over the word (Baker and Griffis 2005, Barr et al. 2006, Yu et al. 2006, Wang et al. 2007, Kroon et al. 2010, Velasco and Roth 2010). Furthermore, this technology has also been increasingly used for calibration and validation of ecosystem carbon cycle simulation models, which requires more detailed components of net CO_2 exchange: ecosystem assimilation and respiration (Hollinger and Richardson 2005, Medlyn et al. 2005, Kroon et al. 2010). Based on directly measured net CO_2 exchange flux, ecosystem gross primary production (GPP) and respiration (R_{eco}) have been successfully derived with different flux-partitioning algorithms in recent years with the definition of GPP as the sum of NEE and R_{eco} (Yi et al. 2004, Reichstein et al. 2005, Stoy et al. 2006, Lasslop et al. 2010). Although varied with detailed function, most flux-partitioning algorithms are common in extrapolation of respiration from nighttime to daytime according to its dependence on temperature or both temperature and soil moisture availability. In different algorithms, the ecosystem respiration can be estimated form nighttime flux data or light response curve of daytime or both day- and nighttime NEE.

The advantage of eddy covariance technology and flux separation algorithms have largely promote studies of ecosystem-scale carbon processes (assimilation and respiration) and water use (evapotranspiration) response to drought environment. Drought impacts ecosystem carbon balance by modifying both ecosystem carbon uptake and release rates. Under soil drought, both GPP and R_{eco} usually showed decrease trend and the decrease magnitude of GPP tend to be higher than that of R_{eco} in most terrestrial ecosystems, leading to a decline trend of NEE or a transform from carbon sink to carbon source (Pereira et al. 2007, Centritto et al. 2011, van der Molen et al. 2011). During a drought and heatwave across Europe in 2003, continental-scale primary productivity was estimated to decrease 30% compared with non-drought years, resulting in a strong net source of CO_2 during drought period and expended the four-year accumulative net carbon sequestration (Ciais et al. 2005). Moreover, in an integrated analysis which collected from 238 flux tower sites distributed across 11 biomes including croplands, shrublands, forests, grasslands, savannas, permanent wetlands, result showed that ecosystem assimilation sensitivity to drought was higher than that of R_{eco}, causing a decline trend of terrestrial carbon sink under drought at global scale (Schwalm et al. 2010). Similarly, ecosystem water flux also declined with the limitation of soil water availability in most ecosystems under drought (Meyers 2001, Zha et al. 2010). On the contrary, water was expected to be used more effectively, i.e. water use efficiency of carbon assimilation (WUE) increased during soil moisture deficit in the majority of plant species (Deng et al. 2006, Monclus et al. 2006). However, drought effect on WUE at ecosystem scale was more complex. Increased ecosystem WUE has been found in Ozark forest (Yang et al. 2009), temperature and subtropical evergreen forests (Yu et al. 2008) under water deficit. On the contrary, in ecosystems of Mediterranean evergreen forests, northeast-china meadow steppe and west-China desert, ecosystem WUE declined with increasing soil moisture drought (Reichstein et al. 2002b, Dong et al. 2011, Liu et al. 2012).

With the expansion of studied spatial scale, more biotic and abiotic variables were related to water and carbon physiological processes and thus drought effect on the gas exchange of studied objects were affected by other factors which may enhance or weaken drought effects (McNaughton and Jarvis 1991, Grossiord et al. 2014). As a result, drought effects on fine scale objective may not linearly correlated with that of larger scales. From leaf to ecosystem scale, for example, leaf distribution in canopy, composition of plant species and their influence on climate drivers, as well as their interaction with each other may have different effect on objective response to drought environment. By integrating stomatal control on gas exchange under drought that derived from leaf-scale perspective, a physiologically mechanistic simulation model resulted in a 200% over-estimation of ecosystem-scale carbon assimilation and WUE under drought in Mediterranean forest ecosystem (Reichstein et al. 2002b). For a desert shrub species, daily branch transpiration linearly coupled with VPD while that at canopy scale showed no response to VPD (Zheng and Wang 2014). Under simulated precipitation addition experiment in a semiarid grassland, water use efficiency at canopy and ecosystem scale was stimulated by 17% and 10%, respectively, while that at leaf scale decreased by 27% (Niu et al. 2011). These results strengthened the necessary of studies on drought effect at different scales.

1.3 Study site and objectives

1.3.1 Study site

The study was conducted in the Beishawo experimental plot (44°25′54″N, 87°54′9″E, 600 m a.s.l.) located on the southern edge of Gurbantünggüt desert in Northwest China and Central Asia (Fig. 1-1). The plot was established in 2009. It has a flat topography and is dominated by homogeneous silver sand soil. Mean soil pH is 8.52. Soil organic carbon and total salt content is 0.80 ~ 7.08 mg g^{-1} and 0.25 ~ 0.69 mg g^{-1}, respectively. The site is characterized by a continental arid climate with dry, hot summer and cold, snow-covered winter. Mean daily maximum air temperature during summer is > 40 ℃, while the mean daily temperature in winter is < -20 ℃. The mean annual temperature is 7.5 ℃. Long-term (1985-2010) annual average precipitation is 163 mm (Liu et al. 2012) and snowfall in winter is the main water source for the budding shrubs and short-lived grasses. Contrary to the low precipitation, the mean annual pan evaporation is approximate 2000 mm.

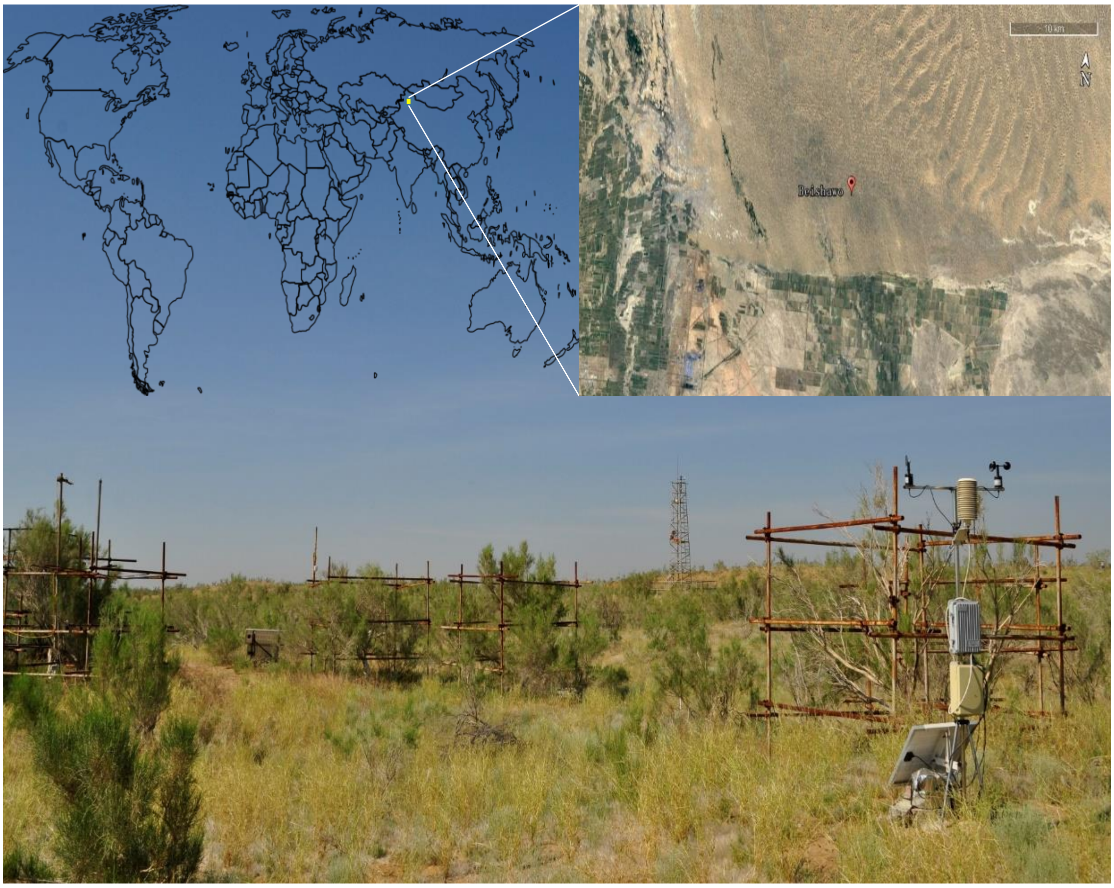

Fig. 1-1 Location and photograph of the study site.

The dominant vegetation is an appropriate 2-meter-high shrub, *Haloxylon ammodendron* with few companion shrubs (e.g. *Tamarix ramosissima*). Photosynthetic organ (assimilation shoots, see Fig. 1-2) of *H. ammodendron* is photosynthetically active from the middle of spring but they become dormant by late autumn. Short-lived and shallow-rooted herbaceous species, e.g. *Erodium oxyrrhynchum*, *Ceratocarpus arenarius* and *Alyssum linifolium,* occur in spring in response to increased soil moisture input from the melted snow water, but die out in late spring when soil become dry. The mean canopy coverage and density of *H. ammodendron* in this study site is estimated at 16% and 584 stems ha^{-1}, respectively (Zheng and Wang 2014, 2015). The mean canopy height is appropriate 2 m, the mean individual canopy projection area is 3.26 m^{2}, and the mean basal diameter is 6.4 cm. Coverage of sapwood area is appropriate 0.77 m^{2} ha^{-1} estimated according to an inventory done by Zheng and Wang (2014). The growing season of *H. ammodendron* at this study site usually starts at the end of April and ends at the end of October while that of under-storey grasses usually last from April to June.

Fig. 1-2 Photosynthetic terminal shoots of *Haloxylon ammodendron*.

1.3.2 Study objectives

As one of the most significant natural disturbance, drought has been revealed to have dramatic effects on ecosystem carbon and water cycles in various biomes at multi scales (Davidson et al. 1998, Easterling et al. 2000, Acuña et al. 2005, Monclus et al. 2006, Hwang et al. 2008), and then has significant influences on regional productivity, biodiversity, and their feedback to climate (Tilman and Haddi 1992, Ciais et al. 2005, Archaux and Wolters 2006, Žalud et al. 2017). Desert is one typical arid ecosystem and is extremely vulnerable to periodic and longtime drought stress. Because located in the center of Eurasia and far from ocean, Central Asia is dominated by temperate desert and semi-deserts (Lioubimtseva et al. 2005, Lioubimtseva and Henebry 2009) and is one of the most responsive regions to climate change and is suffering obvious climate-induced influences (Giorgi 2006).

With increasing air temperature, glaciers, which is a regulator in seasonal variability of regional runoff and a buffering water source for summer, showed a common trend of reducing volume in Central Asia (Dyurgerov and Meier 2000, Shi et al. 2006), which will ultimately result in intensification of water deficit in hot and dry summer periods (Sorg et al. 2012). Based on regional climate model, the annual temperature and annual precipitation in northwest of China are predicted to increase 2.0 ℃ and 19%, respectively under the scenarios of double atmosphere CO_2 concentration (Shi et al. 2006). Another climate simulation model predicted area-averaged annual mean surface air temperature and precipitation in Central Asia would increase 3.18 ℃ and 1.3%, respectively, till 2050, but with more inhomogeneous seasonal distribution: 3.55°C increase of temperature and 2.3% decrease of precipitation in summer (Lal and Harasawa 2001). These results point to a drier tendency in summer or plant growing season in Central Asia although annual mean precipitation was expected to increase. The drier trend in dry season has also been verified in an observational data-based analysis (Chou et al. 2013). With rare of historical observation data in extensive deserts, the current available projections on climate change in arid land of Central Asia have large uncertainties (Shi et al. 2006). Even so, drought is still the dominated limiting effect on ecosystem now in Central Asia and this is expected be continue in the recent coming decades. In addition, the increasing population and extension of irrigated cropland (such as desert oasis) made desert ecosystem in Central Asia becoming more vulnerable to drought and facing increasing risk of desertization (O'Hara 1997, Saiko and Zonn 2000, Geist and Lambin 2004, Lioubimtseva et al. 2005).

Hence, the knowledge on desert ecosystem response to drought in water use and carbon processes are increasingly urgent. The primary aim of this study is to understand drought effects on multi-scale water use and ecosystem scale carbon processes of a typical temperate desert ecosystem in Central Asia. This study will conducted in the southern edge of Gurbantünggüt desert located in northwest of China with three specific objectives as follows:

① Quantify water use and stomatal conductance response to climate drought at leaf, branch and whole plant scales of dominate plant species, and evaluate if there are differences in drought effect on water use among multi scales of typical temperate desert plant species;

② Quantify the response of canopy-scale water use and stomatal conductance to both climate and soil drought during prolonged drought in growing season, and try to explore the low threshold of soil water content for survival of dominate species under natural conditions using continuous four-year monitored sap flow data;

③ Compare ecosystem assimilation, respiration and water use efficiency response to soil water content and evapotranspiration fraction, and evaluate whether evapotranspiration fraction can be viewed as a proxy of soil drought and used to trance drought effect on carbon processes in temperate desert ecosystem.

CHAPTER 2 DROUGHT EFFECT ON WATER USE AND STOMATAL CONDUCTANCE AT LEAF, BRANCH AND INDIVIDUAL SCALES

Abstract

Desert ecosystems exposed to extreme droughts and are vulnerable to climate change. Multi-scale mechanism of hydrological adaptation of desert plants to drought are not fully understood, creating uncertainty in risk assessment of desert ecosystems to climate change by ecological modelling. In this chapter, we investigated multi-scale water-use strategies of *Haloxylon ammodendron*, a dominant desert shrub of central Asia. We found that whole plant water use of *H. ammodendron* was significantly reduced during most of the daytime period. At low light water use was controlled by PPFD and at high VPD it was further conserved by stomatal closure. It appears that water conservation in *H. ammodendron* at leaf scale may behave differently to that at whole plant scale. High stomatal sensitivity of the plant to VPD at whole plant scale means more conservative water use strategy at whole plant scale than leaf scale. Response of transpiration and stomata to climate variables were un-convergent among leaf, branch and individual scales for a dominated desert shrub. So one must be cautious in up scaling leaf scale data to infer canopy scale water conservation to avoid overestimation of plant response to climate drivers. Our results enrich the database of multi-scale water use response of desert plants to climate factors, which are crucial for ecological modelling aiming to predict arid land vulnerability to climate change.

2.1 Introduction

Water use of vegetation directly relates to carbon assimilation and energy partitioning in plants, playing a crucial role in ecosystem functioning and it is largely controlled by climate variables (Schlesinger 1997, Allen et al. 2010). Understanding the mechanism of water use of dominant plants to climate drivers is essential to evaluate arid ecosystem response to climate change. As stomata are the primary channels for gas exchange by controlling transpiration and carbon assimilation, stomatal conductance is a key parameter that describes plant water use and conservation under different climatic conditions (de Arellano et al. 2012, Huntingford et al. 2015). A clear understanding of stomatal response to climate drivers is crucial for accurate estimation of ecosystem water, carbon and energy fluxes.

Arid and semi-arid lands cover nearly 40% of terrestrial surface of the earth, which are expanding and intensifying globally due to climate change (Schlesinger 1997). Previous studies on plant water use and stomatal response to climate drivers largely focused on trees in mesic environment while similar studies in xeric ecosystems particularly in central Asia are very few (Xu and Li 2006, Xu et al. 2007, Zheng and Wang 2014, 2015). The paucity of data from arid ecosystems creates large uncertainty in risk assessment of these ecosystems to global climate change (Yohe et al. 2006). Shrubs and short-lived (annual) grasses are the dominated vegetation in such ecosystems (Schwinning and Ehleringer 2001). With very low species diversity, simple vegetation structure and weak buffering capacity to climate change, desert ecosystems are highly vulnerable to climate change and prone to degeneration (Lioubimtseva and Henebry 2009). Existing limited studies on desert shrubs mainly dealt with water use estimation (Sala et al. 1996, Zheng and Wang 2014), water use response to climate factors, rain pulse events and elevated CO_2 (Pataki et al. 2000, Xu and Li 2006, Qiyue et al. 2014, Zheng and Wang 2014) and quantifying water use sources (Mooney et al. 1980, Ehleringer et al. 1991).

It is generally agreed that desert vegetation exhibits higher tolerance to water shortage by morphological adjustment, adapting to extreme low water potential by stomatal and osmotic regulation (Kozlowski and Pallardy 1997, Nobel 2002). However, water use strategies of desert plants vary widely depending on species and scales of measurement (Xu and Li 2006, Du et al. 2011). For example, *Tamarix ramosissima* sustained stable water use at different surface soil water conditions while that of *Reaumuria soongorica* and *Haloxylon ammodendron* varied significantly under contrasting surface soil water conditions (Xu and Li 2006), indicating interspecific difference in available water among the three co-occurring shrubs. Zheng and Wang (2014) found that whole plant scale water use of *Haloxylon ammodendron* was saturated under high VPD while such phenomena did not occur at branch scale, suggesting plant water use was scale dependent. These results are helpful in understanding water use strategies at seasonal and whole plant scales. However, stomatal conductance and its regulation on transpiration are thought to be more sensitive to changes diurnal environmental variables at leaf scale than that at seasonal and whole plant scales. Unfortunately, such data are currently unavailable.

Stomatal conductance is usually determined by instantaneous gas exchange measurement at leaf scale. At branch and whole plant scales it is estimated from the inverted Penman-Monteith (P-M) function based on continuously monitored sap flow (Granier et al. 1996a). Although sap flow at branch and whole plant scales have been reported for selected Central Asian desert shrubs (Gong et al. 2006, Zheng and Wang

2014), such studies are rather limited and it is desirable to obtain additional data necessary for ecological modelling for reliable risk assessment of desert communities to climate change. In this chapter, we examined water use strategies of a dominant desert plant in Central Asian, *Haloxylon ammodendron*, from both water use (transpiration and sap flow) and stomatal conductance perspectives in response to climate drivers at leaf (assimilating shoot), branch and whole plant scales.

2.2 Material and methods

2.2.1 Measurement of climate factors

An automatic recorded weather station (Vantage Pro2™, Davis Instruments, USA) was installed on the study site to continuously record air temperature (T_{air}), relative humidity (RH), wind speed and direction, precipitation. A quantum sensor (Li190SB, Campbell Scientific, Inc., Logan, USA) was used to measure photosynthesis photo flux density (PPFD) at 3 m. Data was sampled every 1 min and 10 min averages recorded by data logger (DT80, Thermo Fisher Scientific Australia Pty Ltd, Australia). Atmosphere pressure (P_{air}) was provided by an eddy covariance system (Li-7500, Licor Inc., Lincoln, NE, USA) installed at an 11 m-high tower, which was 50 m away from the weather station. Atmospheric vapor pressure deficit (VPD) was then calculated using 10-min averages of air temperature and relative humidity as follows (Campbell and Norman 1998):

$$\mathrm{VPD} = \mathrm{a} * \exp\left(\frac{\mathrm{b} * \mathrm{T_{air}}}{\mathrm{T_{air}} + \mathrm{c}}\right) * (1 - \mathrm{RH}) \qquad (2\text{-}1)$$

where T_{air} is air temperature (°C), RH is atmosphere relative humidity (%) and a, b, c are constants set to 0.611, 17.502 and 240.97, respectively.

2.2.2 Measurement of leaf scale transpiration

Terminal shoots of *H. ammondendron* are modified to green succulent cylindrical structures with stomata (Fig. 1-2), which carry out the main photosynthetic function of the plant (Huang et al. 2003, Kazantseva et al. 2012). These needle-like shoots (assimilating shoots) are the basic organ of carbon assimilation. However, to be consistent with the scaling terminology in gas exchange literature (leaf, branch and tree) we called this basic photosynthetic unit 'leaf' as in previous studies for the same species (Gong et al. 2006, Xu and Li 2006). We measured diurnal variations of leaf scale transpiration and stomatal conductance at an interval of 1 to 1.5 hours from sunrise to sunset using a portable gas exchange system (GFS-3000, Heinz Walz GmbH, Germany) from June 15 to July 12, 2016. All measurements were taken on clear days with minimum cloud in five healthy *H. mmodendron* plants representing the diameter and height distribution of the entire plot. For each measurement we used two sunlit mature leaves (assimilating shoots) in each of the five sample plants (n = 10). The leaves were clamped in the chamber parallel to each other to avoid overlapping. Because the assimilating shoots of *H. ammodendron* are almost cylindrical and covered with stomata equally on the surface (Xu and Li 2006), we assumed that all leaf surface area in the chamber contributed equally to gas exchange. The recorded gas exchange and stomatal conductance were calibrated using the surface area of cylinder calculated from diameter and length of the shoot samples in the chamber.

