Catena 152 (2017) 9–17

Contents lists available at ScienceDirect

Catena

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Slope aspect affects the non-structural carbohydrates and C:N:P stoichiometry of *Artemisia sacrorum* on the Loess Plateau in China

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ARTICLE INFO

Article history:
Received 13 August 2016
Received in revised form 12 November 2016
Accepted 29 December 2016
Available online 7 January 2017

Keywords:
Biomass
Concentration
Soluble sugar
Starch
Environmental factor

ABSTRACT

Slope aspect, as an important topographic factor on the Loess Plateau in China, may influence the productivity and relative characteristics of *Artemisia sacrorum* in this area. Three slope aspects (sunny, half-sunny, and shady slopes) were chosen to study the effects of slope aspect on the biomass, carbon:nitrogen:phosphorus (C:N:P) stoichiometry, and non-structural carbohydrate (NSC) concentrations in *A. sacrorum* in 2014. The maximum *A. sacrorum* biomass was detected in the half-sunny slope, and the ratio of belowground to aboveground biomass significantly changed in the different slope aspects. Slope aspect significantly affected the N:P ratio in the aboveground and the C:P and N:P ratios in the belowground. The maximum C:P and N:P ratios in the rhizosphere and non-rhizosphere soils were reached in the sunny slope, whereas no significant change was observed in C:N ratio. The maximum NSC concentrations occurred in different *A. sacrorum* tissues, that is, aboveground in the sunny slope and belowground in the half-sunny slope. The ratio of soluble sugar to starch concentrations in the aboveground significantly differed among the three slope aspects, but that in the belowground showed no significant difference. Slope aspect was the main environmental factor affecting the plant nutrient and stoichiometry on the Loess Plateau in China.

1. Introduction

C:N:P is the most investigated nutrient relation because these elements often limit organism growth (Elser et al., 2007). Their application in biomass can reflect the relationship between evolutionary processes and the environment (Hessen et al., 2004). Thus, the C:N:P stoichiometry in an organism can determine their position and function. Soil C:N:P stoichiometries are also important (Sardans et al., 2011). Thus, many studies have analyzed the influences of environmental factors on the ecological stoichiometry, which includes nutrients, salts, light, and groundwater table (Li et al., 2013; Rong et al., 2015; Xing et al., 2013). Therefore, identifying the underlying environmental factors that influence C:N:P stoichiometry in the ecosystem is important.

Non-structural carbohydrates (NSCs), the immediate products of photosynthesis, provide substrates for plant growth and metabolism and can be stored by plant tissues. The NSC concentrations in plant tissues affects plant response to environmental stress; this parameter reflects the carbon supply level, plant growth, buffering capacity, and adaptation strategies (Kozlowski, 1992; Myers and Kitajima, 2007). Low levels of NSCs are closely related to risk of drought-induced mortality (McDowell et al., 2008). NSC concentrations are affected by many factors, such as nutrient elements (Nanamori et al., 2004), temperature (Gaudet et al., 1999; Gough et al., 2010; Li et al., 2016), precipitation (Li et al., 2016), and phenology (Gough et al., 2010). Soluble sugars and starch, which are important energy sources for plant growth, development, and metabolism, are usually considered when studying NSC (Körner, 2003). Soluble sugars are a product of photosynthesis and are used to meet current plant needs; starch is the main currency of storage and used to meet future plant needs (Kozlowski and Keller, 1966).

Slope aspect, as an important topographic factor, affects the angle between the ground and the wind direction, as well as the light radiation from the sun. Meanwhile, solar radiation is the main factor that determines soil moisture, near-surface air temperature, soil temperature, soil carbon, nitrogen, and other nutrients; different slope aspects have different spatial and vegetation distribution patterns because of different natural factors, such as light, heat, water, and soil (Auslander et al., 2003). Slope aspect affects the local ecological environment by influencing the solar radiation received by the ground surface (Oke, 2002). For example, in moderate topography, the soil water content and near-surface air and soil temperature significantly differ between sunny and shady slopes (Bennie et al., 2008). Soil temperature and moisture significantly differ in different slope aspects; thus, nutrient mineralization

