Journal of Arid Environments 146 (2017) 44–52

Contents lists available at ScienceDirect

Journal of Arid Environments

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

Hydrologic thresholds and changes in ANPP of artificial sand-fixing vegetation in a desert-oasis ecotone in Northwest China

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ARTICLE INFO

Article history:
Received 7 September 2016
Received in revised form
21 July 2017
Accepted 25 July 2017
Available online 1 August 2017

Keywords:
Artificial sand-fixing region
Haloxylon ammodendron
Hydrologic thresholds
ANPP
Time lags

ABSTRACT

The interactive relationships between ecological and hydrological processes drive plant performance, community structure, and community succession in arid areas. Yet the nature of potential hydrologic thresholds for responses of vegetation remains poorly understood. In this paper, we report on hydrologic thresholds associated with aboveground net primary production (ANPP) of *Haloxylon ammodendron* (HA) and sand-fixation region (SFR) between 1987 and 2012 in the ecotone of desert and oasis in the northwest China. In particular, we focused on precipitation and soil moisture dynamics. Our results showed that 1) ANPP and soil moisture of both HA and SFR decreased from 1987 to 2005, and then reached a stable state; 2) nonlinear models provided a much better fit to the data than linear models, highlighting the presence of a discontinuity in vegetation ANPP changes along precipitation and soil moisture gradients; 3) precipitation, accumulated between preceding-year June to current-year August, of <160 mm, or soil moisture at < 1.4–1.5% may decrease ANPP. Our results provide insights into the thresholds of precipitation and soil moisture in a long-term sand-fixing ecosystem, and highlight the importance of legacy precipitation for the recovery of the sand-fixing ecosystem. Consequently, the findings provide useful references for further understanding of the mechanisms of ANPP changes in a sand-fixing ecosystem with changes in precipitation and soil moisture.

1. Introduction

Sand-fixation with vegetation is a key measure in controlling desertification and promoting ecological restoration of desert ecosystems (Li et al., 2014). In arid and semiarid environments, ecological processes (eg. aboveground net primary production) of sand-fixing vegetation have long been assumed to be a consequence of hydrological processes which determined the sustainability of this practice (McCluney et al., 2012; Moreno-de las Heras et al., 2012). However, the nature of potential thresholds in hydrologic processes of sand-fixing vegetation remains poorly understood. An increased understanding of such thresholds will strengthen the scientific basis for ecological system management of sand-fixing vegetation.

A change in the structure and function of an ecosystem is typically induced by environmental drivers or disturbances (Gao et al., 2011; Sasaki et al., 2007; Turnbull et al., 2012). The dynamics of aboveground net primary production (ANPP), representing the activity of vegetation (Li et al., 2013a; Wang et al., 2011; Zhao and Liu, 2010), is key to the understanding of ecosystem processes (Muldavin et al., 2008). Recent research on changes in ANPP of sand-fixing plants in the Shapotou region of China suggested that the numbers and biomass of shrubs (*Artemisia ordosica and Caragana korshinskii*) decreased over time since sand-fixation (up to 17 years), while the mass of microbes, percent vegetation cover, and the number of plant species attained maxima in dunes stabilized for 40 years (Wang et al., 2005). The Linze region is severely damaged by desertification. Planting of sand-fixing vegetation began here in 1980–1985. In the early period of revegetation in an area of 1700 ha, the main measures for stabilizing shifting sand dunes were planting of wheatgrass squares and sand-fixing shrubs such as *Haloxylon ammodendron* (HA), *Tamarix aphylla*,

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http://dx.doi.org/10.1016/j.jaridenv.2017.07.011
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Populus bolleana, and Hedysarum scoparium. HA, a pioneer species of desert ecosystems in northwestern China, plays a critical role in the reconstruction of desert ecosystems. However, with increasing age, planted HA forests appear to degenerate to different degrees, threatening ecological integrity of the oasis ecosystem. As a result, ecological recovery of HA has become the main focus of research in this area.

In desert ecosystems, precipitation is the most important source of water and determines the main material-transfer processes at the interface of soil, vegetation, and atmosphere (Li et al., 2013b; Wang et al., 2006). Dryland ecosystems have evolved with high variability in precipitation (Puigdefabregas, 1998; Wang et al., 2012). Recent results suggested that HA was not restricted by the minimum threshold of precipitation, but by the maximum of 180 mm (Ma et al., 2007). In addition, precipitation translates into soil moisture by moisture redistribution; soil moisture controls the growth of plants, vegetation succession, and landscape differentiation (Yang et al., 2014a). Volumetric soil moisture in shallow soil layers increased remarkably following sand-dune stabilization (Wang et al., 2005). Soil moisture in the Tengger desert decreased from 3 to 3.5% before to 1.5% about 9–10 years after planting, and became stable 40 years later at about 1.2% (Li et al., 2013b). Excessive soil moisture significantly decreased leaf area index (LAI) and growth of HA (Gao et al., 2010). Hydrologic variables that determine the distribution and abundance of vegetation must be further elucidated across sites with different ecological histories (Gao et al., 2011).