2.2.3 Sap flow measurement at branch and whole plant scales

Branch scale sap flow was measured using the stem heat balance (SHB) method (Sakuratani 1981). The Sakuratani sensors were heated at a constant power (0.1 W) and covered tightly around the branch with two layers of bubble wrap to protect the sensors from outside heat, and one layer of plastic foil to protect the sensors from rain. In total we measured nine branches at the top canopy of five sample plants (one branch each of four sample plants and five branches at different directions in one central sample plant). All branches were < 20 mm diameter. All cross sectional areas of sample branches were calculated as sapwood.

Water use at whole plant scale was measured by using thermal dissipation probes (Granier 1987). Five couple Granier sensors were installed on north side stems of each of the five sample plants and covered with a plastic box and one layer of foil and reflective film to protect against mechanical and thermal disturbance and prevent rain water. The upper probe was continuously heated with constant power of 0.2 W and signals between heated and reference probes were sampled synchronously with environment measurement. Data recorded at one-minute interval from which mean values at 10 min interval were computed and recorded in a data logger (DT80, Thermo Fisher Scientific Australia Pty Ltd, Australia).

Branch and whole plant sap flow were monitored continuously form June 1 to July 31, 2016, representing the pick growing season of *H. ammodendron*. Sap flow density was calculated according to Sakuratani (1981) or Granier (1987). Transpiration was scaled up based on cross sectional area of branch or sapwood area of stem. Stem sapwood area was assessed according to empirical relation between stem diameter (D, cm) and sapwood area (As, cm^2) according to Zheng and Wang (2014) as follows:

$$As = 0.39 * D^{1.73} \ (R^2 = 0.98, n = 32) \quad (2\text{-}2)$$

To be comparable with result at leaf scale, transpiration at branch and whole plant scales were normalized based on leaf area (E_L). The leaf area of a sample branch (A_L, cm^2) was estimated using allometric equation based on branch diameter (D, cm) as previous studies in the same site (Li et al. 2013) as follows:

$$A_L = 740.16 \times D^{1.3} \ (R^2 = 0.696, n = 159) \quad (2\text{-}3)$$

Leaf area of a sample plant was assessed by dividing the product between LAI and canopy projected area by canopy coverage.

2.2.4 Stomatal conductance

Apparent noise and incorrect data caused by power failure or other equipment errors were excluded from the following analysis. We used sap flow data to calculate stomatal conductance (g_s). Stomatal conductance (m/s) at branch and whole plant scales were estimated by inverting Penman-Monteith (P-M) equation according to previous studies (Granier et al. 1996b):

$$g_s = \frac{\gamma \lambda E_L}{\rho_a C_p (e_s - e_a)} \quad (2\text{-}4)$$

where γ is the psychrometric constant (Pa ℃$^{-1}$); λ is latent heat of vaporization (energy required per unit mass of water vaporized (J g^{-1}); Cp is specific heat capacity of air (J kg^{-1} K^{-1}), ρ_a is dry air density (kg m^{-3}); (e_s - e_a) represents the vapor pressure deficit of the air.

Stomatal conductance was converted to mol conductance (mmol m^{-2} s^{-1}) according to ideal gas law (Lide 2010):

$$g_{mol} = \frac{g_{mm} V_o T_o P_{air}}{T_{air} P_o} \quad (2\text{-}5)$$

Where g_{mol} is molar leaf stomatal conductance (mmol m^2 s^{-1}), g_{mm} is leaf stomatal conductance derived from the Penman-Monteith equation (mm s^{-1}) and V_o is molar volume of air (44.6 mol m^{-3}) at standard air temperature (T_o = 273.15 K) and pressure (P_o = 101.3 kPa), P_{air} is air pressure (kPa) and T_{air} is air temperature (K).

2.2.5 Statistical analyses

For quality control, response of hourly transpiration to PPFD and VPD were analyzed only when PPFD was $\geq$ 40 μmol m^{-2} s^{-1} (Ewers and Oren 2000). Daily average E_L, PPFD and VPD were calculated when PPFD $\geq$ 40 μmol m^{-2} s^{-1}. The correlations among transpiration, stomatal conductance and meteorological factors were determined by Pearson's correlation analysis, 2-segment-linear piecewise function was employed to describe hourly E_L and g_s response to climate factors except between g_s and VPD. Response patterns of hourly stomatal conductance to VPD were fitted following Oren *et al*. (1999) against the data collected during high light (hourly average PPFD > 600 μmol m^{-2} s^{-1} in this study) (Dai et al. 1992, Bourne et al. 2015):

$$g_s = g_{sref} - m \times \ln(\mathrm{VPD}) \quad (2\text{-}6)$$

where g_{sref} is g_s when VPD = 1 kPa and m is stomatal sensitivity to VPD. Difference among the three scales (leaf, branch and whole plant) were analyzed with one-way ANOVA followed by Duncan test.

2.3 Results

2.3.1 Daily and diurnal multi-scale transpiration of *H. ammodendron* and climate drivers

During the study period, daily average E_L of *H. ammodendron* at branch scale varied from 0.20 to 0.51 mmol m^{-2} s^{-1} and averaged 0.33 mmol m^{-2} s^{-1} (Fig. 2-1 a), while that at whole plant scale varied from 0.20 to 0.35 mmol m^{-2} s^{-1} and averaged 0.26 mmol m^{-2} s^{-1} (Fig. 2-1 b). Daily PPFD and VPD were relatively stable varying from 504 to 893 μmol m^{-2} s^{-1} and 1.4 to 5.8 kPa, respectively (Fig. 2-1 c, d).

In four clear days, we found significantly ($P < 0.05$) higher daytime E_L of *H. ammodendron* at leaf scale than at branch and whole plant scales, with the maximum leaf scale E_L ranging from 1 to 2 mmol m^{-2} s^{-1}, compared to around 0.5 mmol m^{-2} s^{-1} at branch and whole plant scales (Fig. 2-2 a). Although diurnal maximum E_L values between branch and whole plant scales did not vary significantly, their difference in diurnal patterns were apparent. Whole plant scale E_L peaked at mid-morning, followed by a decrease and finally disappearing just before sunset. Branch scale E_L showed consistently wider picks (plateau) followed by a decline, which lasted till sunrise (Fig. 2-2 a). Diurnal PPFD showed stable maximum around 1400 μmol m^{-2} s^{-1}, usually occurring at midday (Fig. 2-2 b). However, diurnal VPD generally picked before the sunset varying from 3 to 6 kPa. After sunset the VPD value decreased to 0 and remained so till sunrise (Fig. 2-2 b).

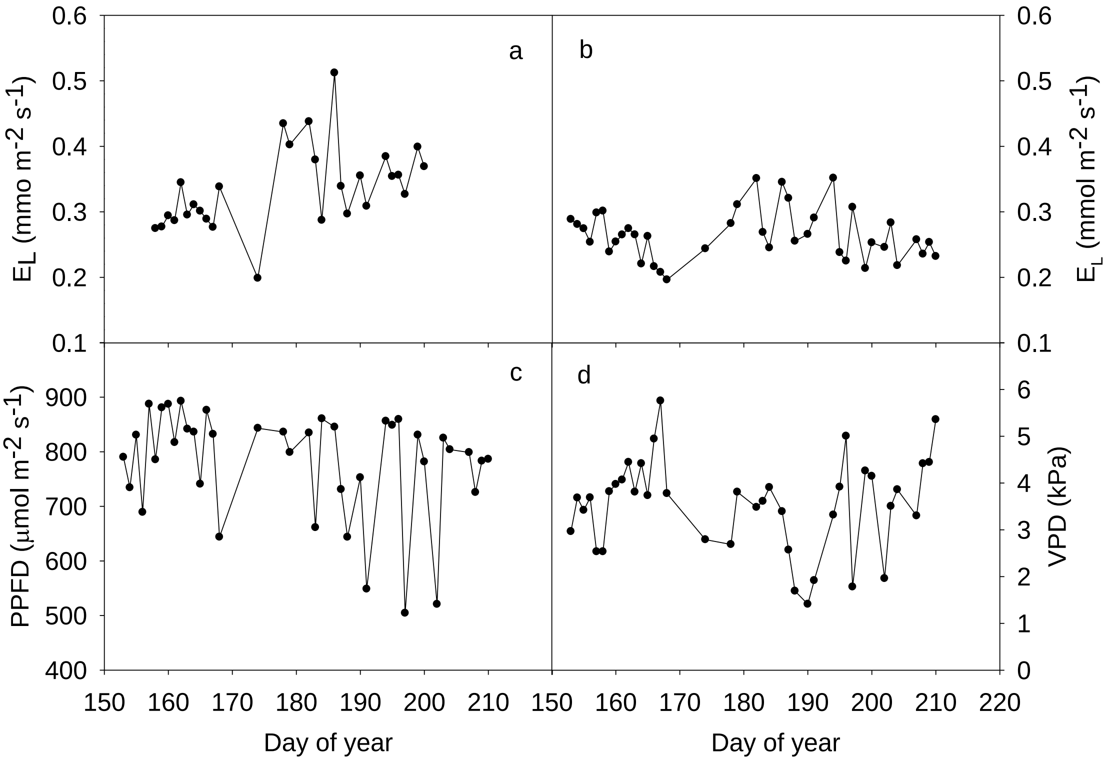

Fig. 2-1 Daily average transpiration rate per leaf area (E_L) of *H. ammodendron* at branch (a) and whole plant scales (b), photosynthesis photon flux density (PPFD, c) and vapor pressure deficit (VPD, d) during daytime across the study period.

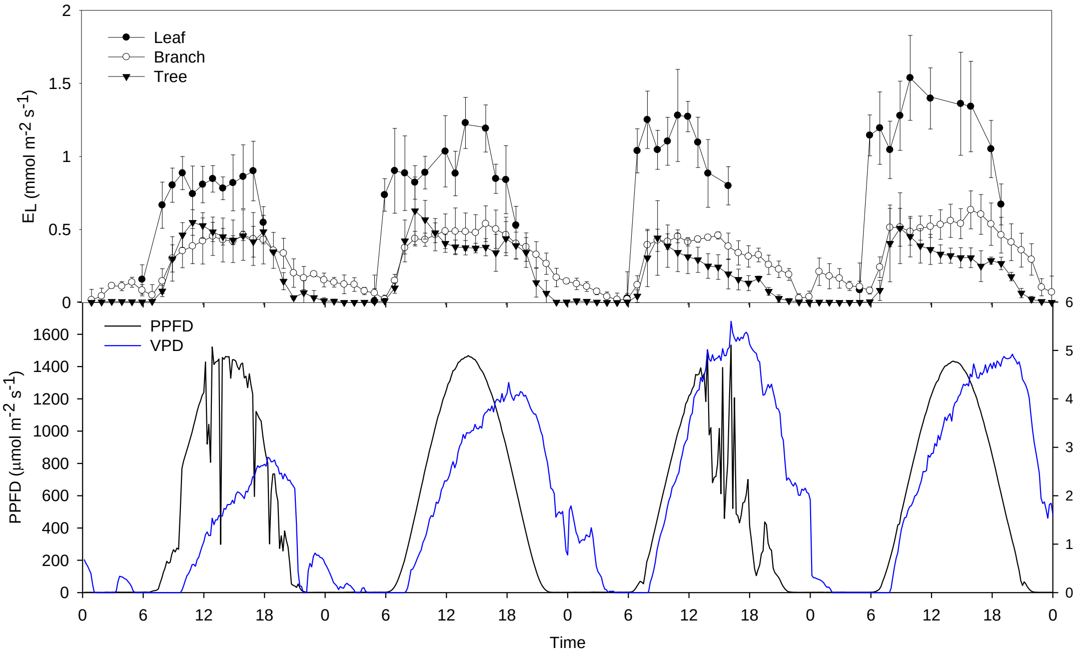

Fig. 2-2 Diurnal transpiration rate of *H. ammodendron* at leaf, branch and whole plant scales in response to climate factors, photosynthesis photon flux density (PPFD) and vapour pressure deficit (VPD) in June 25, 26 and July 1, 4, 2016 at the southern edge of Gurbantünggüt desert, central Asia.

2.3.2 Correlations among multi-scale hourly average E_L, g_s and climate factors

Hourly E_L of *H. ammodendron* showed significant positive correlations with T_{air}, PPFD and VPD at leaf, branch and whole plant scales ($P < 0.001$), except VPD at whole plant scale ($P > 0.5$). In contrast, E_L showed significant negative correlations with RH at all three scales ($P < 0.001$, Table 1). Stomatal conductance (g_s) had the highest negative correlation with VPD among all climate factors ($P < 0.001$). Stomatal conductance (g_s) showed significant correlation with T_{air} and RH at branch scale and with RH and PPFD at whole plant scale ($P < 0.001$).

Table 1 Correlation coefficients among hourly average transpiration rate (E_L) and stomatal conductance (g_s) per leaf area of *H. ammodendron* and environmental factors at leaf, branch and whole plant scales during daytime across study period.

	Leaf		Branch		Whole plant	
	E_L	g_s	E_L	g_s	E_L	g_s
T_{air}	0.68***	− 0.30	0.77***	− 0.34***	0.57***	− 0.04
RH	− 0.67***	0.27	− 0.67***	0.53***	− 0.51***	0.20***
PPFD	0.59***	− 0.00	0.78***	0.04	0.78***	0.34***
VPD	0.56***	− 0.77***	0.57***	− 0.78***	0.08	− 0.89***

***$P < 0.001$.

2.3.3 Response patterns of hourly and daily E_L to climate factors

Response patterns of hourly E_L to PPFD at the three scales were similar, with E_L increasing linearly with increasing PPFD until saturation (Fig. 2-3 a-c). Hourly E_L tended to saturate when PPFD approached 371, 761 and 624 μmol m^{-2} s^{-1} at leaf, branch and whole plant scales respectively. The saturation points of E_L also varied with scales ($P < 0.05$) with mean hourly E_L saturation values 0.86, 0.39 and 0.32 mmol m^{-2} s^{-1} at leaf, branch and whole plant scales, respectively.

We found no significant correlation between hourly E_L and VPD at whole plant scale ($P > 0.05$), but their peak patterns were distinct (Fig. 2-3 f). Hourly E_L during daytime (PPFD ≥ 40 μmol m^{-2} s^{-1}) of *H. ammodendron* increased linearly at low VPD until reaching inflection points when VPD values were 1.6, 2.1 and 2.0 kPa for leaf, branch and whole plant scales, respectively (Fig. 2-3 d-f). After inflection points, hourly E_L showed different response patterns to increasing VPD at different scales, with nearly saturated response at leaf and branch scales and negative liner response at whole plant scale.

Response of daily E_L to PPFD and VPD are shown in Fig. 2-4. Being different from hourly E_L response pattern, the daily E_L stayed relative stable under various daily PPFD and VPD at both branch and tree scales, except E_L response to VPD at tree scale, where daily E_L decreased trend with increasing daily VPD (Fig. 2-4 d).

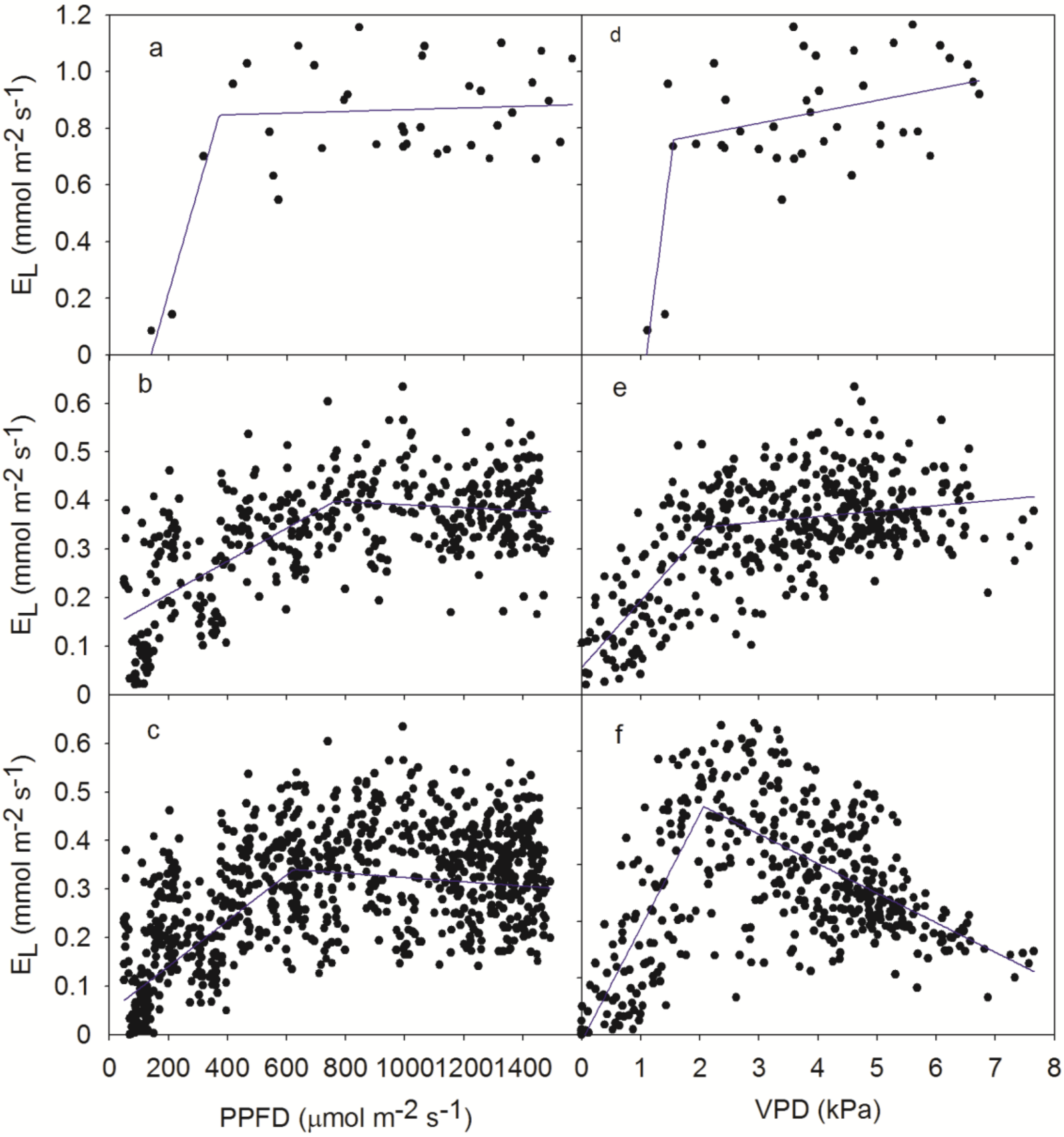

Fig. 2-3 Relationships between hourly average transpiration rete per leaf area (E_L) of *H. ammodendron* during daytime (PPFD ≥ 40 μmol m^{-2} s^{-1}) at leaf (a, d), branch (b, e) and whole plant (c, f) scales in relation to photosynthetic photon flux density (PPFD) and saturate vapour pressure deficit (VPD). Solid lines represent fits according to 2-segment-linear piecewise function.