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http://dx.doi.org/10.1016/j.catena.2016.12.024
0341-8162/

largely varies (Sternberg and Shoshany, 2001). Previous studies found that slope aspect mainly affects sunshine, wind, temperature, transpiration, and plant growth (Naeem et al., 1996). Gong et al. (2008) showed that northern slopes exhibit higher productivity than southern slopes in the hilly grassland of Inner Mongolia in China (Gong et al., 2008). Slope aspect is a main topographic factor of grassland on the Loess Plateau in China and may exert a pronounced effect on productivity, nutrient dynamics, C:N:P stoichiometry, and NSC concentrations.

Artemisia sacrorum has a wide range of distribution, drought resistance, strong root system development, and stable zonal vegetation with a certain cold tolerance; it is largely distributed on the Loess Plateau in China (Wang and Liu, 2002). Given its strong reproductive capacity, high productivity, and quick regeneration characteristics, *A. sacrorum* is a middle source of winter forage for livestock in this area. *A. sacrorum* has dense clusters, and its root system has a network centralized distribution; hence, this plant can directly guard against slope erosion by rainfall and exhibit a favorable mechanism for soil and water conservation. However, the effect of slope aspect on the biomass, C:N:P stoichiometry of plant, and soil, as well as the NSC concentrations of *A. sacrorum*, on the Loess Plateau in China remains unclear.

Three slope aspects (shady, half-sunny, and sunny slopes) with the same rehabilitation time were selected to investigate the effects of slope aspect on the biomass, C:N:P stoichiometry of plant, and soil, as well as the NSC concentrations of *A. sacrorum*. We proposed the following hypotheses: (1) slope aspect significantly but differentially influences the plant biomass in aboveground and belowground parts, as well the ratio of belowground to aboveground biomass; (2) slope aspect changes the C:N:P ratios of plant and soil; and (3) slope aspect significantly changes NSC concentrations and the ratio of soluble sugar to starch concentration.

2. Material and methods

2.1. Experimental site

The experiment was conducted at the Ansai Research Station of Soil and Water Conservation of the Chinese Academy of Sciences. The area is located at the center of the semiarid, hilly-gully region of the Loess Plateau in Northwest China (36°31′N–37°20′N, 108°52′E–109°26′E, 1068–1309 m a.s.l.). This area has a temperate and semi-arid climate with an average annual temperature of 8.8 °C. The average annual precipitation is approximately 505 mm, and >70% of rainfalls are centered between July and September, during which severe rainstorms often occur. The average frost-free period is approximately 157 days. The present soil type is representative loess soil with ranges in contents of: sand = 6.5 to 30.0%, silt = 53.5 to 74.5%, clay = 11.1 to 29.0%; the soil had a bulk density of 1.10 to 1.30 g cm^{-3}, pH = 8.7 to 9.3, organic matter concentration of 1.10 to 13.2 g kg^{-1}, and total N and P concentrations of 0.10 to 0.75 and 0.14 to 0.63 g kg^{-1}, respectively (Messing et al., 2003). Three grasslands abandoned in the same year were selected for the experiment. These grasslands are situated in the sunny slope (S15°W), half-sunny slope (N75°W), and shady slope (N57°E).

2.2. Experimental design and sample collection

In September 2014, three grasslands with different slope aspects were selected as the experimental sites. The histories of the three sites were identified through inquiries from researchers who had worked at the Ansai Research Station of Soil and Water Conservation of the Chinese Academy of Sciences, as well as from relevant land documents. These sites have similar gradients and elevations. Sample information is shown in Table 1, and the location of the experiment sites is shown in Fig. 1.