Variability in ANPP and in the course of succession in planted sand-fixing vegetation results mainly from variability in water inputs, and from factors such as vegetation structure and composition, rate of desertification, and soil characteristics which alter the response of vegetation to water (Lane et al., 1998; Verón and Paruelo, 2010; Yahdjian and Sala, 2006). The relationships between vegetation and water (rainfall and soil moisture) have been studied extensively at different temporal scales and at different levels, from individual plants to ecosystems (Bradford et al., 2006; Shafran-Nathan et al., 2012). The studies revealed two important effects: that of time lags in response to precipitation and that of hydrologic thresholds for specific plant responses. Time lags exhibit different levels of vegetation response to precipitation, and may be annual, seasonal, and individual (Fabricante et al., 2009; Heisler-White et al., 2009; Li et al., 2013b; Sala et al., 2012). Soil acts as a capacitor for moisture. Therefore, soil moisture effects include those of the previous year(s), and those of the previous-cool season precipitation (Bisigato et al., 2013). Previous years or cool-season precipitation controlled a significant fraction of the variability in the current-year plant productivity (Hamerlynck et al., 2013; Jobbágy and Sala, 2000; Reichmann et al., 2013; Sala et al., 2012; Yahdjian and Sala, 2006). However, at the scale of individual rainfall events, time lags reached a maximum of about one month (Li et al., 2013a).

Further, hydrological processes occurring are likely to exhibit thresholds for changes in vegetation structure and function (Gao et al., 2011; Sasaki et al., 2007; Turnbull et al., 2012). Critical thresholds are not linear, but rather abrupt at some threshold level (Asbjornsen et al., 2011; Sasaki et al., 2007), and result in banded or mosaic vegetation patterns in arid ecosystems (McDonald et al., 2009). The cusp-catastrophe model suggested that the potential response of an ecosystem to a change in the strength of one or more environmental factors is determined by the strength of ecohydrological feedbacks (Thom, 1975; Turnbull et al., 2012). Revegetation of desert regions changes the response of ANPP to hydrological processes. Moreover, the soil moisture threshold changes due to altered environmental conditions and human activities. These relationships between planted HA and hydrological processes in the mid-Heihe River region are yet to be identified.

To evaluate the ecological and hydrological processes in sand-fixing vegetation, we chose an area in a desert-oasis ecotone in the middle of the Heihe River. We used 25 years of data on discontinuous precipitation and soil moisture, and corresponding ANPP datasets for an area of sand-fixing vegetation. We addressed the following questions about the influence of sand-fixing vegetation: 1) how did the ecological and hydrological processes change from 1987 to 2013 in an area with sand-fixing vegetation? and 2) how are ecology and hydrology related, and are the relationships likely to exhibit response thresholds to hydrology?

2. Materials and methods

2.1. Study area

We conducted the study in a desert-oasis ecotone (39°21′ N, 100°07′ E, 1389 m) in the middle of the Heihe River Basin, in the northern Linze county of Gansu province (Fig. 1). The climate is arid to semiarid in a temperate continental desert. Mean annual temperature is 7.6 °C with an average low of −27.3 °C in January, and a high of 39.1 °C in July. Inter-annual precipitation is highly variable in amount and spatial distribution, averaging approximately 110 mm/y between 1967 and 2013, with an average of 75% falling between July and September. However, potential evaporation of 2390 mm/y is 20 times the amount of precipitation. Relative humidity is 46%. Wind direction is mainly from the northwest, and the wind speed averages 3.2 m/s, with frequent gales (wind speeds $\geq$ 21 m/s). Plant distribution is patchy over variable soil properties. Predominant vegetation at the study area includes shrubs and semi shrubs (HA, *Tamarix aphylla, Populus bolleana, and Hedysarum scoparium*) as well as grasses (*Bassia dasyphylla*, *Halogeton arachnoideus*). Soils in the study area are classified as aeolian sandy. Bulk density of this aeolian soil is 1.60–1.70 (g/cm^3). Groundwater level is at about ~6 m and cannot be utilized by the natural vegetation. Selected characteristics of the sand-fixation area are shown in Table 1.

2.2. Data

2.2.1. NDVI from Landsat

For this study, we used the growing-season MSS/TM/ETM/LDCM datasets between 1987 and 2012 to evaluate patterns of plant growth (Table 2). Landsat datasets, at 30 m spatial resolution, were acquired for years 1987–2012 from the following website: http:/earthexplorer.usgs.gov/ maintained by the NASA Land Processes Distributed Active Archive Center at the USGS. These datasets were discontinuous in the growing season. Landsat include spectral bands of red and near-infrared that are used to obtain the normalized difference vegetation index (NDVI), a remotely-sensed chlorophyll-sensitive vegetation index that, for semiarid landscapes, strongly correlates with green biomass levels (i.e., leaves and green stems of woody vegetation plus aboveground herbaceous biomass) (Berger et al., 2013; Gamon et al., 2013; Horion et al., 2013; Svoray and Karnieli, 2011). A series of processes such as atmospheric, radiometric, and geometric correction were conducted to ensure data quality. The images were clipped in ENVI 4.7 Software at the border of the sand fixation area.

Landsat data were selected for August of each year, and one scene only. However, the NDVI varied across months, and across days within months due to the occurrence of precipitation events. However, preliminary research indicated that the largest increment of NDVI was 0.015 when rainfall events were <30 mm, which was rare, and the ANPP of annual plants was <5 g/m^2 in early August; changes in ANPP were less distinct than in late August (Li et al., 2013a).