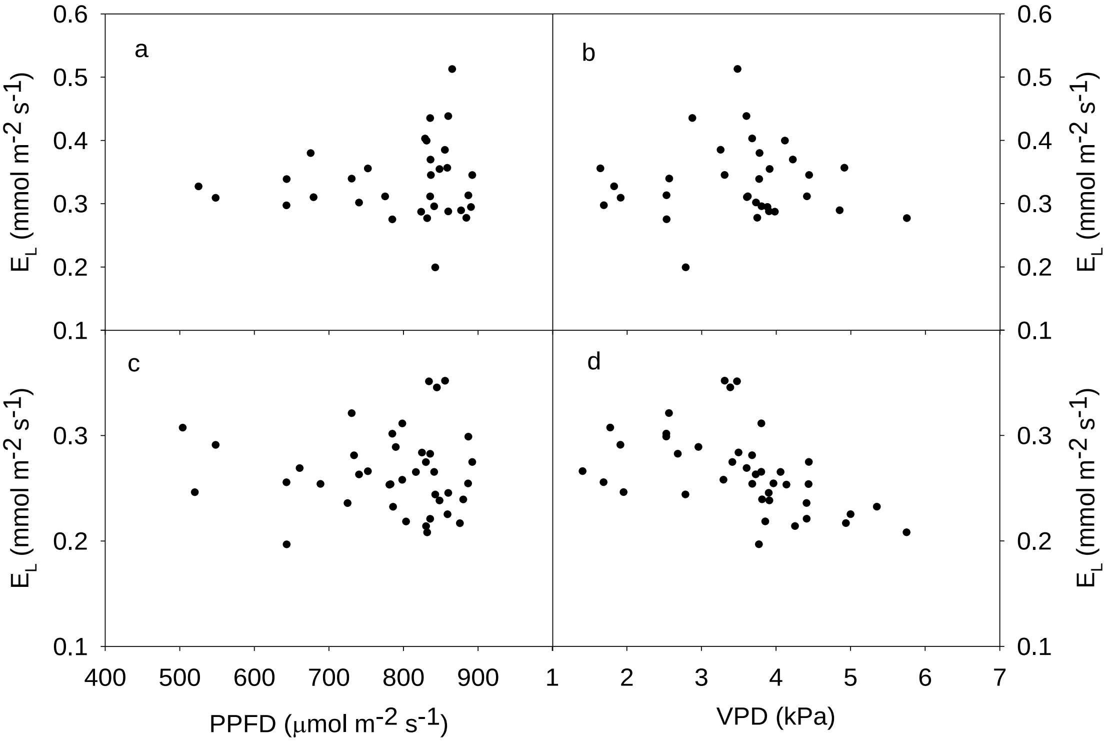

Fig. 2-4 Relationship between daily average transpiration per leaf area (E$_L$) of *H. ammodendron* during day time (PPFD ≥ 40 μmol m^{-2} s^{-1}) at branch (a, b) and whole plant scales (c, d) in relation to photosynthetic photon flux density (PPFD) and saturate vapour pressure deficit (VPD).

2.3.4 Response patterns of g_s to climate factors

Stomatal conductance (g_s) declined sharply with increasing VPD under strong irradiation (when hourly average PPFD > 600 μmol m^{-2} s^{-1}) at all scales (Fig. 2-5a-c). However, stomata level, sensitivity and the reference stomatal conductance (g_{sref}, when VPD = 1 kPa) differed among the three scales. Mean g_s at leaf scale was 20.23 mmol m^{-2} s^{-1}, which was significantly higher than that of branch and whole plant scales (P < 0.01). On the other hand, the mean g_s values were nearly identical to both branch and whole plant scales (Fig. 2-3 b, c). Stomatal conductance at leaf scale had the highest reference value (40.26 mmol m^{-2} s^{-1}), while that at branch scale had the lowest reference value (25.62 mmol m^{-2} s^{-1}). The highest response sensitivity of g_s to increasing VPD (m) was found at whole plant scale, followed by leaf scale and the lowest sensitivity was at branch scale. Under low light conditions (PPFD < 600 μmol m^{-2} s^{-1}) we found little response of g_s to VPD at branch and whole plant scales (insets of Fig. 2-5 b, c).

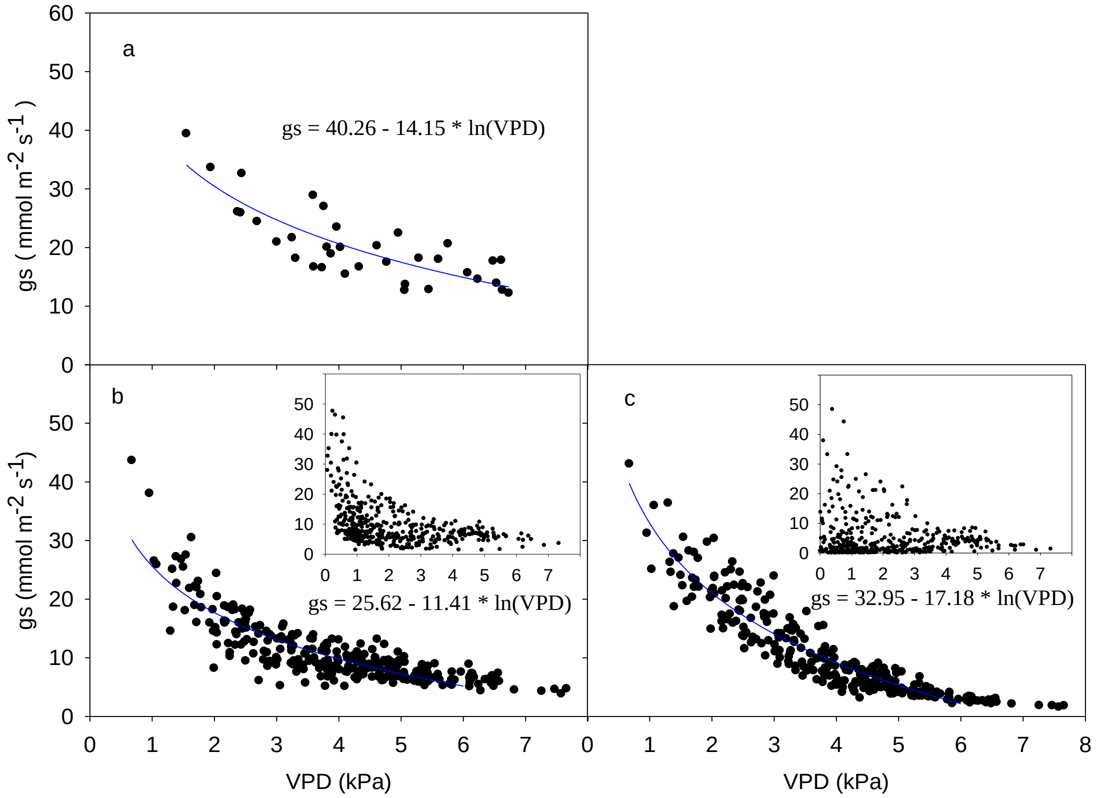

Fig. 2-5 Relationship between hourly stomatal conductance of *H. ammodendron* per leaf area (g_s) and saturate vapour pressure deficit (VPD) at leaf (a), branch (b) and whole plant (c) scales during study period when hourly average PPFD > 600 μmol m^{-2} s^{-1}. The solid lines represent fits according to exponential function. The inset figure denotes the relationship between g_s and VPD at PPFD < 600 μmol m^{-2} s^{-1}. PPFD data at < 600 μmol m^{-2} s^{-1} at leaf scale were not enough to produce an inset figure.

2.4 Discussion

2.4.1 Water use and g_s of *H. ammodendron*

Due to extreme soil and atmospheric drought, the mean diurnal maximum transpiration per leaf area of *H. ammodendron* was found to be much lower than that of the same species reported by Xu and Li (2006) at branch scale (~ 2 mmol m^{-2} s^{-1}) and Gong *et al*. (2006) at leaf scale (~ 6 mmol m^{-2} s^{-1}). This may be related to the lowest soil water content during the period when this study was conducted. Whole plant scale maximum E_L of *H. ammodendron* (0.5 mmol m^{-2} s^{-1}) was also much lower than other shrub species at whole plant scale reported from other arid regions (e.g. 11 mmol m^{-2} s^{-}

^{1}) (Naithani et al. 2012) indicating response of this plant to extreme drought.

Arid and semiarid shrubs are commonly found to have reduced leaf area, which help adapt arid environment, so they have highest g_s per leaf area among all plant functional types (Mencuccini 2003). Among the three scales, mean value of g_s was the highest (20.23 mmol m^{-2} s^{-1}) at leaf scale. But it is much lower than reported by Gong *et al*. (2006) at the edge of an oasis with high soil water content (~180 mmol m^{-2} s^{-1}). Leaf level g_s in our study was slightly higher than that reported by Zheng and Wang (2014) at the whole plant scale. The low g_s in this study may indicate that decreased leaf area of *H. ammodendron* in extreme drought condition cannot improve stomatal conductance considerably and may play limited role to adapt water deficit, compared to stomatal regulation.

2.4.2 Response patterns of water use and g_s to climate drivers

Water use of *H. ammodendron* was consistently controlled by both PPFD and VPD across the three scales, even though the response patterns were relatively diverse. Water use responded similarly to PPFD at the three scales, linearly increasing at low PPFD but saturated under high PPFD, similar to those of semiarid tree species (*Quercus liaotungensis, Robinia pseudoacacia*) reported by Du *et al*. (2011) but different from plants of wet tropical forests (*Cecropia insignis, Pentaclethra macroloba*) in which transpiration increase linearly even under high radiation (O'brien et al. 2004). This may be explained by different canopy structures (generally open and sparse canopies of shrubs in arid and semiarid land vs. closed and dense canopies in mesic tropical regions) and soil moisture conditions between arid and mesic regions. Linear increase of *H. ammodendron* water use with increasing PPFD under low PPFD suggest that water use is mainly controlled by PPFD at low solar radiation due to small stomatal aperture, whose expansion is largely controlled by high light (Sharkey and Raschke 1981). We found water use of *H. ammodendron* to be saturated at all three scales when PPFD was more than 800 μmol m^{-2} s^{-1}, similar results were reported from semiarid region by Du *et al*. (2011). During saturation period of water use under high PPFD, water use was instead controlled by VPD, whose variation lagged behind diurnal PPFD.

Water use of *H. ammodendron* linearly increased with VPD at low VPD (generally < 2 kPa irrespective of scale), indicating that water use is mainly controlled by transpiration pull resulting from VPD following stomatal opening. Under high VPD, which usually occurs during midday and afternoon, leaf and branch scale water uses nearly saturate but at whole plant scale it decreases with increasing VPD, indicating that water use at this scale was limited by partially closed stomatal aperture resulting from decreased leaf water potential due to less water supply to leaf than water loss under high VPD. Whole plant scale water use response pattern to VPD of *H. ammodendron* in arid environment was different from those in semiarid and mesic regions where soil was not as drought as this study desert, which remain saturated despite high VPD (O'brien et al. 2004, Du et al. 2011). This may be explained by the different VPD ranges in different regions (0 - 1.5 kPa in mesic region, 0 - 6 kPa in semiarid region and 0 - 8 kPa in this study), different interspecific functional types or different minimum safe hydraulic boundary between this study and previous studies. Diurnal water use of *H. ammodendron* at whole plant scale was depressed when VPD was more than 2 kPa, which was higher than those found in mesic or mild arid regions (Oren and Pataki 2001, Tang et al. 2006) but similar to that reported in semiarid region (Du et al. 2011). The duration of VPD above 2 kPa was accounted for approximately 50% of the diurnal cycle or 79% of daytime, so water use of this desert species was greatly depressed by water deficit during most of the daytime, leaving the most favorable time for water use and concomitant carbon assimilation in mid-morning.

We found no obvious relationship by plotting g_s against PPFD at branch and whole plant scales. However, different response patterns of g_s to VPD appeared when g_s was grouped under low and high PPFD with the demarcation point of 600 μmol m^{-2} s^{-1}. This indicates that the effect of PPFD on stomatal function is mainly regulated by stomatal aperture under low PPFD, as in tree species in semiarid (Igarashi et al. 2015) and shrub species in arid land with irrigation (Zhang et al. 2012).

Similar to other findings, we found that g_s of *H. ammodendron* decrease exponentially with increasing VPD at all three scales in absence of the limiting role of PPFD and could be described by a linear logarithmic function (Oren et al. 1999, Ocheltree et al. 2014). According to Oren *et al.* (1999), who summarized response of many species of semi-arid and mesic regions, stomatal sensitivity (m) of vascular plants is proportional to g_s at low VPD (= 1 kPa, g_{sref}) with similar empirical and theoretically derived ratio (approximately 0.6), which have been reported for tree species in mesic regions and shrub species in semiarid regions (Bourne et al. 2015, Igarashi et al. 2015). In this study, we found that m/g_{sref} values was 0.35, 0.45 and 0.52 at leaf, branch and whole plant scale, respectively. Whole plant scale m/g_{sref} in this study was similar to the same species found by Zheng and Wang (2014), to a semi-arid shrub (Naithani et al. 2012) and to mesic tree species (Oren et al. 1999), but less than mesic *Eucalyptus* species (Bourne et al. 2015) and two desert shrubs (*Ephedra nevadensis* and *Larrea tridentate*) reported by Oren *et al.* (1999). This suggest that *H. ammodendron* may have strong stomatal regulation on hydraulic safety to prevent excessive xylem cavitation under atmosphere drought at whole plant scale, although unstable seasonal midday water potential was found in other places for the same species (Xu et al. 2007, Naithani et al. 2012, Igarashi et al. 2015).

Furthermore, m and g_{sref} found in this study were slightly higher than that observed by Zheng and Wang (2014) for a longer period but lower than a semi-arid shrub species of sagebrush (Igarashi et al. 2015). This was largely attributed to the use of deeper soil moisture and redistribution of soil water through root systems for sagebrush, while *H. ammodendron* being much dependent on precipitation-derived upper soil water (Xu and Li 2006). With lower LAI and opener canopy, m and g_{sref} of *H. ammodendron* were lower than those found in mesic tree species (Loranty et al. 2010, Bourne et al. 2015), which may be explained by different inter-species functional type and extreme soil and atmosphere drought in this study site compared to mesic regions.

2.4.3 Diurnal response patterns

Various diurnal patterns of water use among the three scales were pronounced as a results of their diverse response to climate drivers. In contrast to the narrow unimodal or bimodal diurnal water use patterns commonly found in vegetation under no or mild water deficit, *H. ammodendron* behaved distinctively with a relatively wide peak around midday time at both leaf and branch scales, similar to the diurnal pattern found at leaf scale in another desert shrub (Gong et al. 2006). However, the patterns were different with patterns that was characterized by narrower and higher peak at midday at branch scale reported by Xu and Li (2006) for the same species, preliminary due to lower soil moisture conditions in this study.

The peak water use at whole plant scale clearly occurred in mid-morning, with a lower gentle peak at sunset, which was similar to diurnal pattern of the same species reported by Zheng and Wang (2014). Peak of water use at whole plant scale occurred ~ 9 h earlier than that of VPD, which was similar to that found by Zheng and Wang (2014) but much earlier than other semiarid shrub or tree species (0 ~ 2 h) (Du et al. 2011, Naithani et al. 2012) and rain forest trees (1 ~ 4 h) (Motzer et al. 2005), indicating severer water deficit and larger stomatal regulation on water use of *H. ammodendron* than other species. Compared with peak water use at midday that was commonly found in other species in mesic and semi-arid regions (Oren and Pataki 2001, Tang et al. 2006, Du et al. 2011), the whole plant water use of *H. ammodendron* during mid- and past mid-day time was largely depressed, which was related much with decreased leaf water potential and whole plant hydraulic conductance following stomatal closure (Tyree 2003, Xu et al. 2011, Zhao 2011).

2.4.4 Scale variations

In this study we found decreasing correlation coefficients between water use and T_{air}, RH, VPD and increasing correlations between water use and PPFD when upscaling from leaf scale to whole plant scale. This phenomenon was also noted by Zheng and Wang (2014) in this plant and other desert shrubs at branch and whole plant scales (Liu et al. 2011), which is related to scale issue in canopy. Whole plant water use can be approximated by integrating all leaves' transpiration in canopy ignoring non-stomatal water loss, diverse diurnal patterns and response patterns of water use and stomatal conductance to climate drivers among leaf, branch and whole plant scales would likely show that leaves in canopy behave unevenly and at least part of leaves and branches may behave differently compared to the whole plant. Such diverse pattern of water use may be attributed to high spatial heterogeneity of climate drivers in closed forest (Jarvis 1995). However, climate drivers are distributed relative evenly in open and sparse canopy of *H. ammodendron* in this study, so the effect of spatial heterogeneity of climate drivers on different leaf behaviors in canopy would be limited.

Spatial heterogeneity of leaf characteristics in canopy could also induce various water use and stomatal response to climate factors at multiple scales. At whole plant scale, partly sunlit leaves in canopy of *H. ammodendron* (sample leaves in this study) showed higher reference stomatal conductance and lower stomatal sensitivity to VPD, allowing stomata to remain at relative high conductance and maintaining high transpiration rate under high VPD. By contrast, whole plant scale showed less reference stomatal conductance and higher stomatal sensitivity to VPD, resulting in lower stomatal conductance and transpiration rate than that at leaf scale under high VPD. The different stomatal behavior between organism scales indicate that *H. ammodendron* has more conservative water use strategy at whole plant scale than leaf scale, which may be effective to protect whole plant water homeostasis. Such ununiform stomatal response to VPD among different scales can only be explained if a small number of leaves maintain relatively high stomatal conductance while most leaves have low stomatal conductance in the canopy under high VPD during midday and afternoon resulting canopy patchiness (Jarvis 1995, Sinoquet et al. 2001). Canopy patchiness of *H. ammodendron* can also be derived to some extent from the higher error bars of leaf scale diurnal water use than those at branch and whole plant scales. Similar water use response of *H. ammodendron* to climate factors has also been reported by Zheng and Wang (2014) at branch and whole plant scale. Canopy patchiness could reduce whole plant water loss and allow partial assimilation by part of the canopy in mild drought, which is considered as one of the key mechanisms to balance water loss and carbon acquisition at whole plant scale under drought (Buckley et al. 1999, O'Grady et al. 2013). Hence, patchiness must be considered in ecohydrology models, in order to avoid systematic error of overestimating vegetation response to climate change.

Another potential reason contributing to diverse transpiration and stomatal sensitivity to VPD and PPFD is hysteresis caused by water stored in trunk. However, we did not find remarkable hysteresis between branch and plant stem sap flow during morning in this study (Fig. 2-2). Zhao (2011) attributed the phenomena to the measurement using portable gas exchange system which changed boundary layer conductance around leaf in leaf chamber leading to overestimation of leaf scale stomatal conductance. In our study site *H. ammodendron* had typical needle-like assimilating shoots (described as leaf) and they were sparsely distributed with open canopy and thus large boundary layer conductance around canopy leaf, so different measurement methods could hardly explain the significant variations in stomatal conductance and transpiration among leaf, branch and whole plant scales. Data poverty has limited a clear understanding of water use strategies of dominated shrubs in such arid ecosystems. This creates problem in accurate evaluation of vulnerability of arid ecosystem to global climate change. Although this study provides useful data revealing water use strategies of *H. ammodendron* at different spatial scales during the main growing season, future study should consider a year round and multi-year assessment of water use strategies of desert shrubs in response to changes in climate variables.

2.5 conclusion

We found that water use of *H. ammodendron* was significantly reduced due to strong atmospheric drought during most of the daytime. Hourly water use was limited by PPFD at low light and it was further reduced by stomatal closure under high VPD. This indicates high tolerance of *H. ammodendron* to drought and strong stomatal regulation on water loss. *H. ammodendron* showed more conservative water use strategy at whole plant scale than leaf scale which resulted from increased stomatal sensitivity to VPD at whole plant scale than leaf scale. This canopy patchiness in stomatal behavior is an important characteristic of sparsely distributed desert plants to balance water loss and carbon assimilation in extreme drought. It appears that for water use partially sunlit leaves of *H. ammodendron* behaves differently even opposite to whole plant scale. Therefore, one must be cautious in up scaling leaf scale studies to canopy scale in order to avoid overestimation of plant water use response to climate drivers. Our results enrich the database of multi-scale water use response of desert plants to climate factors. Such data are crucial for ecological modelling aiming to predict arid land vulnerability to climate change.

CHAPTER 3 DROUGHT EFFECT ON WATER USE AND STOMATAL CONDUCTANCE AT CANOPY SCALE

Abstract

Vegetation water use plays a key role in ecosystem productivity and stability. In arid and semiarid lands, canopy water use and its dynamics depend largely on stomatal sensitivity to drought. In this study, sap flow of a dominant species (*Haloxylon ammodendron*) growing in Central Asia deserts was continuously monitored using Granier-type sensors, from which the canopy stomatal conductance was derived. The responses of canopy water use and stomatal conductance to environmental variables during the second half of the growing season, when annual prolonged drought occurred, was analyzed for four continuous years, from 2013 to 2016. Soil water content (SWC) of 3% was identified as the lower soil water threshold for this species, below which the plant lost the ability for stomatal regulation on water loss and suffered the risk for mortality. Above this threshold, the sensitivity of canopy water use to vapor pressure deficit -VPD (K) was linearly correlated with SWC, which mainly resulted from different stomatal behaviors at varying soil drought intensities. Stomatal sensitivity to VPD (m/G_{sref}) increased linearly with soil moisture deficit, inducing a shift from a more anisohydric to a more isohydric stomatal behavior. The flexibility of stomatal behavior to soil water deficit was one key strategy facilitating the survival of *H. ammodendron* in such an extreme dry environment. These results improve our knowledge on plant adaptive mechanism to extreme, prolonged droughts and are helpful to make more accurate evaluation of vulnerability of arid ecosystems under future climate change.