Three 10 m × 10 m plots were established at each site and were considered true replicates. Before our experiment, three 1 m × 1 m samples were established in each plot. The grass in these samples was measured and recorded (the coverage, maximum/mean height, and number were separately recorded according to species) before harvest. The grass samples were divided into *A. sacrorum* and weeds (other herbaceous vegetation). The aboveground and belowground biomasses of these grass samples were immediately stored in a low-temperature incubator and then transferred to the laboratory. They were minimally cleaned and stored immediately in a refrigerator (−20 °C). After the grass was removed, soil strongly adhering to the roots and collected within the space used by the roots was considered the rhizosphere (0–20 cm, rhizosphere soil samples were from *A. sacrorum*). Bulk soils were sampled from a location approximately 15 cm from the root. Each soil sample was collected at five points (including four corners and the center of the plot), and the collected soil samples were combined into one soil sample. All soil samples were collected up to a depth of 0–20 cm, and the ring knife method was used to determine the soil bulk density (10 cm inner diameter). The soil bulk density was determined at 105 °C for 48 h. Finally, 36 plant samples and 18 soil samples were collected.

2.3. Laboratory analysis

All aboveground and belowground biomasses from each plot were clipped and dried at 65 °C in an oven until a constant weight was obtained. The samples were weighed, ground through a 1 mm sieve, and then stored for chemical analysis. Each soil sample was air-dried. After removing roots, stones, and debris, the soil samples were homogenized and sieved to 0.25 mm prior to analysis. The organic matter concentration in soils, and total C, N, and P concentrations in the plants and soils were then analyzed.

The plant samples for NSC analysis were immediately frozen in liquid N, heated in a microwave oven (40 s at 600 W), dried to a constant weight at 65 °C, ground through a 1 mm sieve, and then stored until chemical analysis. The concentrations of the soluble sugars and starch were determined using an anthrone reagent.

2.4. Chemical analyses: Soluble sugars and starch

Ground material (0.1000 g) of the dried samples was placed into a 10 mL centrifuge tube and added with 2 mL of 80% ethanol. The centrifuge tube was incubated at 80 °C in a shaking water bath for 30 min and then centrifuged at 5000 ×g for 5 min. The supernatant was removed, the residue was extracted two more times as above, and the residue was retained for starch analysis. The supernatants were retained, combined, and then stored at −20 °C for soluble sugar determination.

The starch in the residues was resuspended in 2 mL of distilled water, and the mixtures were incubated at 100 °C in a shaking water bath for 15 min to remove the ethanol. After cooling to room temperature, 2 mL of 9.2 mol L^{-1} $HClO_4$ was added and shaken, and then 4 mL of distilled water was added 15 min later. The mixtures were centrifuged at 5000 ×g for 5 min. The residues were extracted again with 2 mL of

Table 1
Location and floristic composition of the sampling sites.

Slope aspect	Latitude	Longitude	Altitude (m)	Plant community
S15°W	36.85°	109.31°	1269	*A. sacrorum* + *Bothriochloa ischaemum*
N75°W	36.85°	109.31°	1275	*A. sacrorum* + *Phragmites australis*
N57°E	36.85°	109.31°	1278	*A. sacrorum* + *Artemisia capillaries*

Fig. 1. The location of the experiment sites. ARSSWCCAS = Ansai Research Station of Soil and Water Conservation of the Chinese Academy of Sciences.

4.6 mol L^{-1} $HClO_4$. The supernatants were retained, combined, and then stored at −20 °C for starch determination.

Soluble sugar and starch contents were determined spectrophotometrically (Shimadzu, Japan) at 620 nm using an anthrone reagent (Seifter et al., 1949). The sugar concentration was calculated from the regression equations based on glucose standard solutions, and the starch concentration was determined by comparison with glucose standards using a conversion factor of 0.9 (Osaki et al., 1991) on a dry-matter basis.

2.5. Chemical analyses: Total C, N, and P concentrations

The total C concentration of the plants and the organic matter concentration of the soils were determined using the H_2SO_4–$K_2Cr_2O_7$ oxidation method. The total N concentrations of the plant and soil samples were measured using the Kjeldahl method (Bremner and Mulvaney, 1982). The total P concentration of the plants was measured by persulfate oxidation followed by colorimetric analysis, whereas that of the soils was determined colorimetrically after digestion with H_2SO_4 and $HClO_4$ (Schade et al., 2003).