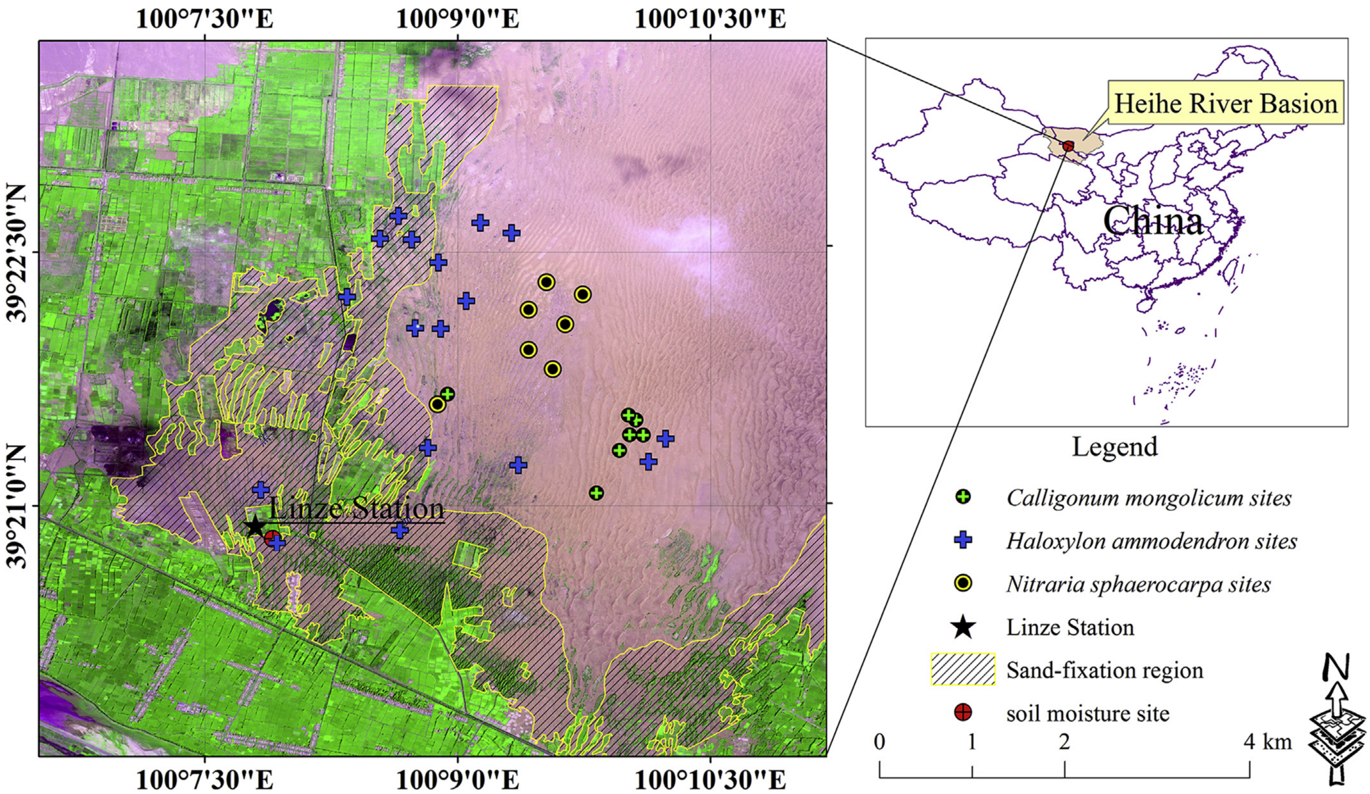

Fig. 1. Map of the study area and location in China.

2.2.2. Shrub sampling and ANPP estimations

Vegetation was sampled in August 2013. Thirty-three sites, 90 m × 90 m, were selected to determine ANPP of the sand-fixation area ANPP; of those sites, 16 contained HA, 7 contained *Calligonum mongolicum* (CM), and 7 contained *Nitraria sphaerocarpa* (NS). A total of 99 shrub quadrats, 25 m × 25 m, and 495 herb quadrats of 1 × 1 m^2 were established across the 33 sites (three shrub quadrats at each site, and five randomly-selected herb quadrats within each shrub quadrat). We determined vegetation cover, richness of shrub species, and the size of each plant (height and crown width) within shrub quadrats; then we selected 3 of each-large, medium, and small-sized plants. Aboveground productivity of each shrub was obtained by clipping the whole plant or its portion, removing new branches and leaves after the height and crown diameter were measured. Herbaceous density and cover were recorded for each species in each herb quadrat. Aboveground biomass of the herbaceous layer was obtained by clipping all biomass in a 1 × 1 m quadrat at ground level with 5 replications in each plot. All samples were oven-dried at 80 °C until constant weights was obtained. Sampling points are detailed in Fig. 1.

The NDVI was extracted for a cell grid of 90 m × 90 m corresponding to 3 × 3 pixels in our study sites for 1987–2013. To obtain ANPP for years 1987–2012, we first established a correlation equation between ground-surveyed ANPP and the corresponding remote sensing NDVI for 2013, and then applied the equation to all other years. Ground survey of ANPP in 2013 used crown-width data of individual to establish a relationship between plant crown width and ANPP for each plant. Then we calculated ANPP for site using characteristics of ground vegetation communities, including the combined crown width of all species converted to mass value per square meter. Ultimately, we determined the average ANPP of the sand-fixation area by establishing the relationship between ANPP and NDVI based on 33 sites, and the average ANPP of HA based on the 9 HA sites in the sand-fixation area.

2.2.3. Precipitation and soil moisture data

Meteorological data were obtained with an open-field weather station located at the study site. Rainfall was measured with a tipping-bucket rain gauge (model TE525, metric; Texas Electronics, Dallas, TX) and stored as 10-min mean data. Considering that precipitation after August in this desert ecosystem had no effect on August ANPP, and on the time lag in ANPP response to precipitation, we selected three time periods of precipitation: 1) previous summer (from June to August), 2) cool season (from previous

Table 1
The community characteristics of typical vegetation in the sand-fixation region.