3.1 Introduction

Vegetation water use is tightly coupled to carbon assimilation and energy balance through the latent heat of transpiration and is one of the most crucial components of the terrestrial water cycle (Farquhar and Richards 1984, Jasechko et al. 2013). It is the result of the interactions between plant physiological functioning and the plant’s immediate environment. In arid and semiarid lands, which cover more than 40% of terrestrial surface of the earth, drought is the premier factor affecting vegetation water use, biodiversity, ecosystem productivity and stability (Schlesinger 1997). Plant hydraulic failure resulting from excessive transpiration water loss is a major cause for tree mortality during drought (McDowell et al. 2008, Allen et al. 2010, Hartmann et al. 2013). Assessment of the stability of arid ecosystems in light of the ongoing climate change, therefore, requires a mechanistic understanding of transpiration water loss to extreme drought environment, particularly for the dominant vegetation.

Stomata are the main channels for gas exchange between vegetation and the atmosphere. Thus, environmental sensing and the regulation of water loss are accomplished by the stomata. Among the environmental variables, atmospheric vapor pressure deficit (VPD) is the main factor driving leaf transpiration and has a strong influence on stomatal conductance (Dai et al. 1992). Stomatal sensitivity to VPD is a valuable tool that plants employ in order to maintain stable tissue water status under drought environments (Tardieu and Simonneau 1998, McDowell 2011). Previous studies have shown that stomatal sensitivity to VPD is variable among species and also among different environmental conditions (Oren et al. 1999, Rogiers et al. 2012). For instance, Bourne *et al*. (2015) found that Eucalyptus species originating from more arid climates had a lower stomatal sensitivity to VPD and that transpiration declined less during a progressive drought than those from humid climates, where water deficit was rare. Cunningham (2004) found that tropical species, with no growing season's drought, showed higher stomatal sensitivity to VPD than the temperate species, which experienced frequent water stress during the growing season. Similarly, Rogiers *et al*. (2012) reported heightened stomatal sensitivity of a grapevine cultivar (*Vitis vinifera*) to VPD under drier soils.

Most of the previous field studies were, however, conducted under sporadic drought or with short-term drought spans. Vegetation behavior in low-frequency and short-term drought-intervals may not be applicable to frequent and long-term drought situations. In arid and semiarid regions, where drought persists for several months, almost on an annual cycle, knowledge of plant stomatal response to VPD under different degrees of drought is necessary in order to predict how water use will respond to continuous, long-term drought events and for evaluating ecosystem vulnerability under climate change.

With extremely low precipitation and high atmospheric vapor demand, deserts are areas of extreme drought, with low biodiversity and primary productivity. Vegetation here is on the verge of extinction due to increasing climate- and human-related influences (Lioubimtseva and Henebry 2009). *Haloxylon ammodendron* C.A.Mey., Bunge is a dominant shrub in deserts located in northwest China and in Central Asia and plays a key role in preventing the vulnerable desert ecosystems here from degeneration. Previous studies revealed that daily water use of *H. ammodendron* was correlated with VPD, photosynthetic photon flux density (PPFD) and air temperature (T_{air}) during its growing season (Zheng and Wang 2015). From the same species, Zheng and Wang (2014) observed varying branch and whole-tree transpiration responses to climate factors and concluded that canopy scale patchiness existed in this desert species. Due to a pronounced higher evaporation than precipitation in such environments, soil water content decreases continuously during summer and autumn. As a result, soil is drier in the second half of the growing season than in the first half (Xu et al. 2007, Xu et al. 2011). Thus, during the second half of the growing season, *H. ammodendron* suffers the highest risk of dysfunction within a year, and its canopy water use response to environment and underlying stomatal regulation at this time determine its survival. Little is, however, known with regard to its stomatal response to environmental variables and the regulation of water use during the prolonged drought condition.

The current study examined: (1) environmental controls on canopy water use of *H. ammodendron* at intra-annual and inter-annual scales during prolonged droughts, (2) influence of the degree of soil drought on canopy water use response to climate factors (3) inter-annual variations of canopy stomatal response to VPD under progressive soil drought.

3.2 Material and methods

3.2.1 Measurement of environment variables and sap flow

Climate factors were measured by a climate station as in chapter 2. Volumetric soil moisture content (SWC) was measured by soil moisture sensor (ThetaProbe, Delta-T Devices Ltd., Cambridge, England) at 20 cm depth. Granier type sensors were used to monitor stem sap flow in the 20 mm depth of the conducting sapwood at approximate 30-50 cm above the ground in six different individual trees. The diameters ranged from 5-20 cm, being representative of the stem size distribution in this study site. The install method of Granier sensors, data sampling and record, calculation of stem sap flow density and sapwood area were same as in chapter 2.

3.2.2 Canopy transpiration and conductance

The sapwood area-weighted average of sap flow density was up-scaled to canopy transpiration per ground area (Tr) based on sapwood coverage of *H. ammodendron* in this study site. Tr was used to calculate canopy conductance (G_s) by inverting Penman-Monteith (P-M) model according to Granier *et al*. (1987) as equation 2-4 and equation 2-5 in chapter 2. With needle-like leaves (assimilating branch) and sparse, open and short canopy, *H. ammodendron* canopy is well-coupled to the surrounding atmosphere and there is no vertical gradient in VPD throughout the canopy. Thus equation 2-4 is applicable in this study.

3.2.3 Data and statistical analysis

According to annual water cycle dynamic and soil moisture conditions in this study site, second half growing season from the first of August to early October when atmosphere temperature higher than 10 °C was defined as annual prolonged drought period in this study and data during this period from 2013 to 2016 was then used for further analysis. Water use of *H. ammodendron* and PPFD were accumulated and VPD was averaged daily during daytime (when incoming hourly average PPFD $\geq$ 40 μmol m^{-2} s^{-1}) while rainfall was accumulated and SWC was averaged every entire day during study periods. One-way ANOVA with Duncan test was performed to show annual difference in water use and environmental factors. The relationships between water use and environmental variables were fitted with liner and quadratic functions except the relationship between G_s and VPD, which was fitted with a linear logarithmic equation proposed by Oren *et al*. (1999) as equation 2-6 in chapter 2 under conditions with high radiation (daily average PPFD > 200 μmol m^{-2} s^{-1}). All statistical analysis was conducted with $P < 0.05$ as a threshold for statistical significance.

3.3 Results

3.3.1 Soil moisture and microclimate

General decreasing trends of all the climate variables from DOY 210 to DOY 290 can be distinguished during the four-year study period between 2013 and 2016, even though apparent day-to-day fluctuations also occurred (Fig.3-1 a-h). Mean daily PPFD was estimated at 28.2, 33.2, 26.1 and 26.0 mol m^{-2} d^{-1} while the respective daily VPD values were 2.5, 2.6, 2.0 and 2.7 kPa, respectively, during the four years. During the study period, accumulative annual rainfall was 44.6, 22.0, 58.8 and 42.8 mm from 2013 to 2016, respectively. During the same periods, volumetric SWC varied from 4.3% to 3.3% in 2013, 2.5% to 1.8% in 2014, 3.7% to 2.7% in 2015 and 5.3% to 3.3% in 2016, with the respective mean values of 3.7%, 2.1%, 3.1% and 4.5% in 2013, 2014, 2015 and 2016, respectively (Fig.3-1 i-l). Changes in volumetric SWC among the years were significant ($P < 0.001$). The inter-annual variations of PPFD and VPD during the study periods (among the four years) were significant ($P < 0.05$), while PPFD between each other among 2013, 2015 and 2016 and VPD between each other of 2013, 2014 and 2016 was not significant ($P > 0.05$).

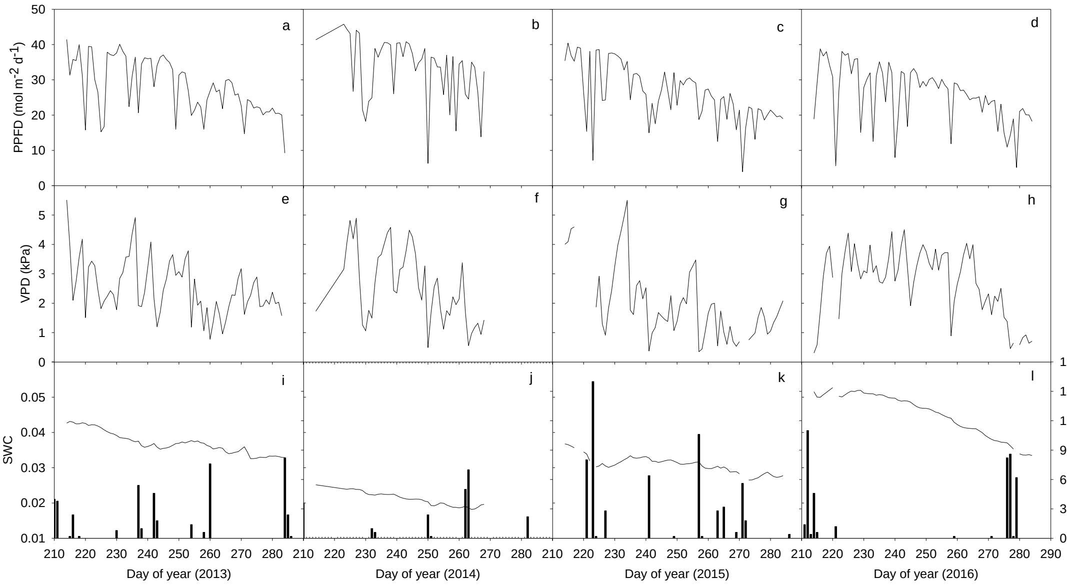

Fig. 3-1 Daily photosynthetic photon flux density (PPFD, a-d), vapor pressure deficit (VPD, e-h), rainfall and volumetric soil water content (SWC, i-l) during the second of growing season (August 1 to early October) between 2013 and 2016. PPFD and VPD were computed every day during daytime when PPFD ≥ 40 μmolm^{-2}s^{-1} while rainfall and SWC were computed every whole day.

3.3.2 Canopy water use

Annual patterns in water use of *H. ammodendron* were variable (Fig. 3-2). Due to equipment failure, only approximate one-month data were available in 2013 and the mean daily water use was 0.044 mm d^{-1}. The average daily water use in 2014 was 0.028mm d^{-1}. In 2015, water use of *H. ammodendron* decreased from 0.044 mm d^{-1} to 0.010 mm d^{-1}, with an average value of 0.026 mm d^{-1}. Daily water use in 2016 remained high at 0.070 mm d^{-1} before decreasing markedly to 0.009 mm d^{-1} at the end of the growing season, with the average daily rates of 0.049 mm d^{-1}. Statistical analysis showed that the inter-annual variations in daily water use among the four years were significant ($P < 0.001$). Daily water use in 2013 and 2016 was significantly higher than in both 2014 and 2015 ($P < 0.05$). Difference in water use between 2013 and 2016 and between 2014 and 2015 were not significant ($P > 0.05$).

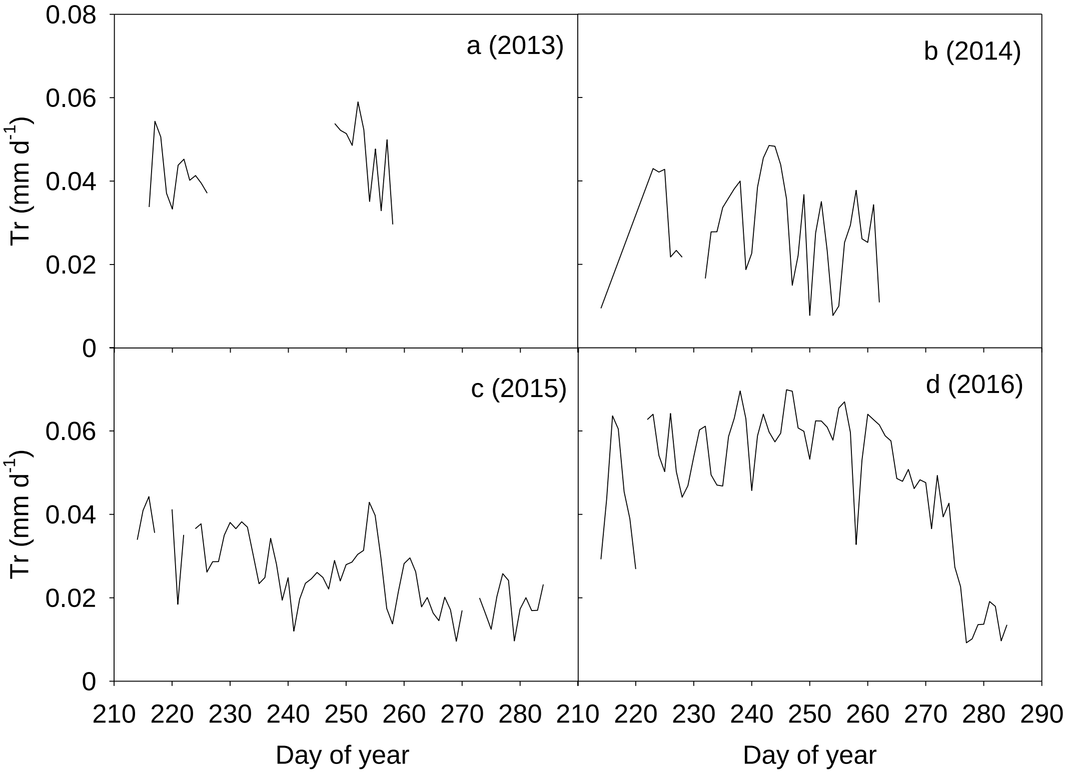

Fig. 3-2 Variations in daily cumulative canopy water use per ground area (when PPFD ≥ 40 μmolm^{-2}s^{-1}) during the second half of the growing season (August 1 to early October) when air temperature >10 °C from 2013 to 2016. Data gaps in 2013 resulted from equipment failure while data gaps in 2014 were due to low air temperatures (< 10 °C) at the end of the measurement period.

3.3.3 Response of daily canopy water use to environmental variables

Water use response patterns of *H. ammodendron* to environmental variables were apparently different in different years and with different environmental variables (Fig. 3-3 a-c). Daily water use during the study periods increased linearly with PPFD (P < 0.05) in 2014, 2015 and 2016, but not in 2013 (P > 0.05, Fig. 3-3 a). In all the years, daily canopy water use increased linearly with VPD (P < 0.01, Fig. 3-3 b). The sensitivity of canopy water use to VPD (K, defined as the slope of linear regression between daily Tr and VPD) increased linearly with the mean daily SWC (P < 0.001) when the average SWC of the second half growing season was above 3% (including fitted K in 2013, 2015 and 2016, Fig. 3-4). The fitted K in the driest year (2014) fell inside the range of those found in the other three years (Fig. 3-4). Daily water use in both 2015 and 2016 were significantly correlated with SWC (P < 0.01), while that in 2013 and 2014 was not significant (P > 0.05, Fig.3-3 c). Relationship between daily canopy water use and SWC in 2016 could be described by a quadratic function (y = -

$324.38x^2 + 29.98x - 0.6312$, R^2=0.77) while that in 2015 was a linear function ($y = 2.0x - 0.036$, R^2=0.29). Although intra-annual water use response to SWC differed among the four years, the inter-annual water use increased linearly with increasing SWC at SWC > 3%, but it was stable at SWC < 3% (Fig. 3-3 c). The correlation between inter-annual canopy water use and SWC was significant ($P < 0.001$).

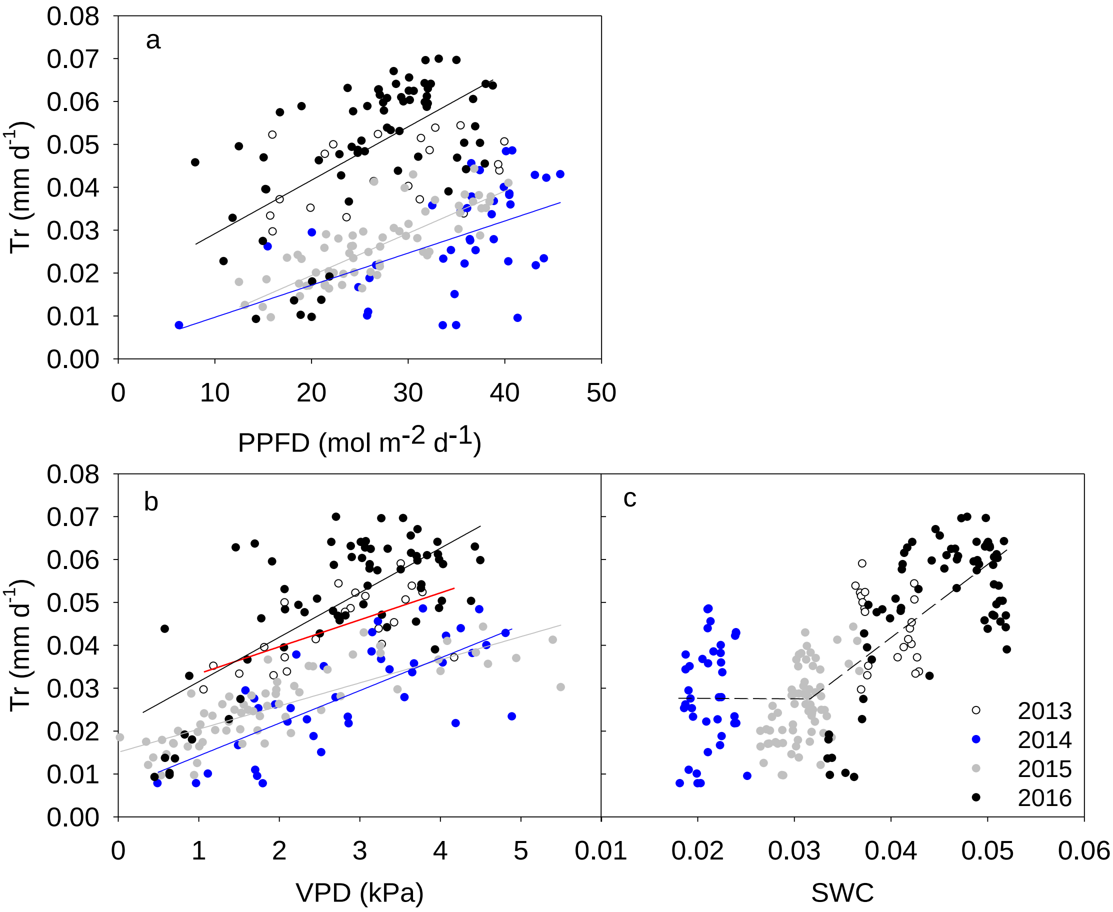

Fig. 3-3 Responses of daily canopy water use (Tr) to daily accumulative photosynthetic photon flux density (PPFD, a), mean vapor pressure deficit (VPD, b) and mean volumetric soil water content (SWC, c) during the second half of the growing season (August 1 to early October) from 2013 to 2016. Lines in first two figures were fitted with liner functions in each of the monitored four years. Line colors represent different years while discontinuous line in the last figure was fitted with a liner function based on all data in the four years.

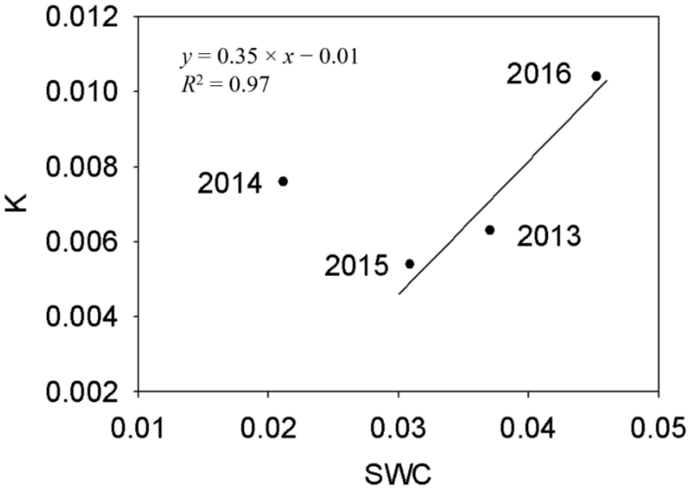

Fig. 3-4 Relationship between annual mean volumetric soil water content (SWC) and water use sensitivity to VPD (K) from 2013 to 2016. Water use sensitivity to VPD (K) was defined as slope of linear regression between daily Tr and VPD. The data were fitted with a linear function between K and annual average SWC at SWC > 3%.