2.6. Data analysis

NSC concentrations were calculated as the sum of starch and soluble sugars in each sample (Li et al., 2002). The data from all treatments were analyzed by ANOVA followed by the least significant difference test. A correlation analysis was based on Pearson's correlation coefficients ($P < 0.05$). Redundancy analysis, a direct gradient analysis, was performed using CANOCO5.0. All ANOVA and correlation analyses were tested for significance at $P < 0.05$ using SPSS 20.0 (SPSS Inc., Chicago, USA), and graphs were plotted using SigmaPlot 12.5.

3. Results

3.1. Biomass, nutrient concentrations, and their stoichiometry

The aboveground and belowground biomasses and total biomass of *A. sacrorum* were significantly affected by slope aspect (Fig. 2). All of these parameters reached their minimum values in the sunny slope. When compared with those in the sunny slope, the biomasses in the half-sunny and shady slopes (500%, 554%, 528% and 184%, 323%, 256%) were higher. Slope aspect also significantly affected the aboveground and belowground biomasses and total biomass of the weeds (Fig. 2). In contrast to the findings for *A. sacrorum*, the maximum value of aboveground and belowground weeds biomasses and total biomass appeared in the sunny slope. Moreover, slope aspect exhibited no significant effect on the total biomass of the entire plot (Fig. 2). The ratio of belowground to aboveground biomass of the shady slope was significantly higher than that of the sunny slope for *A. sacrorum*. The ratio of belowground to aboveground biomass of the three slopes showed no significant difference in the weeds (Fig. 2).

The C, N, and P concentrations of *A. sacrorum* were not significantly affected by slope aspect, except for the C concentration in the aboveground part and the N concentration in the belowground part (Fig. 3A–C). The half-sunny slope had the maximum C concentration in the aboveground part (Fig. 3A). Different from the C concentration, the N concentration in the shady slope reached its maximum value in

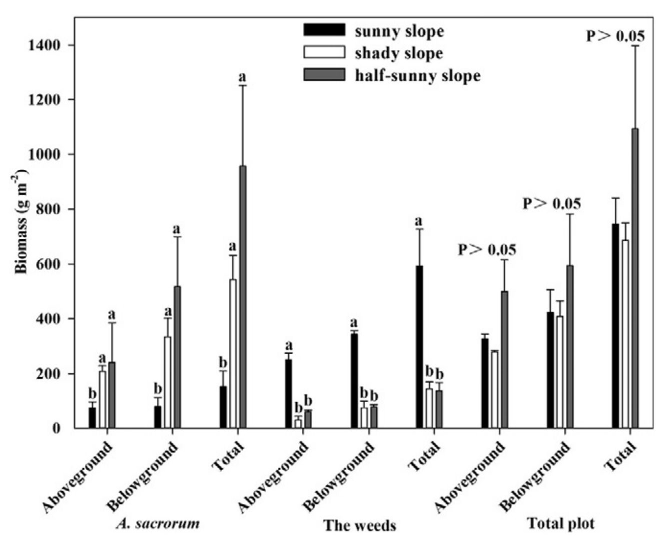

Fig. 2. Effects of slope aspect on plant biomass. Error bars are SE (n = 3). Different letters above bars indicate significantly different at P = 0.05.

the belowground part (Fig. 3B). Slope aspect also significantly affected the C, N, and P concentrations of the weeds but did not significantly affect the C concentration in the aboveground part (Fig. 3A–C). The maximum N and P concentrations in the aboveground part were found in the shady slope (Fig. 3B and C). Compared with the sunny and shady slopes, the half-sunny slope had the maximum C and N concentrations in the belowground part (Fig. 3A and B). The maximum P concentration in the belowground part was found in the shady slope (Fig. 3C).