Coenotype	Dominant species			Coverage (%)	Density (N/m^2)	Species
	Coverage (%)	Height (cm)	Density (N/m^2)			
Haloxylon ammodendron	55.2 ± 8.2	179.5 ± 60.8	0.22 ± 0.06	59.7 ± 7.6	102.6 ± 46.4	6
Tamarix aphylla	13.6 ± 4.6	204.3 ± 112.6	0.42 ± 0.12	15.3 ± 5.5	33.8 ± 7.36	13
Populus bolleana	65 ± 0.53	1450 ± 870	0.15 ± 0.01	72 ± 5.2	29 ± 0.15	6

The data stand for Mean ± SD.

Table 2
Regression statistics for the relationships between the growing season aboveground net primary production and precipitation in fixing-sand region and *Haloxylon ammodendron*.

Site		variables			Overall model			
		p	r^2	Slope	F	df	p	R^2
Haloxylon ammodendron	intercept	0.574		−12.932	9.965	2.12	0.003	0.56
	PPT ($June_{t-1}$–$February_t$)	0.048	0.18	0.423				
	PPT ($March_t$–$August_t$)	0.001	0.38	0.544				
	intercept	0.381		−18.031	20.708	1.13	0.001	0.58
	PPT ($June_{t-1}$–$August_t$)	0.001	0.58	0.509				
Sand-fixation region	intercept	0.388		−14.915	29.935	2.12	0.000	0.80
	PPT ($June_{t-1}$–$February_t$)	0.001	0.29	0.648				
	PPT ($March_t$–$August_{t)}$)	0.000	0.51	0.669				
	intercept	0.300		−15.814	64.747	1.13	0.000	0.82
	PPT ($June_{t-1}$–$August_t$)	0.000	0.82	0.663				

Both standardized regression sum of squares (R^2) and standardized partial regression sum of squares (r^2) are show, PPT represents the cumulative precipitation. t and t-1 represent the current year and previous year, respectively.

September to current February) and 3) warm season (from March to August). We also used 15 months cumulative precipitation.

We used previously-published soil moisture data for years 1970, 1977, and 1990 (Liu et al., 2002; Yang, 1987, 1991). The aeolian soil water potential was measured from April to August 2002–2012 using the oven-drying method. The soil at depths of 20, 40, 60, 80, 100, 120, 140, 160, 180 and 200 cm was sampled with three replicates at three random positions in each shrub quadrat, using an auger. Soil samples were dried at 105 °C for 12 h.

2.3. Statistical analysis

We determined the relationships between ANPP and crown width at individual scale, and NDVI and ANPP at site scale by linear regression. Also, we used multiple regression with forward selection to assess the sensitivity of ANPP to seasonal patterns of precipitation with cumulative precipitation from previous-year June to current-year August as predictors of ANPP. In addition, we analyzed nonlinear relationships between ANPP (SFR and HA) and hydrological processes (precipitation and soil moisture), and found that the best fitting curve for this relationship was sigmoidal. We used Origin 8.0 (OriginLab Corp., Northampton, MA, USA) for mapping, and statistics software SPSS (10th edn.; SPSS, Chicago, IL, USA) for data analysis.

3. Results

3.1. ANPP change in the sand-fixation region and in HA over 30 years

3.1.1. The relationships between crown width and plant productivity

The relationships between ANPP and plant crown width for HA, CM, and NS were significant ($p < 0.001$), and R^2 ranged between 0.78 and 0.93 (Fig. 2). On average, the slope of the relationship was steeper for HA that was <15 years old than for older (>15 years old); this was due to the faster growth of HA stable or recession.

3.1.2. The relationship between ANPP and NDVI and the change of hydrological processes

At the scale of a site (90 m × 90 m), ANPP of HA was well ANPP of HA was well-represented by the NDVI, and the determination coefficient was about 0.78 (Fig. 3). In the sand-fixation region, the regression relationship for ANPP used of other vegetation types and the corresponding NDVI, and the adjusted R^2 was 0.82. So the use of NDVI as a surrogate variable for ANPP was available for HA and for SFR.

Since 1985, plant productivity in the SFR including that of *Populus bolleana* and HA, fluctuated from 80 to 120 g/m^2, and in the HA