3.3.4 Response of canopy stomatal conductance to VPD in different years

As shown in Fig. 3-5a, during the second half of the growing season in each of the four years, daily canopy stomatal conductance in 2014 varied from 0.54 to 2.33 mmol m^{-2} s^{-1}, with a mean rate of 1.23 mmol m^{-2} s^{-1}, which was significantly lower than in the other years ($P < 0.05$). Mean daily scale daytime canopy stomatal conductance in 2013, 2015 and 2016 were 2.30, 2.10 and 2.54 mmol m^{-2} s^{-1}, respectively. There were no ($P >$ 0.05) significant differences among those 3 years.

Daily stomatal conductance was significantly correlated with daily mean VPD in each year, expressed by linear logarithmic functions ($P < 0.05$). Stomatal sensitivity to VPD (slope of fitted function, m) and reference stomatal conductance (G_s when VPD = 1 kPa, G_{sref}) were lowest in the driest year of 2014. In addition, m/G_{sref} was 0.46, 0.22, 0.52 and 0.35 in 2013, 2014, 2015 and 2016, respectively. The m/G_{sref} decreased linearly with increasing annual average SWC when annual average SWC >3% ($P <$ 0.001, Fig. 3-5 b).

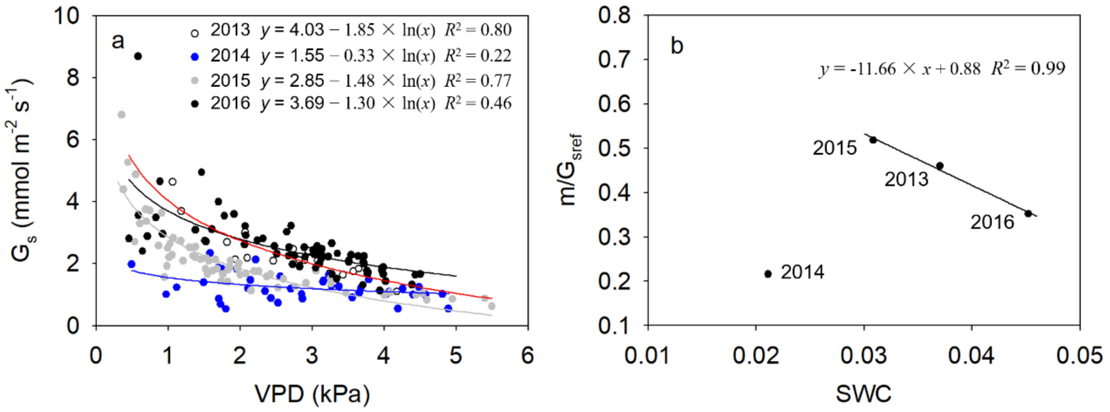

Fig. 3-5 Relationships between mean daily canopy stomatal conductance (G_s) and daily average vapor pressure deficit (VPD) under conditions of high radiation (daily average PPFD > 200 μmol m^{-2} s^{-1}) during the second half of the growing season (August 1 to early October) from 2013 to 2016 (a) and inter-annual relationship between the ratio of stomatal sensitivity to reference stomatal conductance (m/G_{sref}) and annual average volumetric soil water content (SWC) (b).

3.4 Discussion

3.4.1 Soil drought intensity decides response of canopy water use to climate

Plant water use is a physiological process that is mainly controlled by surrounding environmental variables, particularly solar radiation, soil water availability and VPD and the physiological status of the leaf, mainly the leaf water status (Law et al. 2002, Nicolás et al. 2008). Daily canopy water use of *H. ammodendron* increased linearly with PPFD in 2014, 2015 and 2016. This is consistent with results found by Zheng and Wang (2014) in the same species. Similarly, canopy water use increased linearly with increasing VPD in all the years and the sensitivity of daily water use to VPD (K- defined as the slope of fitted linear function between Tr and SWC), increased linearly with annual average SWC, except during the driest year (2014). The linear correlation between canopy water use and VPD was similar to that reported previously under similar drought conditions (Clausnitzer et al. 2011), but differed from those found in the first half of the growing season (Fig. 2-3) and in other relatively moist conditions, in which saturated water use occurred at high VPD (Jung et al. 2010a, Zheng and Wang 2014). This is likely due to decreased sensitivity (response magnitude) of stomatal conductance to VPD during prolonged drought. The linear correlation between SWC and water use sensitivity to VPD clearly indicated the influence of environmental variables on canopy water use. Similar results have also been reported by Chen *et al*. (2014), in which *Ziziphus jujube* had decreased sap flow sensitivity to VPD with increasing soil water stress in semiarid Northwest China. These results indicated that soil water availability was a fundamental variable affecting plant water physiology in arid and semiarid ecosystems (Daly and Porporato 2005, Cammalleri et al. 2013).

Intra-annual *H. ammodendron* water use was significantly and linearly correlated with SWC only in 2015, suggesting there was no consistent intra-annual direct relationship between them. However, on a long-term scale (inter-annual scale), the daily canopy water use increased linearly with increasing SWC when SWC was higher than 3%. This demonstrated that in the second half of the growing season in each year, associated with prolonged drought, SWC remained relatively low and could not induce any variations in canopy water use. Patterns of canopy water use during this period were mainly controlled by VPD, while the magnitudes (water use sensitivity to VPD) were determined by SWC levels. Thus the underlying indirect regulation of SWC on canopy water use only become apparent at inter-annual scale, when the inter-annual SWC varied significantly, something that was not apparent in the short-term. Although different water use responses to VPD have been found in contrasting soil water conditions in previous studies (Clausnitzer et al. 2011, Chen et al. 2014a), long-term relationship between SWC and canopy water use response to VPD has not been well investigated, mainly due to insufficient available data. Our results suggest the need for long-term monitoring (inter-annual) the interaction between plant water use and environmental variables, in order to accurately evaluate ecosystem functions and vulnerability in the arid lands, which suffer frequent and extended droughts.

Linear increase of inter-annual water use with increasing soil water availability when the average SWC > 3% suggested that, on a long-term scale, canopy transpiration of *H. ammodendron* was limited by restricted soil water availability during a prolonged drought. Moreover, strong inter-annual water use response to shallow SWC (20 cm depth) indicated that shallow soil water was also one of the main water sources for *H. ammodendron*. Xu *et al*. (2007) investigated natural root distribution of *H. ammodendron* in the same desert and found that more than 90% of feeder roots are located within 0 to 0.9 m top soil layer. Xu and Li (2006) found that transpiration and leaf water potential were sensitive to rain pulse events and precipitation-derived upper soil water was the main water source of *H. ammodendron*. The results from both studies are consistent with ours.

An interesting finding of this study was that when SWC was < 3%, the annual canopy water use of *H. ammodendron* was unresponsive to SWC, demonstrating that

3% was the lowest threshold of SWC for this species, below which it was likely to suffer high risk of mortality. The relative stable canopy water use when SWC was less than 3% hence reflects the lowest transpiration rate of *H. ammodendron* to allow for the necessary carbon assimilation and leaf temperature regulation (through evaporative cooling), both of which are necessary for plant survival in the desert conditions (Jiang 1992, McDowell et al. 2008, O'Grady et al. 2013). Hartmann *et al*. (2013) reported that transpiration of Norway spruce (*Picea abies*) stabilized at low value before mortality occurred, when relative extractable soil water content was approaching zero under extreme drought. Similarly, transpiration of piñon (*Pinus edulis*) was projected to have a weak response to SWC and precipitation pulses before mortality under prolonged drought, based on mixed effects models (Plaut et al. 2013).

3.4.2 Soil drought intensity decides stomatal regulation ability on water loss

Stomata are the main channels through which CO_2 and H_2O exchange between plant and atmosphere occurs. Stomatal conductance (G_s) is, therefore, a crucial physiological function balancing plant transpiration and assimilation. G_s is markedly affected by environmental conditions and its regulation of hydraulic homeostasis was species-dependent (Hetherington and Woodward 2003). Based on the magnitude at which the water status variation was maintained through stomatal regulation among various environment conditions, the terms of isohydric and anisohydric were used to describe stomatal regulation on water use in previous studies (Tardieu and Simonneau 1998). Isohydric refers to tight stomatal regulation on plant water loss that maintains a relatively constant leaf water potential regardless of soil moisture conditions, whereas less stomatal regulation on transpiration, leading to considerable water status variation under varying soil water conditions, is anisohydric (Domec and Johnson 2012). Although the terms have been previously used to describe species- or variety-specific stomatal function, recent reports showed inconsistent stomatal behaviors (isohydric and anisohydric) for certain varieties (Lovisolo et al. 2010, Zhang et al. 2012). In our study, G_s of *H. ammodendron* was significantly correlated with VPD and could be described with linear logarithmic functions each year. In 2015 when the annual average SWC as low as 3%, the calculated m/G_{sref} was 0.52, still close to that of theoretical ratio (0.60) derived from a hydraulic model which assumes perfect stomatal regulation of constant leaf water potential with respect to VPD (Oren et al. 1999), indicating that *H. ammodendron* imposes a tight stomatal regulation on water loss (more isohydric) when the annual average SWC was as low as 3%. With increasing annual average SWC among second half growing seasons, m/G_{sref} decreased linearly from 0.52 in 2015 to 0.35 in 2016, when soil moisture was highest among the four years, demonstrating a relative slack stomatal regulation on water loss (more anisohydric) during years when soil water deficit was relative relaxed. Xu *et al*. (2010) found that midday leaf water potential of *H. ammodendron* showed considerable response to rain events when soil water content was more than 3%, indicating that *H. ammodendron* behaved more ansiohydrically, consistent with our results. Furthermore, Zhang *et al*. (2012) reported that one grape variety (*Vitis Vinifera*) showed more isohydric-like stomatal behavior under low SWC but switched to anisohydric-like behavior with increasing SWC, which was consistent with stomatal strategies of *H. ammodendron* during prolonged drought. Such inter-annual progressive variation of stomatal behavior from more anisohydric to more isohydric under increasing soil moisture deficit during a prolonged drought indicated that the species had flexible stomatal regulation ability on water use. Adjustment of stomatal regulation ability on water use according to soil water availability is the main mechanism for plant to balance maximizing production when soil moisture was attractable and keeping hydraulic security when soil moisture was more limited (Domec and Johnson 2012, Zhang et al. 2012). This is crucial for the survival of *H. ammodendron* under the harsh desert environment associated with extended periods of drought each year. Although mechanisms driving stomatal regulation under varying soil moisture conditions are less known, Domec and Johnson (2012) reported that the variation of hydraulic signal might allow stomatal function of some species to switch between more isohydric and more anisohydric.

As *H. ammodendron* canopy is sparse and boundary conductance between canopy and atmosphere is large enough to be neglected, canopy water use was mainly controlled by stomatal conductance (Xu et al. 2010). The decreasing stomatal sensitivity to VPD (m/G_{sref}) introduced relative high stomatal conductance and transpiration rates. Thus increasing annual water use sensitivity to VPD (K) found in this study when SWC > 3% resulted mainly from the decreased stomatal sensitivity to VPD in wetter soils.

During the driest year (2014) when SWC was less than 3%, *H. ammodendron* had the lowest mean daily canopy stomatal conductance and stomatal sensitivity (m/G_{sref}). Even so, canopy transpiration in 2014 was comparable to that in 2015 when SWC was higher, indicating the failure of stomatal regulation on water loss, which largely relate to hydraulic conductance (Xu et al. 2010). However, following the driest year (2014), stomatal regulation on water use recovered in the following two relatively wetter years (2015 and 2016), indicating that whole plant hydraulic apparatus was preserved although stomata failed to regulate water conservation in extreme drought year (2014). The capacity of *H. ammodendron* to keep hydraulic apparatus intact, even under extreme drought may be related to variation of leaf and/or root morphology that relate to hydraulic architecture (Schafer 2011). Another study found that leaf area of *H. ammodendron* decreased continuously from July to August when upper-layer (0-50 cm) SWC (volumetric) was less than 3% (Dai 2015). On the other hand, another studies found higher leaf area per branch for *H. ammodendron* under double precipitation treatment than that under no precipitation treatment (Zou et al. 2010). Xu *et al*. (2010) reported that shoot and root hydraulic conductance were equally important for water transport, and concluded that a decrease in leaf area (leaf shedding) was responsible for decrease of shoot hydraulic resistors of *H. ammodendron*. These studies showed that adjustment of morphology that relates to hydraulic architecture is a dominant mechanism for *H. ammodendron* to maintain its hydraulic apparatus intact and survive under extreme drought.

Throughout the four-year study period of the second half growing season, we revealed positive linear correlation between K and SWC and progressive inter-annual variation of stomatal behavior from more anisohydric to more isohydric at higher soil water deficit, during prolonged droughts. These results will enrich our knowledge on coordinated regulation between soil water content and climate on canopy water use, deepening the understanding of flexible stomatal regulation on survival of plant under annual prolonged drought in arid area. Considering the apparent inter-annual variation in adaptive response of water relations of *H. ammodendron* during prolonged drought, long-term studies are necessary for better description of desert ecosystem physiology and how they may respond to future climate changes.

3.5 conclusion

During prolonged droughts, 3% is the lower soil water threshold, below which *H. ammodendron* lost its ability for stomatal regulation on water loss, subjecting it mortality risk. Above this threshold, SWC had a positive linear correlation with water use sensitivity to VPD (K). The indirect effect of SWC on canopy water use through VPD could only be found on a long-term (inter-annual) scale. Stomatal behavior of *H. ammodendron* progressively shifted from more anisohydric to more isohydric, with increasing soil water deficit during prolonged drought when soil water content was above the lower threshold. The influence of SWC on K was linked to different stomatal behaviors in order to regulate water loss and ensure survival of *H. ammodendron*, depending on drought intensity and duration. The flexible stomatal response to environment and the regulation of water loss is a key mechanism for *H. ammodendron* to balance production when soil moisture was attractable and survival when soil moisture was more limiting. Our results emphasized the importance of long-term observations of interaction between plant water relations and the environmental variables and the underlying adaptive mechanisms in arid lands.

CHAPTER 4 DROUGHT EFFECT ON WATER AND CARBON EXCHANGE AT ECOSYSTEM SCALE

Abstract

Responses of ecosystem assimilation, respiration and water use to global climate change vary considerably among terrestrial ecosystems constrained by both biotic and abiotic factors. In this study, net CO_2 exchange between ecosystem and atmosphere (NEE) was measured over a 4-year period (2013-2016) using eddy covariance technology at a desert ecosystem in Central Asia. Ecosystem assimilation (gross primary production, GPP) and respiration (R_{eco}) were derived from NEE through fitting light response curve of NEE based on day- and nighttime data, and their responses to soil water content (SWC) and evaporative fraction (EF) were accessed during growing season. Results indicated that both GPP and R_{eco} were linearly decreased with declining of SWC, with the sensitivity of GPP to SWC 3.8 times higher than that of R_{eco} during the entire growing season, as a result, carbon sequestration capacity decreased under soil drought. At seasonal scale, significant correlation between GPP and SWC was found only in spring while that between R_{eco} and SWC was found in all growing seasons and the sensitivity increased steadily from spring to autumn. WUE showed a weak correlation with SWC. EF had a low correlation with SWC, GPP and R_{eco}, indicating the index was not a good proxy of soil drought, and energy partitioning was not tightly coupled with ecosystem carbon exchanges in this desert ecosystem. The seasonal variation of environment and vegetation in structure and phenology under drought was responsible for the special observed results in desert ecosystem under extreme drought.

4.1 Introduction

Carbon exchange between terrestrial ecosystem and atmosphere is one of the most important ecosystem functions and tightly related to water cycle and energy partitioning, and thus affects ecosystem feedback to climate changes. Net carbon exchange (NEE) is always used to character potential of terrestrial ecosystem to neutralize greenhouse effect resulting from increase of atmosphere CO_2 concentration (Pereira et al. 2007, van der Molen et al. 2011). However, it covers underlying two opposite processes, carbon fixation through ecosystem assimilation and carbon release to atmosphere through ecosystem respiration, and cannot supply sufficient information to understand ecosystem detailed carbon processes. Both ecosystem assimilation and respiration are the crucial issues in ecosystem carbon balance and are deeply influenced by environmental factors, such as soil water deficit (Doughty et al. 2015). Assessing assimilation and respiration and their response to environmental factors are essential for estimating ecosystem ecological function and predicting accurately the evolutionary trend of ecosystem and climate, which drove by the feedback response each other between them. The micrometeorology-based eddy covariance technology is the dominant method to quantify net carbon exchange between terrestrial ecosystem and atmosphere, and the methods to derive its underlying two components, ecosystem gross primary production (GPP) and respiration (R_{eco}) have been developed in recent years (Reichstein et al. 2005, Lasslop et al. 2010), which provide possible way to evaluate response of carbon processes to climate change at ecosystem level.

Soil moisture can strongly modulate hydrologic and climatic conditions and act as one of a key, if not dominant factor driving carbon and water cycle in terrestrial ecosystems, especially in drylands (Ford et al. 2014). Arid and semiarid regions account for nearly 1/3 of carbon sequestration in the word and are sensitive to climate change (Li et al. 2015a). In addition, drylands are estimated to have high turnover rate of carbon pools and are increasingly important in driving inter-annual variability of global carbon cycle (Poulter et al. 2014). Under water deficit that is predicted to be severer in both magnitude and frequency in dry regions (Chou et al. 2013), physiology even community structure of plants and microbiology, and environment (temperature, radiation) are expected to change, which in turn affect both terrestrial carbon fixation and release (van der Molen et al. 2011). Drought intensity, timing and ecosystem history are also proved to affect drought effects on both carbon and water cycle in assimilation, respiration evaporation and transpiration, making the effect of drought on carbon and water cycle more complex (Barr et al. 2007, Schwalm et al. 2010, Hoover and Rogers 2016). Most ecosystem show a decrease in assimilation resulted from reduction in both photosynthetic capacity and stomatal conductance under drought (Kaiser 1987, Tenhunen et al. 1987, Cornic 2000, Xu et al. 2008). There is a 30% reduction in continental-scale GPP during a heat and drought year across Europe and a decrease of R_{eco} along with GPP (Ciais et al. 2005). Although GPP can affect substrate availability of autotrophic and heterotrophic respiration through root exudates and then control ecosystem respiration in terrestrial ecosystem under drought, the magnitude and timing of water deficit effect on these two opposite carbon processes may be different (Yang and Zhou 2013). Short-term drought may suppress R_{eco} earlier and more than GPP because upper litter and soil where heterotrophic respiration mainly occurred suffer drought first, whereas vegetation photosynthetic capacity could be maintained by accessible deep-layer soil water (Reichstein et al. 2002a). At global scale, both assimilation and respiration decreased under relative drought, assimilation was proved to be 50% higher in sensitivity to drought than respiration, and the sensitivity of assimilation and respiration to drought was highest in climatic summer among growing seasons (Schwalm et al. 2010). However, as a different issue, a summer drought induced a decrease of GPP by 9%-12% and concurrent increase of R_{eco} by 2%-21% for evergreen and deciduous broadleaf forest in northwest America (Welp et al. 2007).

With coupling to the relationship between carbon assimilation and water vapor loss, ecosystem water use efficiency for primary carbon uptake (WUE) related to more aspects of ecosystem gas exchange, including biotic and abiotic effects on carbon and water processes, and become an integrated ecosystem trait for adaptation to water limited environment (Scartazza et al. 2014). Ecosystems with different vegetation structure and climate environment suffer various drought conditions and then have different active or negative influence degree on ecosystem WUE. A boreal aspen forest in central Saskatchewan, Canada showed increased WUE from the time of drought onset and reached higher values during the peak drought (Krishnan et al. 2006). By contrast, two nearly monospecific *Quercus ilex* L. forests and one typical mixed macchia forest in Mediterranean all showed a consistent decrease trend with more soil water deficit during growing season (Reichstein et al. 2002b). Similarly, a spring drought induced more suppression on ecosystem GPP than ET in a meadow steppe ecosystem in Northeast China and thus, ecosystem WUE reduced 25% compared with normal-precipitation year (Dong et al. 2011). However, most of previous studies on drought influence on ecosystem carbon assimilation and respiration, evapotranspiration and water use efficiency mainly focused on noncyclic drought and not included extreme drought ecosystems, such as temperate desert which are predicted to be more vulnerable to extreme and periodic drought.