The C:N and C:P ratios in the aboveground part of *A. sacrorum* were not significantly affected by slope aspect, but the N:P ratio was significantly affected, and the averaged ratios were 36.0, 622.1, and 17.4, respectively (Fig. 4A–C). The maximum N:P ratio in the aboveground part of *A. sacrorum* in the shady slope was 20.4 (Fig. 4C). In contrast to those in the aboveground part of *A. sacrorum*, the C:N and N:P ratios in the belowground part were significantly affected by slope aspect (Fig. 4A and C). Slope aspect significantly affected the C:N, C:P, and N:P ratios in the aboveground and belowground parts of the weeds (Fig. 4A–C). The C:N, C:P, and N:P ratios of the aboveground part were significantly lower in the shady slope than in the sunny and half-sunny slopes (Fig. 4A–C). The C:N, C:P, and N:P ratios in the three slopes of the belowground and aboveground parts significantly differed; the minimum C:P and N:P ratios were found in the shady slope, but the minimum C:N ratio was found in the half-sunny slope (Fig. 4A–C).

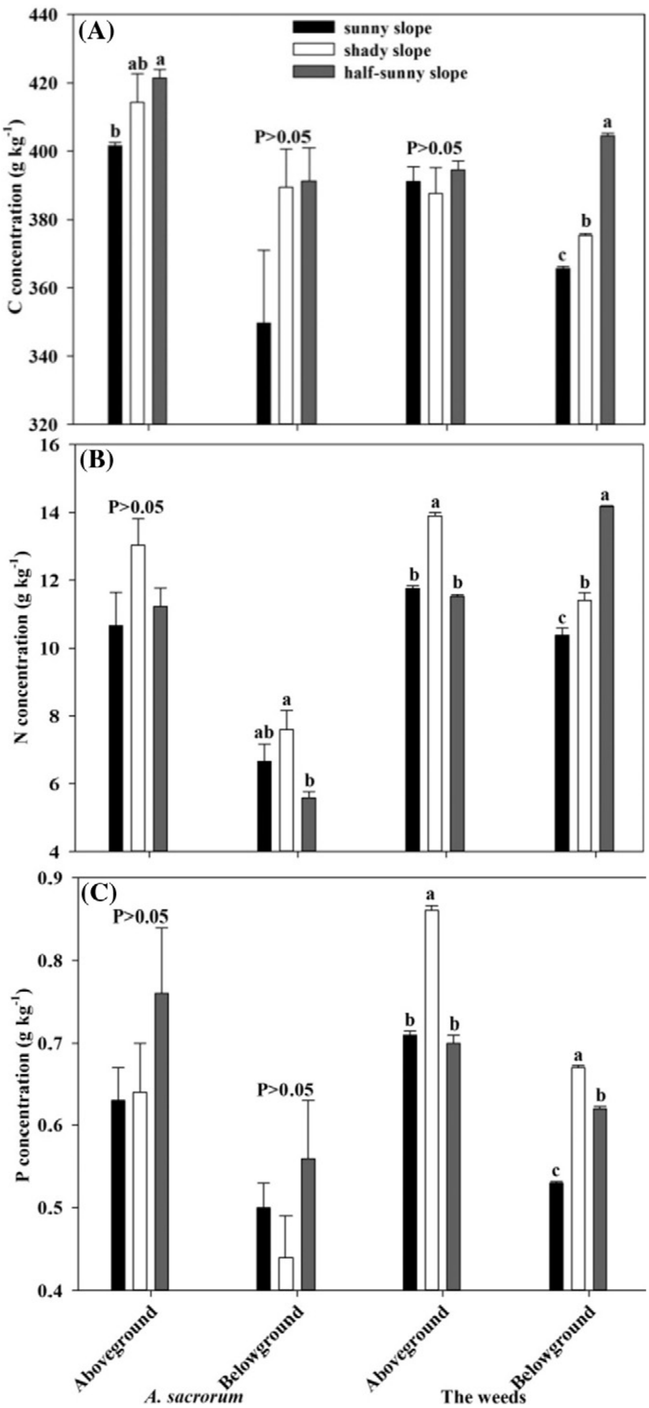

Fig. 3. Effects of slope aspect on plant C, N and P concentrations. Error bars are SE (n = 3). Different letters above bars indicate significantly different at P = 0.05.