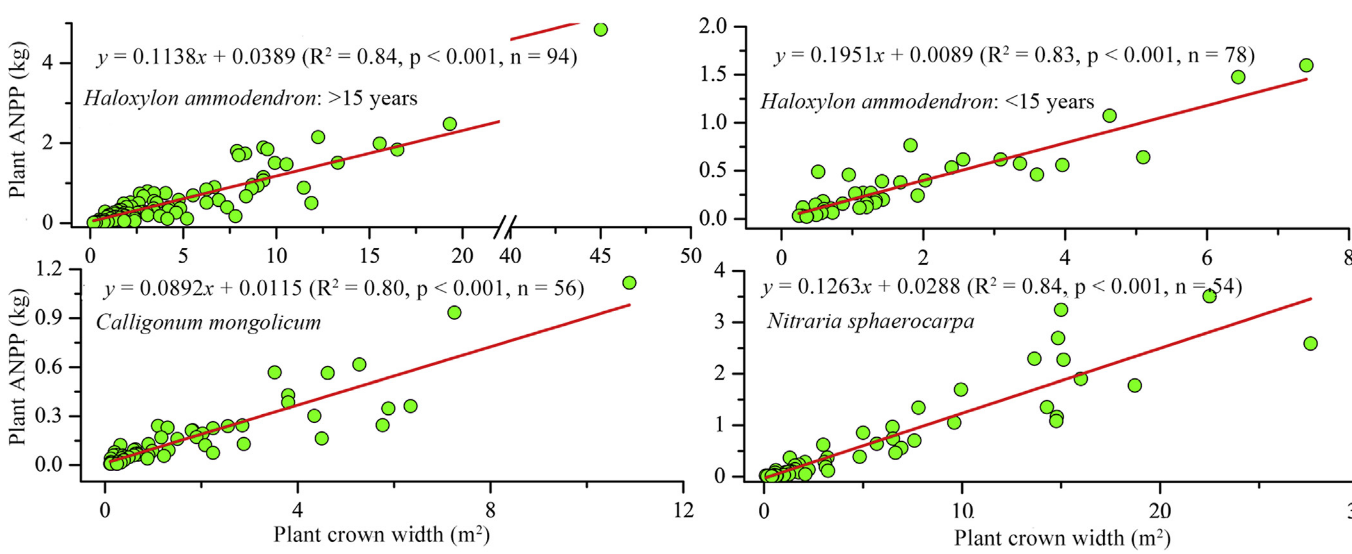

Fig. 2. The relationship between the crown width and individual plant productivity for different vegetation types.

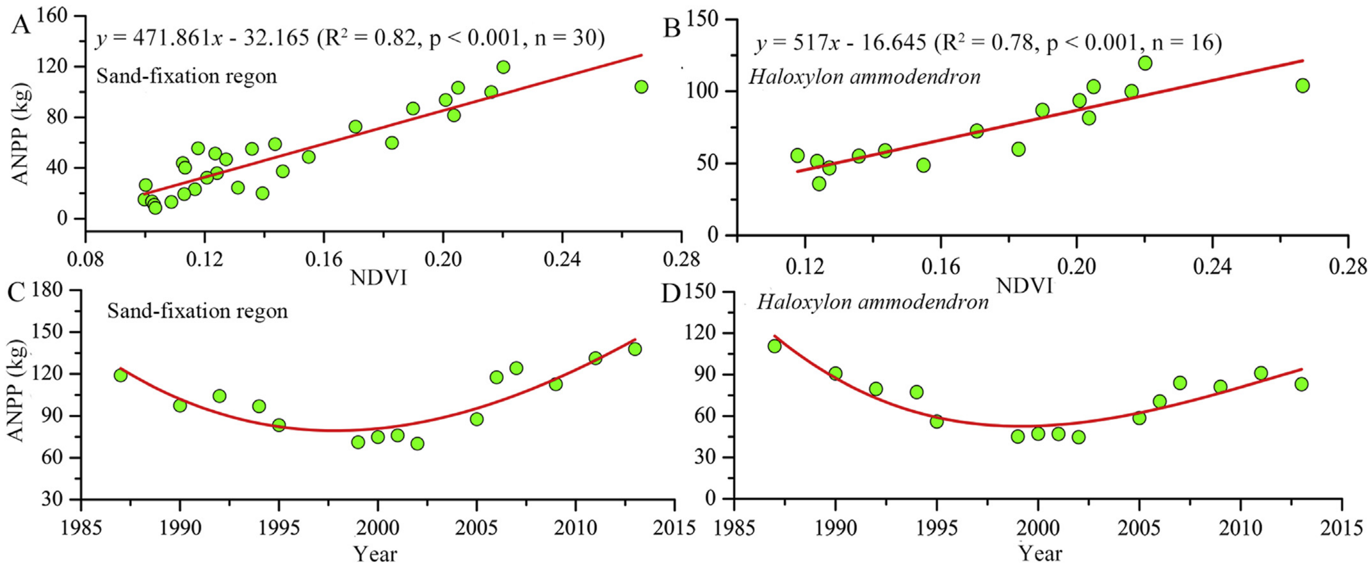

Fig. 3. The relationship between normalized difference vegetation index and aboveground net primary production at sand-fixation region and *Haloxylon ammodendron*, and aboveground net primary production changes with year following sand-fixation.

alone from 50 to 110 g/m^2 (Fig. 3). The lowest ANPP in the SFR and HA was observed around the year 2000; compared with the SFR, the higher slope of HA ($slope_{HA} = -5.04$, $p < 0.001$; $slope_{SFR} = -3.44$, $p = 0.001$) before the year 2000 subsequently declined ($slope_{HA} = 3.76$, $p < 0.001$; $slope_{SFR} = 5.47$, $p < 0.001$).

3.2. Changes in hydrological processes

In years 1987–1996, 1997 to 2003, and 2004 to 2013, current mean spring/summer precipitation was 95, 64, and 94 mm, respectively; mean previous fall/winter precipitation was 28, 21, and 34 mm, and the mean previous summer precipitation was 72, 54, and 69 mm, respectively (Fig. 4A).

After 40 years of sand-stabilization with HA, soil moisture changed the dune structure from shifting to part-mobile and semi-fixed dunes, although fluctuations were noted with changes in precipitation. Soil moisture in HA reached the lowest level about 25 years after planting, decreasing from 2.5% before to 1.4–1.5% after 25 years; subsequently, soil moisture was characterized by stable and small increases (Fig. 4B).

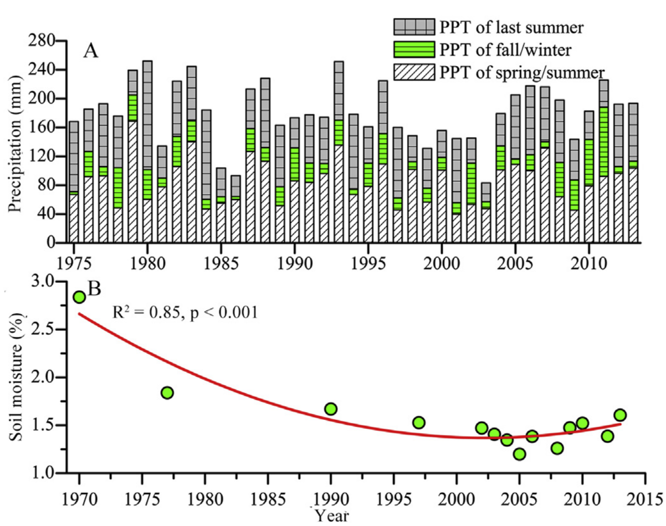

Fig. 4. The precipitation and soil moisture changes with year following sand-fixation. PPT represents the cumulative precipitation.