Evaporative fraction (EF) is the ratio of latent heat flux and total available energy (sum of latent and sensible heat) at the land surface, representing the ratio of incoming energy used for evapotranspiration. When the surface is rich in moisture, most of the net radiation is used to evaporate surface water and $EF \rightarrow 1$, while when land surface moisture is limited for evaporation, more available energy is used for heat conduction and convection (Kurc and Small 2004) and then EF decreased even $EF \rightarrow 0$ under extreme drought. In view of this, EF has been widely viewed as a proxy of water deficit, ranging from 0 when fully dry and 1 when fully wet, and used to describe drought effect on carbon cycle processes (Schwalm et al. 2010). However, ecosystem EF also related to soil water holding capacity, vegetation rooting depth, and vegetation transpiration ability which usually also mediated by other factors besides soil moisture, such as solar radiation, air temperature and vegetation phenology. So EF not always tightly correlated to soil water content. For example, there was no significant relationship between EF and soil moisture in both surface layer and root zone in various croplands in southwest France (Nichols and Cuenca 1993). But whether EF can achieve as a proxy of soil drought and trance drought effect on ecosystem carbon process has not been explored in desert ecosystem.

In this chapter, we measured net CO_2 exchange during growing seasons over continuous four years (2013-2016) in a desert ecosystem in Central Asia using eddy-covariance technology to mainly examine: (i) whether ecosystem assimilation and respiration response to soil drought with the same sensitivity in extreme-drought desert ecosystem; (ii) whether evaporative fraction can be viewed as a proxy of soil water deficit and used to describe the response of both ecosystem assimilation and respiration to drought in extreme-drought desert ecosystem.

4.2 Material and methods

4.2.1 Measurement of environment variables and eddy fluxes

During early spring to early winter in continuous four years (2013-2016), environment variables including air temperature (T_{air}), air relative humidity (RH), wind speed and direction, photosynthetic photons flux density (PPFD), Volumetric soil water content (SWC) were measured as in chapter 2 and chapter 3. All the environment variables were measured every 1 min and 10min averages were recorded by weather station logger and standing alone data logger (DT80, Thermo Fisher Scientific Australia Pty Ltd, Australia) synchronously.

Net ecosystem CO_2, H_2O and energy fluxes were measured by an open-path eddy covariance system, installed in an 11 m-height tower that 50 m away from the automatic weather station. This eddy covariance system includes a 3D sonic anemometer (WindMaster, Gill Instruments Ltd, Lymington, UK) which measures wind vector and air temperature, and an open-path infrared gas analyser (Li-7500, Licor Inc., Lincoln, NE, USA) which measures CO_2 and H_2O concentration with sampling rate of 10 Hz.

4.2.2 Data treatment and statistical analysis

Raw flux data were computed and calibrated in a software named EddyPro^{TM} (www.licor.com/eddypro, Licor Inc., Lincoln, NE, USA), primarily including coordinate rotation, sonic temperature correction, frequency and WPL correction (Fratini and Mauder 2014). Spikes in half-hourly net ecosystem CO_2 exchange (NEE) were removed based on similar previous studies (Papale et al. 2006). All rain-day and night-time data under non-turbulent conditions were deleted based on a u*-threshold criterion which was determined according to Reichstein *et al.* (2002b). Ecosystem assimilation and respiration were separated by fitting light response curve of NEE based on day- and nighttime hourly data based on previous studies (McMurtrie et al. 1992):

$$NEE = \max\left(-QUE_{app} \times PPFD;\ GPP_{sat}\right) + R_{eco} \tag{4-1}$$

where QUE_{app} (µmol CO_2 μmol^{-1} photons) was the apparent quantum use efficiency of ecosystem carbon uptake, GPP_{sat} (µmol CO_2 m^{-2} s^{-1}) was the gross carbon uptake under saturating photon flux density, and R_{eco} (µmol CO_2 m^{-2} s^{-1}) was ecosystem respiration estimated as NEE when PPFD was 0. Those three parameters were fitted by scattering PPFD and NEE every 5 days with a 15-day window following Reichstein *et al.* (2005).

The fitted 5-day mean R_{eco} then was described by a regression model in each year taking T_{air} and SWC as predictors similar to Reichstein *et al.* (2002):

$$R_{eco} = R_{ecoref} \times (a + b \times SWC)^{\frac{T_{air}-T_{ref}}{10}} \times \frac{SWC - SWC_0}{(SWC_{1/2} - SWC_0) + (SWC - SWC_0)} \tag{4-2}$$

where R_{ecoref} was the ecosystem respiration at 15 ℃ and optimal soil moisture condition, and T_{ref} was fixed to 15 ℃, and $SWC_{1/2}$ and SWC_0 were the SWC at which the half-maximal R_{eco} occurred and at which R_{eco} was 0, respectively. In addition to the measured hourly T_{air} and SWC, the established R_{eco} regression model was used to estimate hourly R_{eco}. Ecosystem gross primary production (GPP) was calculated as the sum of net CO_2 uptake and R_{eco}:

$$GPP = -NEE + R_{eco} \tag{4-3}$$

In keeping with micrometeorology, negative value of NEE indicate the carbon uptake by ecosystem while positive value means release from ecosystem to atmosphere in this study. Ecosystem water use efficiency of gross carbon uptake (WUE) was calculated as

$$WUE = \frac{GPP}{ET} \tag{4-4}$$

Evaporative fraction (EF) was described as a function of tower-based heat fluxes given by:

$$EF = \frac{LE}{H+LE} \tag{4-5}$$

where H was sensible heat flux (W m^{-2}) and LE was latent heat flux (W m^{-2}) above the canopy.

Season is determined by calendar month and local phenology in this study site, i.e. climatic spring consists April, May and June, climatic summer consists July and August, and climatic autumn includes September and October. These three climatic seasons constitute total growing season in the study site. In order to avoid seasonal variation effect of daytime length, the systematic complexity and uncertainty associated with calm conditions during nighttime (Irvine et al. 2002) and be comparable with EF, daily average instead of accumulative flux data during daytime was used for the following analysis. Daytime was defined as when PPFD larger than 40 μmol m^{-2} s^{-1} as in chapter 2 and chapter 3.

In order to compare assimilation and respiration response to drought, linear function was used to describe ecosystem GPP and R_{eco} general response to SWC and the fitted slope was viewed as their sensitivity to soil drought. All statistical analysis was conducted with $P < 0.05$ as a threshold for statistical significance.

4.3 Results

4.3.1 Environment variables

During the measured periods from 2013 to 2016, daily average T_{air} increased from spring, peaked in middle summer and then decreased continuously, ranging from -1.71 ℃ to 39.05 ℃ with average of 22.19 ℃ (Fig. 4-1 a). Daily average of PPFD reached top value (around 900 μmol m^{-2} s^{-1}) at early spring and the top value was kept until early autumn, forming a wide top pattern in growing season (Fig. 4-1 b). The mean daily PPFD was 649.94 μmol m^{-2} s^{-1} during the continuous four years. Daily average VPD had the similar seasonal pattern as T_{air} but with more steep increase and decrease rate, and the maximum of both them appeared at middle summer (Fig. 4-1 c). The maximal and mean daily VPD were approximate 6 kPa and 2.10 kPa, respectively. Although part of data failed to be recorded in both 2013 and 2014, Volumetric SWC at 20 cm depth always have highest values in middle spring followed by continuous decreasing from late spring until the end of growing season (Fig. 4-1 d). SWC in the study site during the studied four years ranged from 2% to 10% and averaged at 4.34%.

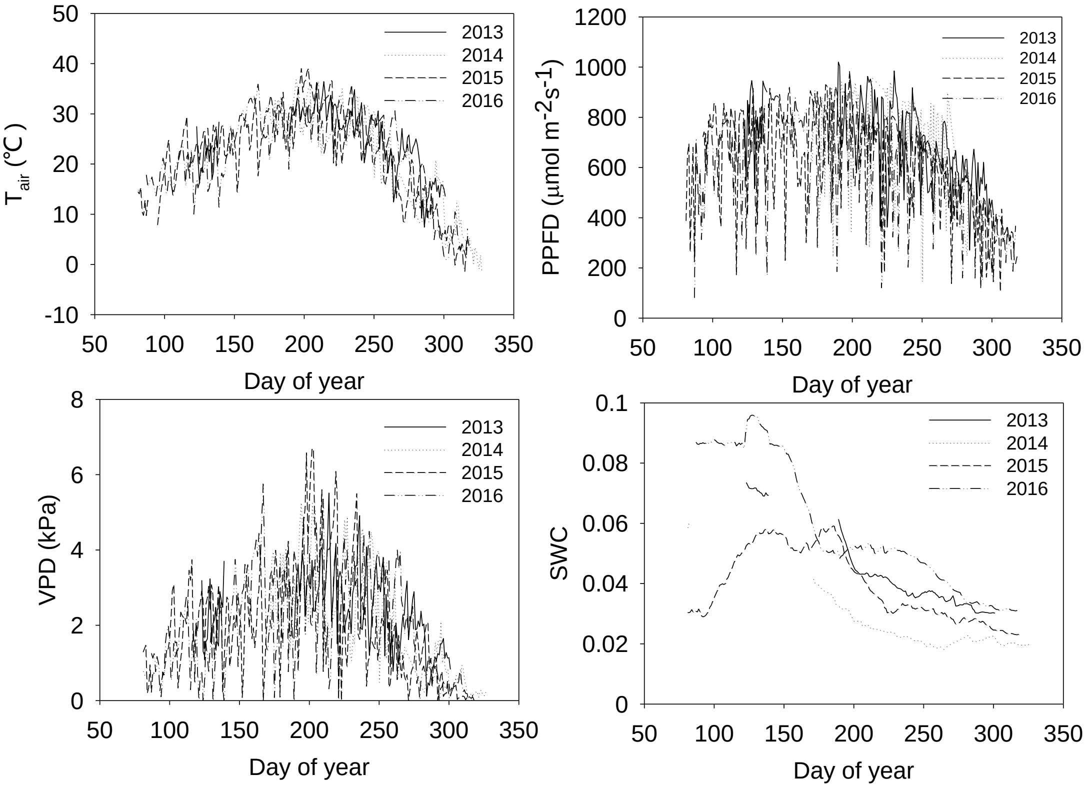

Fig. 4-1 Seasonal variation of daily average T_{air} (a), PPFD (b), VPD (c) during day time when PPFD ≥ 40 μmol m^{-2} s^{-1} and SWC (d) during growing seasons from 2013 to 2016. Part of data missed resulting from power or sensors failure.

4.3.2 Response of assimilation parameters to SWC

During the growing season from 2013 to 2016, the fitted aggregate 5-day ecosystem apparent quantum use efficiency of carbon uptake (QUE_{app}) ranged from 0.001 to 0.009 μmol μmol^{-1} and averaged 0.004 μmol μmol^{-1} (Fig. 4-2 a). The fitted 5-day aggregate gross primary productivity rate under saturating photon flux density (GPP_{sat}) ranged from 1 to 4 μmol m^{-2} s^{-1} and averaged 2.13 μmol m^{-2} s^{-1} (Fig. 4-2b). Both QUE_{app} and GPP_{sat} were significantly correlated with SWC ($P < 0.01$) and linearly increased with increasing SWC (Fig. 4-2).

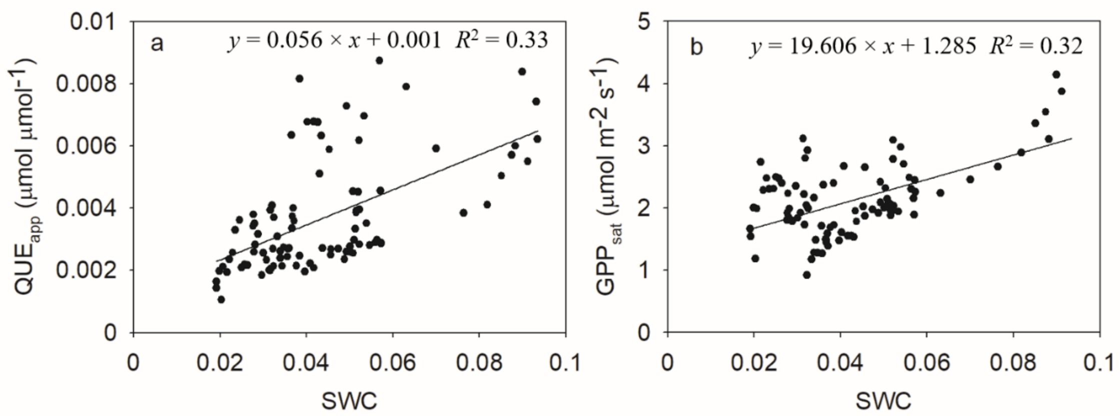

Fig. 4-2 Responses of fitted 5-day aggregate ecosystem QUE_{app} (a) and GPP_{sat} (b) to SWC during growing seasons from 2013 to 2016.

4.3.3 Response of ecosystem respiration to T_{air}

During the four growing seasons from 2013 to 2016, the fitted aggregate 5-day average ecosystem respiration (R_{eco}) varied from 0.06 to 1 μmol m^{-2} s^{-1} and averaged 0.44 μmol m^{-2} s^{-1}, while daily average R_{eco} ranged from 0.19 to 1.68 μmol m^{-2} s^{-1} with average of 0.59 μmol m^{-2} s^{-1}. Both the fitted aggregate 5-day R_{eco} and daily R_{eco} were significantly correlated with air temperature (T_{air}, $P < 0.001$) and increased exponentially with increasing T_{air} (Fig. 4-3).

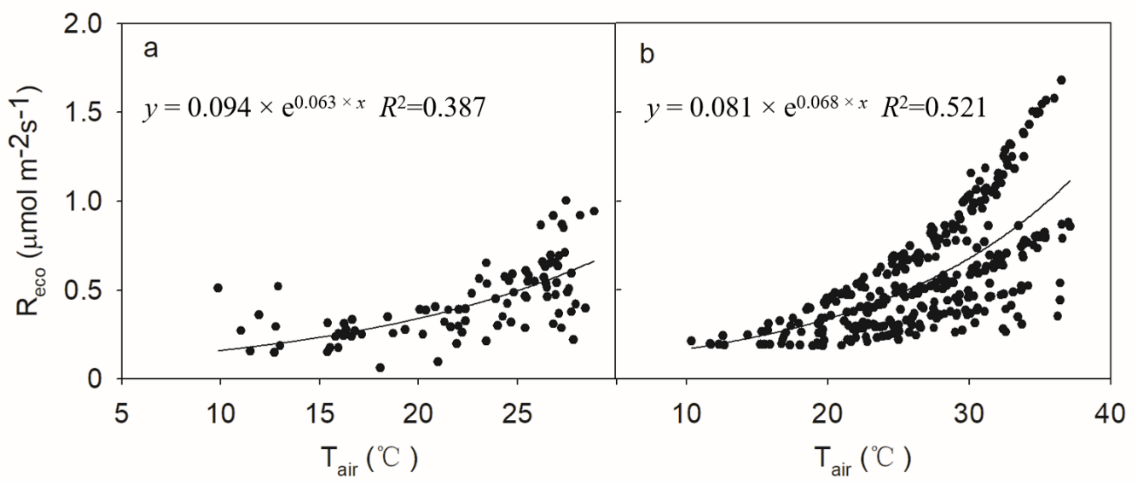

Fig. 4-3 Response of 5-day integrated (a) and daily average (b) ecosystem respiration to air temperature.

4.3.4 Seasonal variation of GPP, R_{eco} and their response to SWC

During the four-year study period, daily mean R_{eco} increased in spring and decreased in autumn, with peak rates of 2 μmol m^{-2} s^{-1} occurring in summer. The average R_{eco} during the period was 0.59 μmol m^{-2} s^{-1}. The daily average GPP increased rapidly from early spring, reaching a maximum in mid spring, but then declining continuously until the end of the growing season. Daily GPP varied from 0 to 6 μmol m^{-2} s^{-1} and averaged 1.79 μmol m^{-2} s^{-1} over the entire growing season (Fig. 4-4 a). Both ecosystem GPP and R_{eco} were positively and significantly ($P < 0.001$) correlated with SWC. The sensitivity to soil drought (defined as the slope of regressed linear function between GPP/R_{eco} and SWC) of ecosystem GPP was approximately 3.8 times higher than that of R_{eco} (Fig. 4-4 b). As a result, net ecosystem CO_2 exchange (NEE) declined significantly ($P < 0.001$) with increasing SWC following a quadratic function (Fig. 4-5 b).

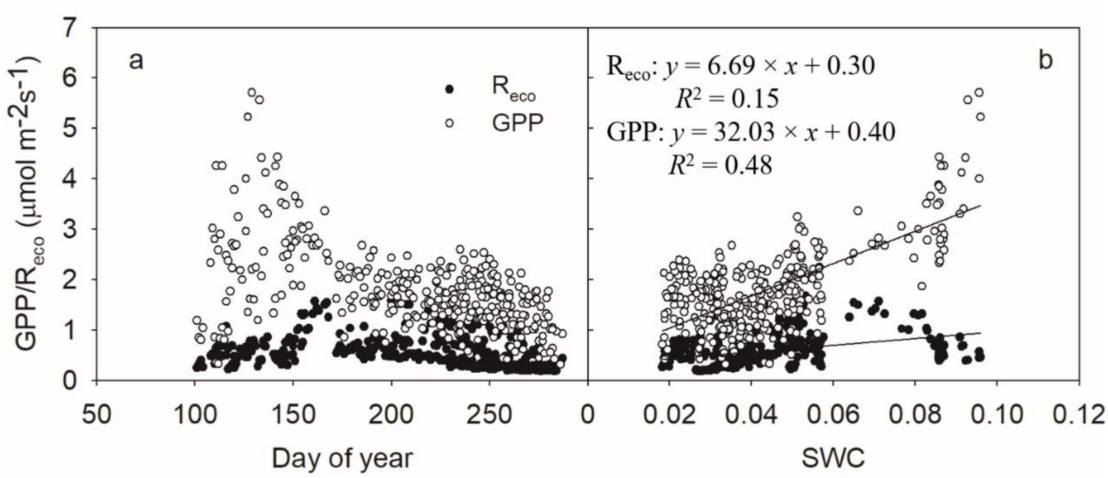

Fig. 4-4 Seasonal variation of daily average ecosystem GPP and R_{eco} during daytime when PPFD ≥ 40 μmol m^{-2} s^{-1} (a) and their response to SWC at 20 cm depth (b) during growing seasons from 2013 to 2016.

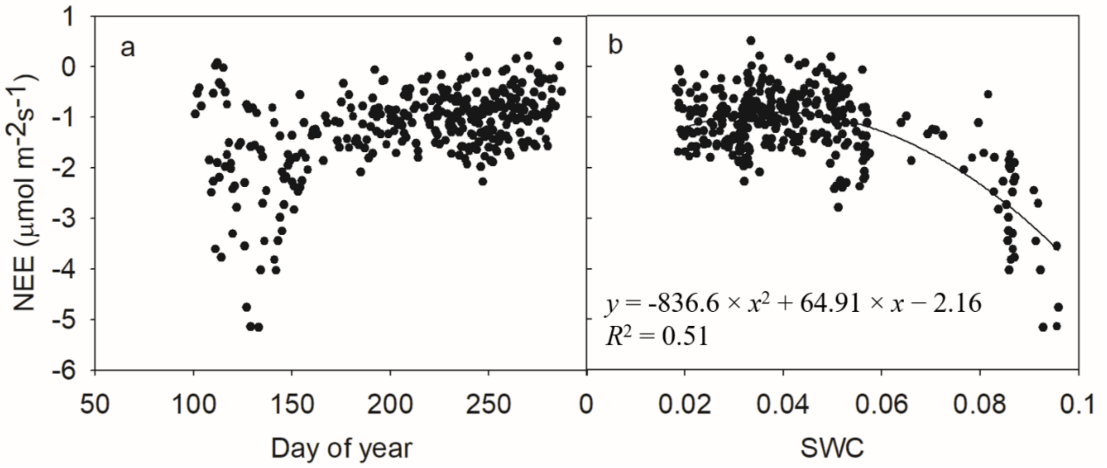

Fig. 4-5 Seasonal variation of daily average ecosystem NEE during daytime when PPFD ≥ 40 μmol m^{-2} s^{-1} (a) and its response to SWC at 20 cm depth (b) during growing seasons from 2013 to 2016.