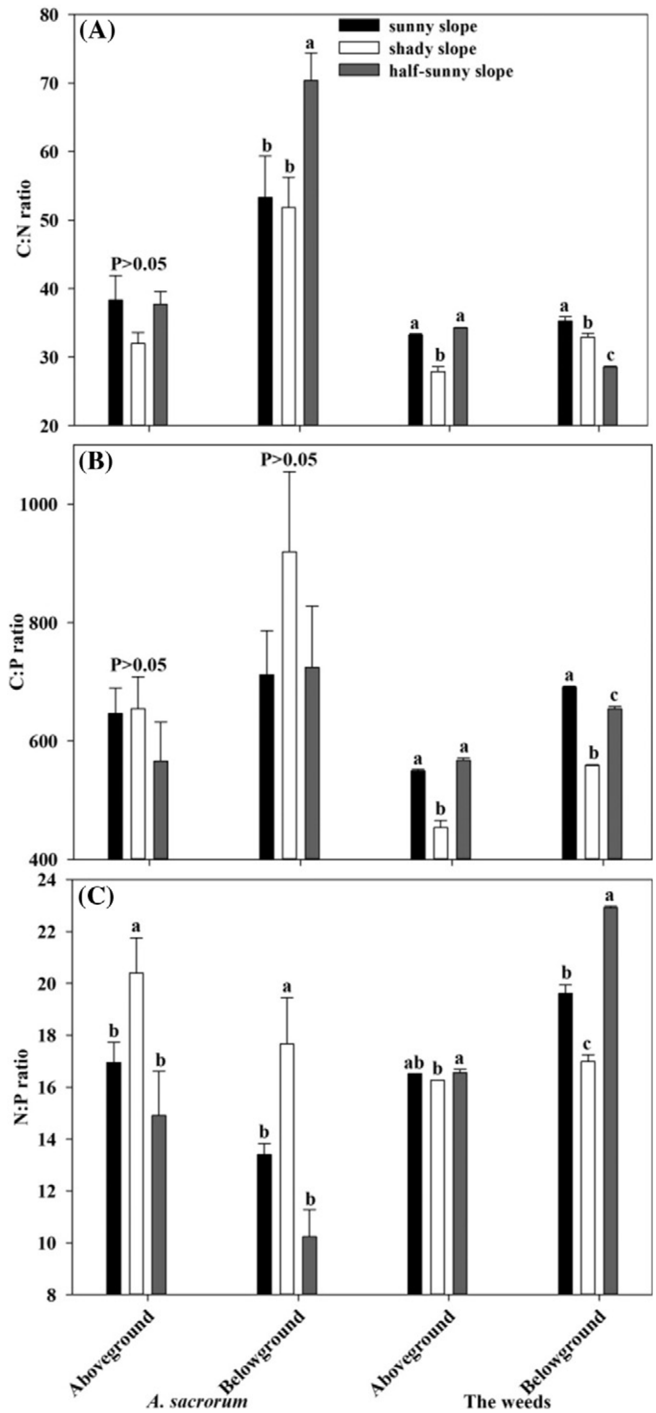

Fig. 4. Effects of slope aspect on plant C, N and P stoichiometry ratios of C:N, C:P, and N:P. Error bars are SE (n = 3). Different letters above bars indicate significantly different at P = 0.05.

3.2. Soil nutrient concentrations and their stoichiometry

Slope aspect significantly influenced the C and N concentrations but not the P concentration of the rhizosphere and non-rhizosphere soils. The maximum C and N concentrations of the rhizosphere and non-rhizosphere soils were reached in the sunny slope (Fig. 5A).

The C:P and N:P ratios of the rhizosphere and non-rhizosphere soils were significantly affected by slope aspect; by contrast, the C:N ratios of the rhizosphere and non-rhizosphere soils were not significantly affected (Fig. 5B). The C:P and N:P ratios in the shady and half-sunny slopes (25%, 75% and 21%, 71%) were significantly lower than those in the sunny slope of the rhizosphere soil. Similarly, the C:P and N:P ratios in the shady and half-sunny slopes (21%, 35% and 25%, 45%) were significantly lower than those in the sunny slope of the non-rhizosphere soil (Fig. 5B).