3.3. The relationships between ANPP and hydrological processes

3.3.1. The linear regression relationship between ANPP and precipitation

ANPP of SFR and HA was affected more by the cumulative previous-to-current summer precipitation than by precipitation in other periods including that in the hydrological year, and in cool and warm seasons. However, the adjusted R^2 values indicated that the lower proportion of the variation (56–58%) in the simulated data was explained by a linear regression (Table 2).

3.3.2. The nonlinear relationship between ANPP and precipitation

Variability in ANPP of SRF and HA exhibited a nonlinear (sigmoidal) function of precipitation accumulated from previous-year June to current-year August. For SFR, ANPP varied significantly with precipitation from 160 to 190 mm, and increased from 75 to 120 g/m^2 (Fig. 5). ANPP exhibited a high value of 120 g/m^2 at > 190 mm of rain, and a low value of 75 g/m^2 at < 160 mm of rain. However, precipitation of 160 mm was a threshold which abruptly changed the ANPP of HA (Fig. 5). At HA, ANPP fluctuated near 85 g/m^2 when precipitation was >160 mm; however, it fluctuated near 45 g/m^2 when precipitation was <160 mm. For SFR and HA, the nonlinear model had relatively narrow bootstrap confidence intervals (95% CI), especially around the threshold points where the rate of change in ANPP was sudden, particularly for HA.

3.3.3. The nonlinear relationship between ANPP and soil moisture

Changes in ANPP of HA were characterized by an abrupt nonlinearly increasing function of soil moisture, which was based on an average from April to October at soil depth of 0–180 cm (Fig. 6). The nonlinear function indicated that when soil moisture was <1.4%, the ANPP of HA was low at near 45 g/m^2, and when soil moisture was >1.5%, the ANPP was high at 85 g/m^2; these values corresponded to the precipitation levels of 160 and 190 mm, respectively. The soil moisture threshold for ANPP change in HA was

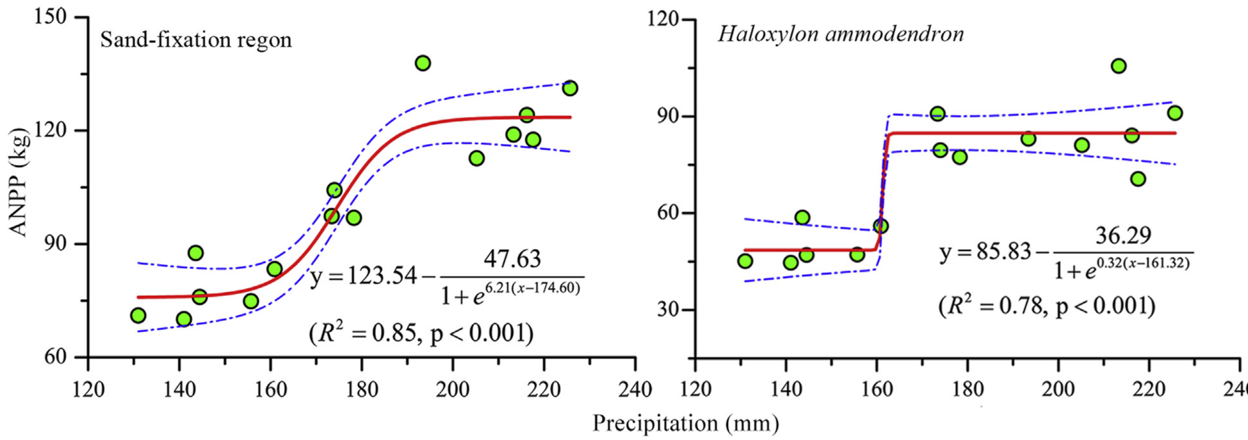

Fig. 5. Best-fit models of aboveground net primary production of sand-fixation region as a function of precipitation from previous year June to current August. Note that the nonlinear models fitted the data well, highlighting the discontinuity in vegetation changes along the precipitation. Each point corresponds to a year. Blue dashed lines indicate the 95% bootstrap confidence interval. The red solid line is the line fitted to predicted values from the sigmoid regression. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

approximately 1.4–1.5%, and marked by an abrupt rather than a continuous change in ANPP from 45 to 85 g/m^2.

4. Discussion

4.1. The relationships between plant growth and soil moisture

Our results showed that crown width determined plant productivity, and that NDVI was a suitable indicator for ANPP (Fig. 2; 3). The empirical relationships provided a convenient method to obtain ANPP without the need for destructive sampling of vegetation. We used direct field measurements and remotely-sensed NDVI data to establish a new high-accuracy database for a variety of species in the middle of the Heihe River basin. For HA, the change in ANPP and soil moisture may be expressed as a “decrease-stabilization-slight increase”; with an increase in plant age, these results may be explained as a self-thinning process (Chang et al., 2008) stemming from the balance of soil loading on water bearing force