4.3.5 Seasonal variation of GPP and R_{eco} response to SWC

In spring, both GPP and R_{eco} were positively and significantly ($P < 0.05$) correlated with SWC (Fig. 4-6 a). The sensitivity of GPP to SWC was 11.32 times higher than that of R_{eco} (Fig. 4-6 d). In both summer and autumn, R_{eco} was positively and significantly ($P < 0.001$) correlated with SWC while GPP was not ($P > 0.05$, Fig. 4-6 b-c). Among the three seasons, the sensitivity of R_{eco} to SWC continually increased from spring to autumn (Fig. 4-6 d). Sensitivity of GPP to SWC was highest in spring, despite the lack of significant correlation between GPP and SWC in both summer and autumn (Fig. 4-6 d).

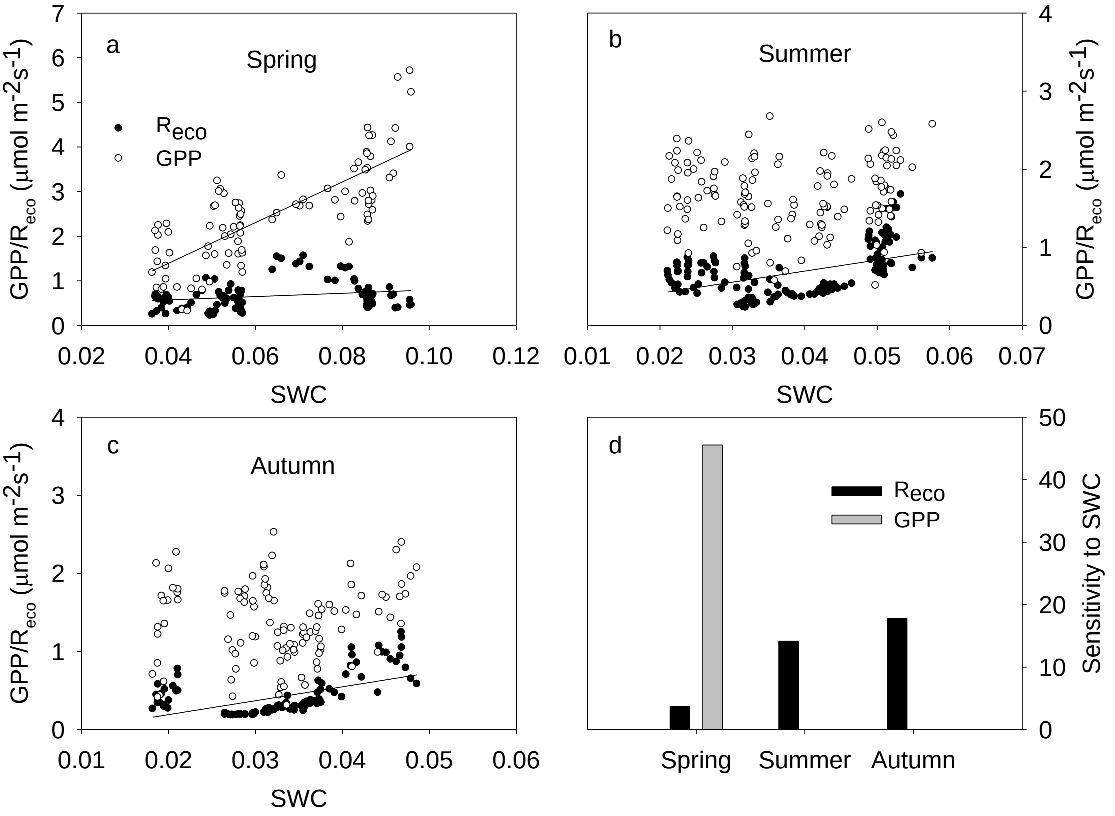

Fig. 4-6 Response of daily average ecosystem GPP and R_{eco} during daytime when PPFD ≥ 40 μmol m^{-2} s^{-1} to SWC in spring (a), summer (b) and autumn (c), and the sensitivity of both GPP and R_{eco} to SWC (defined as the slope of linear regression between SWC and GPP, R_{eco}) in three seasons (d) during growing seasons over 2013 to 2016.

4.3.6 Seasonal variation of daily ET, WUE and their response to SWC

During the growing season, daily average ecosystem evapotranspiration (ET) ranged from 0.11 to 2.54 μmol m^{-2} s^{-1} with average of 0.76 μmol m^{-2} s^{-1}. At seasonal scale, daily ET declined near linearly from spring to autumn (Fig. 4-7 a). Daily ET showed significant correlation with SWC and the relationship between them could be described using a cubic function (Fig. 4-7 b).

Daily average ecosystem water use efficiency (WUE) showed relative stable and varied from 0.02 to 16.03 μmol $mmol^{-1}$ with average of 3.62 μmol $mmol^{-1}$ during growing season (Fig. 4-8 a). Daily average WUE had significant correlation with SWC and showed increase and then decrease trend with increasing of SWC with the highest WUE appeared when SWC was around 7%, which could be fitted through a cubic function (Fig. 4-8 b).

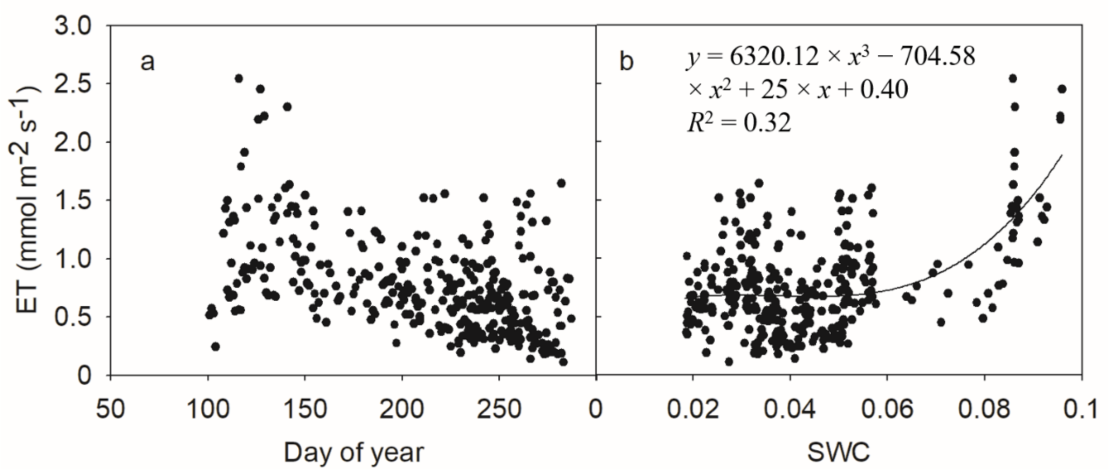

Fig. 4-7 Seasonal variation of daily average ecosystem ET during daytime when PPFD ≥ 40 μmol m^{-2} s^{-1} (a) and its response to SWC at 20 cm depth (b) during growing seasons from 2013 to 2016.

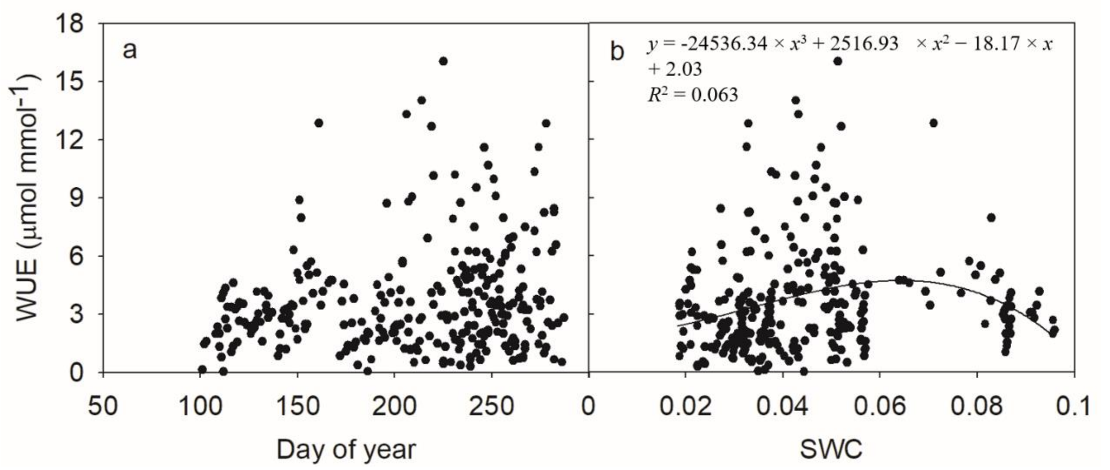

Fig. 4-8 Seasonal variation of daily average ecosystem WUE during daytime when PPFD ≥ 40 μmol m^{-2} s^{-1} (a) and its response to SWC at 20 cm depth (b) during growing seasons from 2013 to 2016.

4.3.7 Seasonal variation of evaporative fraction and its correlation with SWC, GPP and R_{eco}

During the growing season between 2013 and 2016, daily average evaporative fraction (EF) in daytime ranged from 0.04 to 0.65 and averaged 0.20. Daily EF was higher in spring and then declined in summer and autumn, but with strong seasonal fluctuations (Fig. 4-9 a). There was a significant ($P < 0.01$) positive correlation between EF and SWC and EF could be described as a linear function of SWC (Fig. 4-9 b). Daily EF was positively correlated with GPP, but negatively correlated with R_{eco}, and both relationships were poor but statistically significant ($P < 0.05$, Fig. 4-9 c).

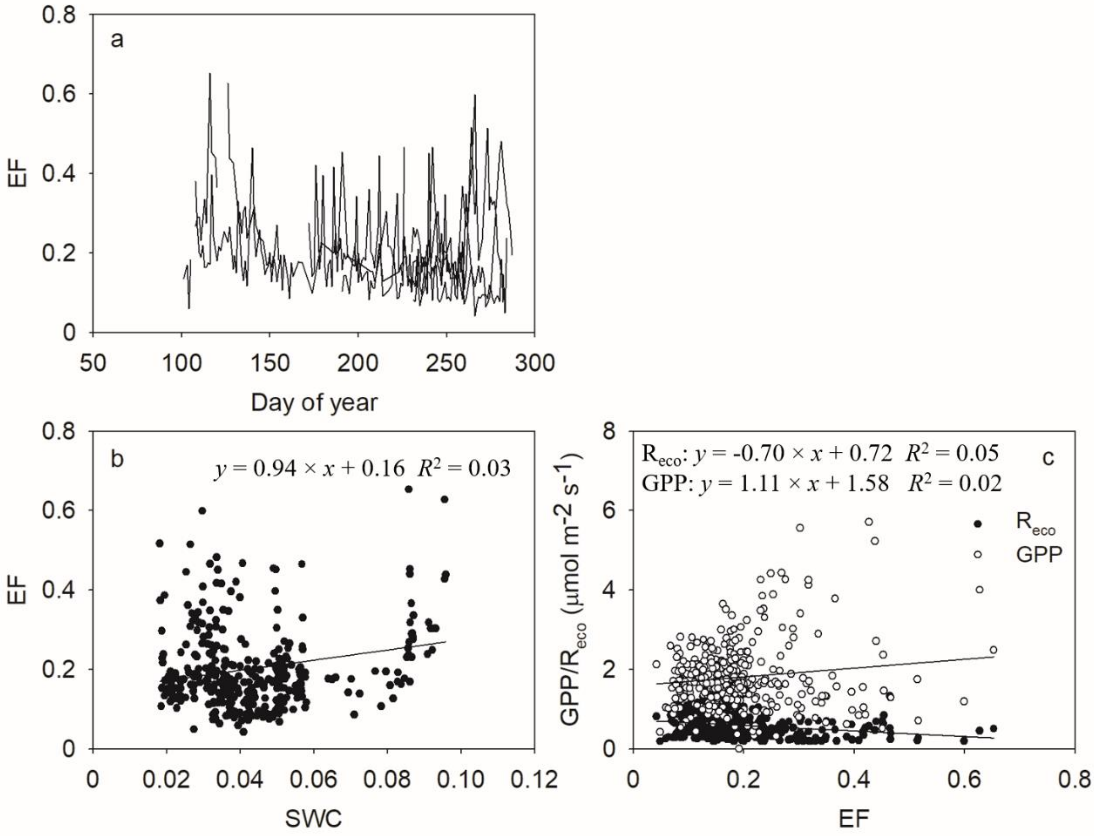

Fig. 4-9 Seasonal variation of daily average EF during growing seasons from 2013 to 2016 (a), response of daily EF to SWC (b) and response of daily GPP and R_{eco} to EF (c).

4.4 Discussion

4.4.1 Different drought effect on ecosystem assimilation and respiration

Soil water is the main water source of terrestrial surface ecosystem and its magnitude always related to drought intensity and has considerable effect on ecosystem process, especially carbon cycle in arid and semiarid lands (Jia et al. 2016). The significant correlation between ecosystem assimilation, respiration and soil water content at 20 cm depth indicated that soil water in surface layer was the main water source for this desert ecosystem. In addition to shallow-rooted herbaceous plants in under-canopy layer, the canopy shrub, *H. ammodendron*, was also proved to absorb soil water from shallow layer. An excavation experiment investigated near this study site showed that surface area of feeder roots of natural *H. ammodendron* decreased continually from surface to deeper layer and approximate 70% of feeder roots distributed within 0 to 50 cm soil layer (Xu et al. 2007). Furthermore, branch transpiration and leaf water potential of *H. ammodendron* were found to be sensitive to rain pulse events and precipitation-derived upper soil water (Xu and Li 2006). The shallow root system of dominated plants in this desert ecosystem decided the importance of shallow soil water in affecting ecosystem carbon cycle.

Suffering drought, plants generally lose part of turgor in guard cells and close partly the stomatal conductance, which in turn limit assimilation. Furthermore, plant photosynthetic ability could also be depressed by enzymatic activity which decreased under water deficit. During growing seasons from 2013 to 2016 in this study desert, both fitted aggregate 5-day ecosystem apparent quantum use efficiency of carbon uptake (QUE_{app}) and gross primary productivity rate under saturating photon flux density (GPP_{sat}) linearly decreased with decreasing soil water content (Fig. 4-2), indicating the decreased ecosystem assimilation capacity under drought. As a result, ecosystem gross primary production (GPP) linearly decreased with increasing soil drought intensity during total growing seasons at the site scale (Fig. 4-4). Similarly, ecosystem respiration also decreased linearly with soil drought, however, its sensitivity to drought was lower than that of ecosystem assimilation, leading to a decline of carbon sequestration capacity in this temperate desert ecosystem under increasing soil drought intensity. The similar results had also been found in a temperate desert grassland in Inner Mongolia where the inter-annual ratio between sensitivities of GPP and R_{eco} to soil water content varied from 1.96 to 4.10 times (Yang and Zhou 2013). This result was also similar to that found at global scale (Schwalm et al. 2010) but the difference between the sensitivities of ecosystem assimilation and respiration to drought in this study (3.8 times) was higher than that of global terrestrial average level (0.5 times). This results stand for the conclusion that differential sensitivity to drought between ecosystem assimilation and respiration increased as drought intensity increased, which derived from a synthesized analysis on published observational and experimental results (Shi et al. 2014). The results found in this study indicated that the sensitivity of carbon sink to drought in this extreme drought desert was much higher than that of global terrestrial average level.

Due to seasonal variation of vegetation structure, phenology, soil water availability and climate variables, sensitivity of ecosystem assimilation and respiration to soil drought were not always constant in various seasons. During spring in this study when short-life herbaceous plants were active, sensitivity of ecosystem assimilation to drought was higher than that at whole growing season, however, ecosystem assimilation behaved no response to drought during summer and autumn when herbaceous plants dried out (Fig. 4-6 b-c). In addition, ecosystem GPP during spring when herbaceous plants were active was the highest in whole growing season. Both of them showed that herbaceous plants dominated carbon uptake magnitude and its response to soil drought in this desert ecosystem. This may resulted from dominated coverage of herbaceous plants in this study site (approximate 80%). The dominated role of understory herbaceous plants in affecting ecosystem carbon cycle in this desert ecosystem was similar to a humid savanna ecosystem in western Kenya (Otieno et al. 2015) and a seasonal drought Mediterranean oak woodland with scattered trees and a herbaceous ground layer (Pereira et al. 2007). The density and height of herbaceous plants mainly dominated by spring melted snow water, so the effect of winter precipitation on the following circannual ecosystem carbon cycle should be paid more attention in future in temperate desert ecosystems. On the other hand, these results also indicated that assimilation of canopy shrub, *H. ammodendron*, had weak response to drought during summer and autumn which was the driest period in whole growing season (Fig. 4-6 b-c). This may related to high adaptive capacity of *H. ammodendron* to desert drought or extreme drought conditions during summer and autumn in the measured four years. Although most of feeder roots of *H. ammodendron* distributed in shallow soil layer, the deep roots could also extend to an average depth of 3.32 m (Xu et al. 2007), which may benefit from deep soil water and then maintain survival of *H. ammodendron* and loosen the response of assimilation to extreme drought. Not similar to ecosystem assimilation, sensitivity of ecosystem respiration to drought continually increased from spring to autumn accompanied with lower soil water content (Fig. 4-6). The seasonal pattern of ecosystem assimilation and respiration sensitivity to drought was different with that of integrated global terrestrial ecosystem where the highest sensitivity of both ecosystem assimilation and respiration to drought occurred in climatic summer (Schwalm et al. 2010). This may resulted from unstable vegetation structure and special phenology of dominated vegetation among intra-annual growing seasons in this study.

4.4.2 Soil drought effect on desert ecosystem water use efficiency

For closed forests, canopy vegetation contribute most of ecosystem CO_2 and H_2O exchange, so soil water deficit affect ecosystem WUE mainly through stomatal conductance which is the main exchange way for both CO_2 and H_2O (Liu et al. 2005, Ponton et al. 2006, Yang et al. 2009). However, soil drought effect on WUE of desert ecosystem that dominated by sparse vegetation may be different and more complex, which including the non-negligible effects of under-canopy vegetation and/or bare soil surface. In this study, both ecosystem assimilation (GPP) and water loss (ET) increased with increasing soil water content, but their sensitivity to SWC were not consistent, inducing different WUE variation trend under various soil moisture levels. As soil was extreme drought when SWC approximately less than 6%, both GPP and ET had weak response to SWC, as a result, ecosystem WUE showed a weak response to increasing SWC. As SWC was larger than 7%, both GPP and ET increased dramatically with increasing SWC and the response rate of ET to SWC was higher than that of GPP, causing ecosystem WUE decreased following increasing SWC. The results showed that there was a drought threshold triggering ecosystem WUE response to drought. Ecosystem water use efficiency of this desert showed weak or no response to SWC when it was less than the drought threshold, above which, however, soil drought could induce the increase of ecosystem WUE. Most of the SWC data larger than 7% occurred during spring while the SWC data less than 6% mainly occurred during summer and autumn. Thus the ecosystem water use efficiency may influenced by both soil water content and vegetation phenology, whose contribution, however, cannot be separated from each other based on current collected data in this study. In a temperate semi-arid steppe in Northern China, ecosystem water use efficiency increased with improved annual precipitation input in a simulated experiment (Niu et al. 2011), which was contrast with results in this study. The response of ecosystem WUE to SWC in whole growing season was also different with the results found in various closed forest ecosystems (Reichstein et al. 2002b, Beer et al. 2009, Wagle and Kakani 2014). The special response pattern of ecosystem WUE to soil drought may result from single or common effects of soil drought intensity, season and related seasonal variation of vegetation species composition and their phenology. Although cannot be separated from other controlling variables, shallow-rooted herbaceous plants was expected to play important influence on seasonal pattern of ecosystem WUE response to soil drought with consideration of its active period during only spring and its dominate coverage in this desert ecosystem.

4.4.3 Suitability of EF as a soil drought index to trance carbon exchange in desert ecosystem

Generally, low evaporative fraction (EF) meant low proportion of available energy devoted to evaporate water, which in turn restricted mainly by available evaporative water (Kurc and Small 2004). Therefore, EF could be used as a proxy of soil drought and had been integrated into satellite-based ecosystem GPP simulation models (Running et al. 2004, Yuan et al. 2015). In this study, EF significantly correlated with SWC and ecosystem assimilation and respiration although the correlation was not robust (Fig. 4-9). These results were similar to that found at site scale of cropland (Yuan et al. 2015) and that found across global scale which including 11 biomes and 238 tower sites (Schwalm et al. 2010). However, the correlation (R^2) between EF and ecosystem GPP, R_{eco} were much less than that between SWC and carbon exchanges, even EF and SWC had opposite effects on ecosystem respiration (SWC actively correlated with R_{eco} while EF negatively correlated with R_{eco}, Fig. 4-4 b and Fig. 4-9 c). Therefore, energy partitioning not tightly coupled with carbon cycle, and EF was not a strong proxy of soil drought and failed to trance response of ecosystem carbon cycle to drought precisely as soil moisture did in this desert ecosystem.

Besides available soil water, evaporative fraction is also correlated with other biological and abiotic processes which may decouple the correlations between ecosystem energy partitioning and available water source, carbon exchanges. In water-limited Southern Great Plains of Unite states, EF acted as a linear function of soil moisture only when soil moisture located between wilting point and crucial value and when daily net radiation above the normal level, and the relationship between them varied substantially from year to year (Ford et al. 2014). Similarly, EF was also found to decrease linearly with more soil water deficit only when soil water content less than approximate 50% of field capacity in a tussock grassland (Hunt et al. 2002). In this study site, short-life herbaceous plants broke out in the early spring and then died in late spring, approximate more than 80% of ground surface was covered by dry herbaceous plants in summer and autumn. The existence of withered grass layer tended to increase the ecosystem albedo, reduce the proportion of available energy to evaporative surface water and then tended to weaken the correlation between soil moisture and evaporative fraction as found in this study (Fig. 4-9 b). In this context, evaporative fraction had become a week proxy of soil drought during total growing season in this study desert and thus behaved low correlation with ecosystem carbon cycle. Schwalm *et al*. (2010) found that relative low EF related with absence of new foliage during spring when soil moisture was abundant in an integrated analysis including 29 deciduous broadleaf forests, and concluded that it was not prognosticative to view EF as an index of soil water status. This integrated analysis together with results found in this desert study commonly indicated that EF was not a faithful proxy of soil moisture status during periods when vegetation structure varied resulted from different phenology of various plant species in a mixed ecosystem. This was different with other ecosystems where vegetation structure were stable and dominate species phenology were relative consistent during most of growing season and thus evaporative fraction acted robust link to drought and ecosystem carbon cycling (Schwalm et al. 2010, Yuan et al. 2015).

Another phenomenon of failure for evaporative fraction to trance drought effect on carbon cycle in this studied desert was that EF and SWC showed opposite effect on ecosystem R_{eco} (Fig. 4-4 b and Fig. 4-9 c). In temperate area, air temperature is one of the dominated factors affecting ecosystem respiration (Flanagan and Johnson 2005, Yvon-Durocher et al. 2012). In this study site, both fitted 5-day aggregated and daily average ecosystem respiration significantly correlated with air temperature and increased exponentially with increasing air temperature (Fig. 4-3). Soil respiration was also found to be tightly correlated with air temperature in the same study site (Guan 2015). During spring when herbaceous plants were active, evaporative fraction was high while air temperature and related ecosystem respiration was at relative low level (Fig. 4-1 a and Fig. 4-4 a). On the contrary, during summer and autumn when herbaceous layer died, evaporative fraction was limited to some extent by the coverage of dry grass, while air temperature and related ecosystem respiration in this period were at high level (Fig. 4-1 a and Fig. 4-4 a). The special seasonal regime of vegetation phenology, air temperature and related ecosystem respiration jointly induced the negative effect of evaporative fraction on ecosystem respiration, which was contrast to the effect of soil drought on ecosystem respiration. In tropical evergreen broadleaf forests, decrease of EF during onset of dry season linked to less rainy days and higher solar radiation, which in turn promoted both assimilation and respiration of forests that commonly have deep root system to access deep soil water stores. As a result, similar relationship generated as this study in desert that EF and carbon exchange negatively correlated (Schwalm et al. 2010). These emphasized the complexity of interaction between energy partitioning and ecosystem carbon cycle. In addition, vegetation rooting depth, precipitation pulse, and canopy shrub also affect both energy partitioning and carbon cycle processes with different strategies, these together imposed the uncertainty in trancing drought effect on ecosystem carbon cycle using evaporative fraction in this desert ecosystem.

4.5 Conclusion

Carbon and energy flux were measured using eddy-covariance technology during growing seasons from 2013 to 2016 in a *H. ammodendron*-dominated desert near southern edge of Gurbantünggüt desert in Central Asia. Ecosystem GPP and R_{eco} were separated by fitting light response curve of NEE and their sensitivity to drought were analysed with SWC and EF as proxy of drought. In the whole growing season, both GPP and R_{eco} linearly decreased with more soil water deficit but the sensitivity of GPP to SWC was 3.8 times higher than that of R_{eco}, inducing a decrease of carbon sequestration capacity under soil drought. At seasonal scale, GPP significantly correlated with SWC only in spring while R_{eco} significantly correlated with SWC in each growing seasons and the sensitivity increased continually from spring to autumn. The ecosystem carbon cycle and its response to drought mainly driven by short-life herbaceous plants. EF decoupled with SWC mainly resulted from death of herbaceous plants in late spring which covered large portion of the desert surface and influenced the partitioning of available energy. The seasonal regime of air temperature and activity of herbaceous plants jointly leaded negative correlation between EF and R_{eco} that contrast with relationship between R_{eco} and SWC. Energy partitioning not tightly coupled with ecosystem carbon cycle in this desert, and EF was not a competent proxy of soil drought and not suitable to trance response of ecosystem carbon cycle to drought as soil moisture did in this desert ecosystem.

CHAPTER 5 GENERAL DISCUSSION

Drought is expected to have strong effects on ecosystem material and energy cycles at a large proportion of terrestrial ecosystems. Drought effect has attracted abundant field and laboratorial studies, however, there are still many key aspects that are far from clear, especially in arid ecosystems resulting mainly from rare long-term field measurement (Lioubimtseva and Henebry 2009, Fu et al. 2017). Another fact that make drought effect complex is that drought effects are study scale, species, drought intensity, and plant phenology dependent.

Gas exchange models, especially physiology process-based models are usually used to estimate ecosystem- or larger-scale fluxes based predominantly on simulations of leaf-scale water and carbon physiology processes and simulation of canopy and vegetation structure and related spatial distribution of environment variables, such as solar radiation and air temperature (Baldocchi and Harley 1995, Pury and Farquhar 1997, Adiku et al. 2006). Considering the simplified ecosystem structure and basic physiology processes, a large number of leaf scale input parameters which are often hard to obtain accurately may induce estimation (output) errors at larger scales (Amthor 1994). Moreover, leaf and larger scale structures (whole plant, for example) may behave differently, which also induce scale-related simulation errors. The latter was verified in current study for the dominate species, *H. ammodendron*, in a typical desert ecosystem located in Central Asia. The different diurnal pattern, air drought response of transpiration and stomatal conductance per leaf area among leaf, branch and whole plant scales showed that whole plant has some characters that do not occurred at smaller scales (i.e. leaf or branch scale), which usually are crucial strategies for their survival under stress of severe arid environment. Canopy patchiness can be employed to explain perfectly the un-convergent transpiration and stomatal response to air drought over leaf, branch and whole plant scales. Based on current and previous studies, drought-induced canopy- or larger-scale patchiness need to be introduced into gas exchange simulation models via suitable methods for more accurate simulation. Although the phenomenon of canopy patchiness of *H. ammodendron* has been reported by previous studies through comparing branch- and whole-plant scale transpiration response to environment variables (Zheng and Wang 2014), the advantages of this study are comparison in transpiration response to climate drivers and the underlying un-convergent stomatal regulation on water loss at total organic scales (i.e. leaf, branch and whole plant scale), which deepen our understanding of the process of canopy patchiness.

Vegetation response to drought are also depend on dry intensity or severity. The relationship between drought intensity and its effect on biome functions is not always consistent among various intensities. Drought effects are predicted to be mutational when drought extends its low threshold (Nepstad et al. 2007, Plaut et al. 2013). However, the drought threshold is not included in gas exchange simulation models mostly. The absence of drought threshold in models will introduce large errors when drought is approaching and lower than the threshold value and thus make the models are insensitive to extreme drought conditions. Drought threshold of plants is usually estimated through comparing plant response to different drought intensities under controlling experiment conditions (Desprez-Loustau et al. 2006, Nepstad et al. 2007, García‑Fernández et al. 2013). However, the results got in artificial conditions may cannot represent natural status. On the other hand, the rare of long-term field measurement and of appearance of extreme drought events further induced difficulty in integrating drought threshold into gas exchange simulation models. Fortunately, our field measurement experiment experienced different-degree soil drought during the second half of growing seasons over four years from 2013 to 2016 in a desert ecosystem. Through comparing different transpiration and stomatal response to soil drought intensities during prolonged drought period (second half of growing season), 3% is estimated as the low soil drought threshold for survival of *H. ammodendron*, bellow which the dominate desert species in Central Asia lost the ability in stomatal regulation on water loss and suffered the high risk of hydraulic failure and mortality. To our knowledge, the current study is the first time to estimate the drought threshold for dominate plants under natural conditions in temperate desert based on long-term (multi-year) field measurements.

Drought has significant effects on water partitioning and thus has tight correlation with carbon cycles at ecosystem scale. Drought effects on ecosystem assimilation and respiration have been abundantly studied in forest ecosystems considering their strong carbon sequestration capacity (Baldocchi 1997, Monson et al. 2002, Sun et al. 2006). With simple vegetation structure and low productivity, desert has not attract abundant studies on carbon sequestration capacity and its response to drought, leaving large gap in estimating each other feedback effects between desert ecosystem and climate change. Recently, desert ecosystem was proved to be a non-negligible part of carbon sink (Schlesinger et al. 2009, Li et al. 2015b), which reinforced the necessary of studies on drought effects on desert carbon sequestration. The results obtained in this field measurement through eddy covariance method during continuous four years verified that desert is a carbon sink and its assimilation sensitivity to soil drought was higher than that of ecosystem respiration over whole growing season, resulting to a decrease trend of carbon sequestration under soil drought. We also tried to use ecosystem evaporative fraction to trance drought effect on ecosystem assimilation and respiration in desert ecosystem for the first time. The low correlation between evaporative fraction and soil water content, ecosystem gross primary production and respiration revealed that energy partitioning for transpiration was not coupled to soil drought and carbon cycles, and evaporative fraction was not a suitable proxy of soil drought in this temperate desert ecosystem. This results indirectly highlighted the importance of short-lived herbaceous plants in controlling ecosystem carbon cycle and its response to soil drought in arid regions where trees or shrubs are sparse.

Although with limitation in number of study sites, the current study fills many important gaps of drought effects on desert ecosystem functions, and the results are expected to deepen our understanding on water and carbon cycles in arid ecosystems with desert as an extreme example.

CHAPTER 6 CONCLUSIONS AND FUTURE STUDIES

6.1 Conclusion summary

Drought is a crucial factor influencing nearly all biotic and abiotic processes in a large portion of terrestrial ecosystems on the earth. With enhanced effect of human activity on earth surface and related climate change, drought is becoming more limiting in many regions, especially in arid and semi-arid lands. In the current study, drought effects on key processes of water and carbon cycles were examined at different scales in a typical desert ecosystem in Central Asia.

H. ammodendron is the dominate species in the studied plot and is also the main study material in this research. All the data base for this analysis are obtained from field measurement. At leaf scale, portable gas exchange system was used to measure leaf transpiration rate. Transpiration of branch and whole plant was measured through sap-flow technology of stem heat balance and thermal dissipation, respectively. Ecosystem water and carbon dioxide fluxes were monitored using eddy covariance method above *H. ammodendron* canopy. Ecosystem GPP and R_{eco} were partitioned form NEE by 'top-down' models which include light response curve of NEE and air temperature and soil moisture response of R_{eco}. Stomatal conductance for water vapor was also estimated through 'top-down' model of Penman-Monteith (P-M) equation. Main meteorological factors and soil water content were also measured synchronously. The data was continually measured during growing season of *H. ammodendron*. SWC and VPD was viewed as soil and atmosphere drought, respectively, and EF was also tested whether it was a suitable drought proxy in this studied desert ecosystem.

Transpiration per leaf area were compared among leaf, branch and whole plant scales in diurnal pattern and their response to air drought and other climate variables. Stomatal conductance at three scales was also compared in their response to air drought. *H. ammodendron* showed higher maximum transpiration and stomatal conductance at leaf scale than that of branch and whole plant scales. Transpiration at three scales increased linearly with increasing VPD when it was at low level. However, at high VPD level, leaf- and branch-scale transpiration nearly saturated while that at whole plant scale decreased. Stomatal sensitivity to VPD (m/G_{sref}) increased continually from 0.35 at leaf scale to 0.52 at tree scale, showing that averaged whole plant-scale stomatal conductance was more sensitive to air drought than that at leaf and branch scales, and that *H. ammodendron* had more conservative water use strategy at whole plant scale than leaf and branch scales. Diverse diurnal patterns and response patterns of water use and stomatal conductance to air drought among leaf, branch and whole plant scales would likely show that a small number of leaves maintain relatively high stomatal conductance while most leaves have low stomatal conductance in the canopy under high VPD during midday and afternoon resulting canopy patchiness. Canopy patchiness could reduce whole plant water loss and allow partial assimilation by part of the canopy in mild drought, which is considered as one of the key mechanisms for arid species to balance water loss and carbon acquisition at whole plant scale under drought. Therefore, one must be cautious in up scaling leaf scale studies to canopy scale in order to avoid overestimation of plant response to drought.

Soil and air drought effects on canopy-scale water use and stomatal conductance for water vapor were also studied during second half growing season (from the first of August to early October when atmosphere temperature higher than 10 ℃) when annual prolonged drought occurred in continuous four years (2013-2016). When volumetric SWC was larger than 3%, daily canopy water use and its sensitivity to VPD (defined as the slope of linear regression between daily T_r and VPD) were linearly decreased with decreasing SWC. Meanwhile, canopy stomatal sensitivity to VPD (m/G_{sref}) increased linearly from 0.35 to 0.52, showing a transfer from more anisohydric to more isohydric with decreasing SWC. When SWC was less than 3%, daily canopy water use showed no response to variation of SWC, water use and stomatal sensitivity to VPD was higher and lower than that in the driest year when SWC larger than 3%. These results indicated that 3% was the lower soil water threshold for this species, below which this plant lost its ability in stomatal regulation on water loss and suffered high risk of mortality. The flexible stomatal response to air and soil drought and its regulation on water loss according to drought intensities was one key mechanism for *H. ammodendron* to make a balance between maximizing production when soil moisture was attractable and keeping hydraulic security when soil moisture was more limited in such severe and frequent drought environment.

At last, soil drought effects on ecosystem water and carbon key processes were examined and whether evaporative fraction (EF) can be viewed as a drought index was also tested during growing seasons in continuous four years (2013~2016). Both ecosystem GPP and R_{eco} were linearly decreased with declining of SWC, with the sensitivity of GPP to SWC 3.8 times higher than that of R_{eco} during the entire growing season, as a result, carbon sequestration capacity decreased continually with increasing soil drought. At seasonal scale, ecosystem GPP correlated significantly with SWC only in spring when under-canopy herbaceous plants were active while R_{eco} coupled significantly with SWC in all growing seasons (spring, summer and autumn) and the sensitivity of R_{eco} to SWC increased continually from spring to autumn. However, GPP sensitivity to SWC in spring was higher than that of R_{eco} in each of growing seasons. Ecosystem water use (ET) increased weakly when SWC less than 6% and then increased largely when SWC higher than 6% as SWC increased. As a result, ecosystem WUE showed a weak response to SWC. This was induced mainly by the sparse vegetation coverage in the severe drought ecosystem. Short-life herbaceous plants have considerable effect on the response of ecosystem carbon and water key processes to drought in this desert ecosystem. EF showed a weak correlation with SWC and explained only 2% and 5% of GPP and R_{eco} variation, respectively. So EF was not a good proxy of drought and failed to trance the response of ecosystem GPP and R_{eco} to soil drought in this desert ecosystem. The seasonal regime of herbaceous plant activity and climate variables jointly decoupled ecosystem energy partitioning process and carbon assimilation and respiration processes.

6.2 Future studies

Ecosystem response to drought is the integration of all biotic and abiotic effects and their interactions induced primarily by water deficit. Ecosystem crucial water and carbon processes have been examined in this study during drought conditions, which include transpiration of dominate shrub, *H. ammodendron*, and ecosystem water use, assimilation and respiration. However, there are some important aspects that have not been examined in this study resulting from limitation of time and equipment. In order to deeper understand drought effects on desert ecosystem, several potential works need to be studied in future, which including:

(I) The results in this study showed that contribution of *H. ammodendron* to ecosystem water and carbon response to drought was limit. So short-life herbaceous plants are non-negligible and need to be paid more attention in their response to drought. Under-canopy herbaceous species are shallow rooted and are predicted to have more strong response to drought than deep-rooted *H. ammodendron* and then have considerable contribution to ecosystem water and carbon response to drought. Thus, water and carbon exchange between herbaceous plants and atmosphere need to be monitored in long term. In addition, soil respiration and its response to drought need also to be explored in this desert ecosystem.

(II) Physiology-based models have been one powerful method to study ecosystem key processes and to predict evolution trend of ecosystem under climate change. All biotic and abiotic changes under water deficit need to be integrated into a process-based desert model to simulate ecosystem- and larger-scale ecological functions. The important physiology response of the dominate species to drought found in this study, such as canopy patchiness, stomatal sensitivity to drought and soil water low threshold, are crucial for accurate simulation of canopy water use during severe and prolonged drought. Moreover, establishment of a practical simulation model needs abundant field data for test and calibration, which also highlight the importance of longer-term and detailed field measurement.

(III) Vegetation response to drought also related to plant water usage among various water sources. Soil water at different depths, rainfall water, dew water and underground water are possible water sources for the dominated species in desert ecosystems and their contribution to vegetation transpiration are expected to vary with growing season and species. Stable isotope is a powerful technology to trance water cycle and plant water sources. Partitioning vegetation water sources using stable isotopic technologies can provide more information for ecosystem water cycle processes and accurately evaluate drought effects on plant and ecosystem functions, and also can provide support for policy making in ecosystem protection under the background of climate change. All this point to the necessary of water sources partitioning in future in this frangible arid ecosystem.

LIST OF FIGURES

LIST OF ABBREVIATIONS

symbol	meaning	unit
A_L	Leaf area	cm^{-2}
As	Sapwood area	cm^2
D	Branch diameter	cm
EF	Evaporative fraction	%
E_L	Transpiration per leaf area	mmol m^{-2} s^{-1}
ET	Evapotranspiration per ground area	mmol m^{-2} s^{-1}
GPP	Ecosystem gross primary production	µmol m^{-2} s^{-1}
GPP_{sat}	gross primary production under saturate photon flux density	µmol m^{-2} s^{-1}
g_s	stomatal conductance per leaf area	mmol m^{-2} s^{-1}
G_s	Canopy stomatal conductance per ground area	mmol m^{-2} s^{-1}
g_{sref}	stomatal conductance when VPD = 1kPa	mmol m^{-2} s^{-1}
G_{sref}	Canopy stomatal conductance when VPD = 1kPa	mmol m^{-2} s^{-1}
H	Sensible heat	W m^{-2}
K	Sensitivity of transpiration to vapor pressure deficit	mmol m^{-2} s^{-1} kPa^{-1}
LE	Latent heat	W m^{-2}
m	Stomatal sensitivity to vapor pressure deficit	mmol m^{-2} s^{-1} kPa^{-1}
NEE	Net ecosystem CO_2 exchange	µmol m^{-2} s^{-1}
PPFD	Photosynthesis photon flux density	µmol m^{-2} s^{-1}
QUE_{app}	Apparent quantum use efficiency	µmol $µmol^{-1}$
R_{eco}	Ecosystem respiration	µmol m^{-2} s^{-1}
RH	Atmosphere relative humidity	%
SWC	Volumatic soil water content	cm^3 cm^{-3}
T_{air}	Air temperature	℃
T_r	Transpiration rate	mmol m^{-2} s^{-1}
VPD	Atmosphere vapor pressure deficit	kPa
WUE	Ecosystem water use efficiency	µmol $mmol^{-1}$

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