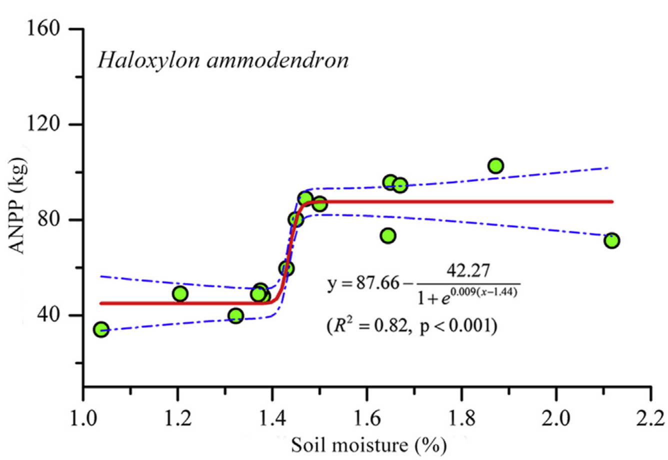

Fig. 6. Best-fit models of aboveground net primary production of sand-fixation region as a function of soil moisture. Note that the nonlinear models fitted the data well, highlighting the discontinuity in vegetation changes along the soil moisture. Each point corresponds to a year. Dashed lines indicate the 95% bootstrap confidence interval. The red solid line is the line fitted to predicted values from the sigmoid regression. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

(Li et al., 2014). Ma et al. (2007) indicated that the change from moving to revegetated sand dunes increased plant density to 1650 plants/hm^2 with soil moisture at 2.0–2.5% abruptly increasing water demand via evapotranspiration; subsequently, when soil moisture decreased, plant density also decreased to 375–450 plants/hm^2 after remaining stable for about 14 years. Soil moisture reached the lowest level (1.0–1.3%), then slowly began to recover to 1.5%, and remained stable for about 30 years following revegetation; remnants of the HA growth flourished to a theoretical density of 675–900 plants/hm^2. This was a result of the balance of soil loading on water bearing force (Li et al., 2014). Our results are in agreement with those of previous studies. For example revegetation decreased soil moisture in the Tengger desert (Wang et al., 2006, 2011); the decline in ANPP was caused mainly by a decrease in the density and by degeneration of HA in the desert area of Minqin (Chang et al., 2008). Therefore, we conclude that revegetation changed the water cycle of this sand-fixing ecosystem by redistribution of soil moisture.

Revegetation affected the properties of soil and therefore changed the trajectory of vegetation succession. In our study area, Wang et al. (2015) found that the organic matter, total-N and available-P at 0–5 cm soil depth increased with an increase in plant age. Soil structure became more developed, including increasing soil stability by binding soil particles together especially in the upper soil profile (Wang et al., 2006), then surface soil moisture increased and deep soil water decreased because of lower infiltration of precipitation; this is consistent with the conclusion from a different study that the temporal and spatial pattern of soil moisture in a moving dune changed significantly with revegetation (Li et al., 2013b). This stimulated the growth of grasses, while the cover of shrubs decreased. After 30–40 years, plant community structure tended to stabilize, deep soil moisture recovered slowly facilitating the re-establishment of shrubs, and surface soil moisture at the 0–40 cm layer enabled many annual plants to grow. Ultimately, the sand-fixing vegetation consisted of few old HA, more young HA, and many annual plants (Wang et al., 2015).

4.2. Thresholds and time lags of ANPP response to precipitation in SFR and HA

Our results showed that variation in ANPP during the growing season responded to cumulative precipitation from previous June to current August at the scale of years; this response was observed in both HA and SFR (Fig. 5). These results support the conclusion that precipitation during two preceding years accounted for a large fraction of the inter-annual variability in current production (Reichmann et al., 2013). These results are also consistent with observations in the Patagonian steppe that shrub production had the highest correlation with precipitation received in the preceding 14 months (Jobbágy and Sala, 2000; Sala et al., 2012). Thus, plant production is expected to be lower in wet years preceded by dry years than in wet years preceded by wet or by normal years (Yahdjian and Sala, 2006). One possible reason for this is that the soil moisture carryover from previous years provides enough support for the biotic functions of the vegetation to mediate the ANPP response to the variability in mean annual precipitation (Reichmann et al., 2013; Robertson et al., 2009; Thomey et al., 2011). Additionally, the carry-over effect may influence the density of meristems where plant growth occurs (Yahdjian and Sala, 2006); here, meristem density (tiller density) may be reduced under low precipitation, also reducing ANPP in the subsequent year. The opposite effect would be observed in years with high precipitation (Oesterheld et al., 2001). These results highlighted the importance of legacy precipitation.

Our results also indicated that the appropriate precipitation for HA growth is greater than 160 mm, and that critical precipitation at which plants undergo water stress is less than 160 mm. Ma et al. (2007) indicated that the precipitation amounts in the HA-growing region exhibited an upper limit, which was <180 mm of annual precipitation. These results emphasize the importance of precipitation thresholds for ANPP responses of HA and SFR in dry environments, consistent with the conclusion that these thresholds exist in banded or mosaic vegetation patterns in arid environments (Bisigato et al., 2013; Thom, 1975; Turnbull et al., 2012). However, the precipitation threshold in SFR exhibited an “unstable range” from 160 mm to 190 mm. In this “unstable range”, the ANPP at SFR appears to gradually change from about 75 g/m^2 to about 120 g/m^2 (Fig. 5). The reasons for this may be that *Populus bolleana* and annual plants act as secondary contributors to the overall ANPP in the SFR region, with a linear response to precipitation within certain limits; such effect could moderate the overall non-linear response.

Many biological-state changes, in which organisms transition from a lower to a higher state of physiological activity, require a minimal triggering precipitation (Schwinning and Sala, 2004). In this study, the threshold needed for a significant ANPP response was 160 mm, past which ANPP increased more than 2 fold (average of 45 and 90 g/m^2 ANPP for precipitation <160 and >160 mm, respectively) (Fig. 5). These results diverged from those for other species in different regions. For example, major recruitment of shrubs in dry environments was linked to winter rainfall above a certain threshold in southern Ethiopia and northern Kenya (Coppock, 1993; Ellis et al., 1993; Puigdefabregas, 1998). Rates of stem growth increased more than eightfold with a threshold of over 100 mm of summer precipitation (Sponseller et al., 2012). In grass communities, spring and summer precipitation thresholds for CO_2 uptake were 23 and 51–148 mm respectively, while in shrub communities, these values were 59 mm for spring, and 57–140 mm for summer; further, the spring response affected the summer threshold values (Emmerich and Verdugo, 2008). The differences in precipitation thresholds between HA and other vegetation types were most likely the result of different demands for water in dissimilar ecosystems (Muldavin et al., 2008). Our results provided a positive feedback to assess the potential response of HA to fluctuations in precipitation.

4.3. Threshold of soil moisture for ANPP response of HA

Our results showed that soil moisture of 1.4–1.5% resulted in significantly higher ANPP response in HA; this indicated that the appropriate soil moisture for HA growth was >1.5%, and that the critical soil moisture at which these plants experienced water stress was <1.4 mm. Meanwhile, our results indicated that small reductions in ANPP occurring near the specific threshold of 1.4–1.5% soil moisture can cause abrupt changes in ecosystem state. These results are consistent with conclusions of earlier studies that appropriate soil moisture significantly enhances canopy and leaf photosynthetic capacity, and that extremely high soil moisture is not conducive to photosynthesis in HA (Asbjornsen et al., 2011; Bisigato et al., 2013; Gao et al., 2010); The most striking finding in our study spanning 26-years of data is that the overall threshold of soil moisture (1.4–1.5%) for HA in the middle reaches of the Heihe River is within the broad range of soil moisture thresholds reported for the world's HA communities. In the Minqin Oasis, for example, the withering coefficient of HA is at 0.824% soil moisture, the critical soil moisture content at which natural vegetation degenerates is between 0.824% and 1.30%, and HA grow normally when soil water content is above 1.3% (Ma et al., 2007). Also, Yang et al. (2014b) estimated that the suitable and minimal aeolian soil water conditions for the growth of HA were about 2.0% and 1.0%, respectively, in the Ulan Buh Desert. These results emphasize the importance of the soil moisture threshold for ANPP response of HA in dry environments.

Whether the growth of HA requires the absorption of groundwater has always been a controversial topic (Ma et al., 2007). Studies showed that the growth of HA utilized groundwater when groundwater table was less than 5 m (Zhang, 1990); however, other studies indicated that if the groundwater was deep, HA also thrived, because HA can obtain water from precipitation (Ma et al., 2007). In our study area, the groundwater table is above 6 m depth. Related research showed that more than 90% of the feeder roots of HA were in the 0–1 m soil layer, and no roots were found below 5 m (Wang et al., 2015). Such a shallow root system indicated that this species depended on precipitation as its primary water source (Xu and Li, 2006; Xu et al., 2007). Stored aeolian soil water might be the main water source for the growth of HA (Ma et al., 2007). In addition, for the nonphreatophyte HA, efficient morphological adjustment, combined with strong stomatal control, contributes to its acclimation to variability in precipitation (Hao et al., 2009; Xu et al., 2007).

5. Conclusions

We evaluated the ecological and hydrological processes and their relationships in the sand-fixing vegetation region in a desert-oasis ecotone in the Heihe River Basin. Our results showed that variation in ANPP of HA and SFR during the growing season responded to total precipitation from previous June to current August, and to soil moisture during the growing season at the scale of years. Specifically, when soil moisture decreases to 1.5%, or if precipitation received in the previous 15 months is less than 160 mm, ANPP of HA may abruptly decrease. From a management perspective, identifying of such critical thresholds permits effective planning before damage to vegetation becomes irreversible, and may increase sustainability of the sand-fixing vegetation in our study area.

Our study provided strong evidence for the existence of hydrologic thresholds in ANPP responses in HA vegetation. This study had the following limitations: 1) ANPP was a result of a multivariable combination, and quantitative expression of precipitation or soil moisture was not sufficient to understand the mechanism of change in ANPP, necessitating model simulation for a further study; 2) the selected remote sensing data of TM were limited to one scene each year in August, and differed to some extent from other months or from other days in the same month due to precipitation events;

however, the ANPP data addressed the objectives of the study, despite some effects on accuracy. Our results highlighted the inherent complexity of desert ecosystems and the importance of legacy precipitation and hydrological thresholds to the recovery of desert ecosystems. The findings provide useful references for further understanding of the mechanisms of ANPP changes in sand-fixing ecosystem due to changes in precipitation and soil moisture.

Acknowledgements

This study was supported by the Key Project of Chinese National Programs (973 program) for Fundamental Research and Development (grant no. 2013CB429903), and the National Science Foundation for Distinguished Young Scholars of China (grant no. 41125002). We thank Dr. Guo-hua Wang and Ge-fei Zhang for the vegetation surveys. We also thank Dr. Hu Liu and Kathryn Piatek for language assistance. We also gratefully acknowledge the journal's anonymous reviewers and editors for their critical reviews and comments that helped to improve and clarify the manuscript.

Conflicts of interest

The authors declare that they have no conflict of interest.

Author contributions

Conceived and designed the experiments: WZ, FL. Performed the experiments: FL. Analyzed the data: FL, WZ. Wrote the manuscript: FL, WZ.

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