3.3. NSC concentrations

The soluble sugar, starch, and NSC concentrations of the belowground part of *A. sacrorum* varied and were significantly affected by slope aspect; the result was the same for the starch and NSC concentrations but different for the soluble sugar concentrations of the aboveground part (Fig. 6A–C). The maximum starch and NSC concentrations of the aboveground part were found in the sunny slope, whereas those of the belowground part were found in the half-sunny slope. Different from those of *A. sacrorum*, the soluble sugar, starch, and NSC concentrations in the aboveground and belowground of the weeds varied and were significantly affected by slope aspect. The maximum soluble sugar, starch, and NSC concentrations in the aboveground and belowground parts were found in the shady slope.

The ratio of soluble sugar to starch concentrations in the aboveground part of *A. sacrorum* significantly differed in the different slope aspects; the reverse result was found for that in the belowground part (Fig. 6A and B). The maximum ratio of soluble sugar to starch concentrations in the aboveground part was found in the half-sunny slope. Contrary to the results for *A. sacrorum*, the ratio of soluble sugar to starch concentrations in the belowground part of the weeds was significantly affected by slope aspect, whereas that in the aboveground part showed no significant difference. The maximum ratio of soluble sugar to starch concentrations in the belowground part of the weeds was found in the shady slope (Fig. 6A and B).

3.4. Effect of environmental factors of RDA on plant functional traits

Constrained RDA analyses showed that environmental factors affected the functional traits of *A. sacrorum* (Fig. 7A). The total variation was 26.24, and explanatory variables accounted for 99.4%. The first two axes explained 91.9% of the total variance, 85.4% for the first axis and 6.5% for the second axis. In the seven environmental factors, the N concentration of the rhizosphere soil was the most significant variable that affected the functional traits of *A. sacrorum* ($P = 0.004$), and this variable explained 63.5% of the total variance. The slope and C concentration of the rhizosphere soil were the next most significant environmental variables, and they explained 60.4% ($P = 0.008$) and 50.4% ($P = 0.018$) of the total variance. The slope and N and C concentrations of the rhizosphere soil exhibited a positive correlation with the first axis, with correlation coefficients of 0.834, 0.855, and 0.761, respectively (Fig. 7A). Therefore, the slope and N and C concentrations of the rhizosphere soil were important factors that affected the functional traits of *A. sacrorum*.

Constrained RDA analyses showed that environmental factors affected the functional traits of the weeds (Fig. 7B). The total variation was 19.2, and explanatory variables accounted for 99.3%. The first two axes7 explained 93.3% of the total variance, 81.0% for the first axis and 12.3% for the second axis. In the seven environmental factors, in contrast to the result for *A. sacrorum*, slope aspect was the most significant variable that affected the functional traits of the weeds ($P = 0.01$). This variable explained 57.3% of the total variance. The slope and C and N concentrations of the rhizosphere soil were the next most significant environmental variables, and they explained 46.8% ($P = 0.024$), 46.0% ($P = 0.028$), and 41.8% ($P = 0.026$) of the total variance, respectively. The slope aspect, slope, and C and N concentrations of the rhizosphere soil showed a good positive correlation with the first axis, with correlation coefficients of 0.816, 0.721, 0.694, and 0.729, respectively (Fig. 7B). The species richness negatively correlated with the second axis and had the largest correlation coefficient of 0.946 (Fig. 7B). Therefore, the functional traits of the weeds were mainly affected by the slope aspect, slope, and C and N concentrations of the rhizosphere soil.

4. Discussion

4.1. Effects of slope aspect on plant biomass and C:N:P ratio

Slope aspect significantly affected grass biomass; this finding supports our hypothesis and is consistent with that of another study (Gong et al., 2008). However, we found that the biomass of *A. sacrorum* was higher in the half-sunny slope than in the other slopes. This result contradicts with previous findings. Gong et al. (2008) found that the productivity of the shady slope is higher than that of the sunny slope, and they speculated that slope aspect significantly affects plant biomass through species richness (Gong et al., 2008). By contrast, the *A. sacrorum* biomasses had no correlation with the species richness (Fig. 7A). Constrained RDA analyses also showed that the slope and N and C concentrations of the rhizosphere soil significantly affected the functional

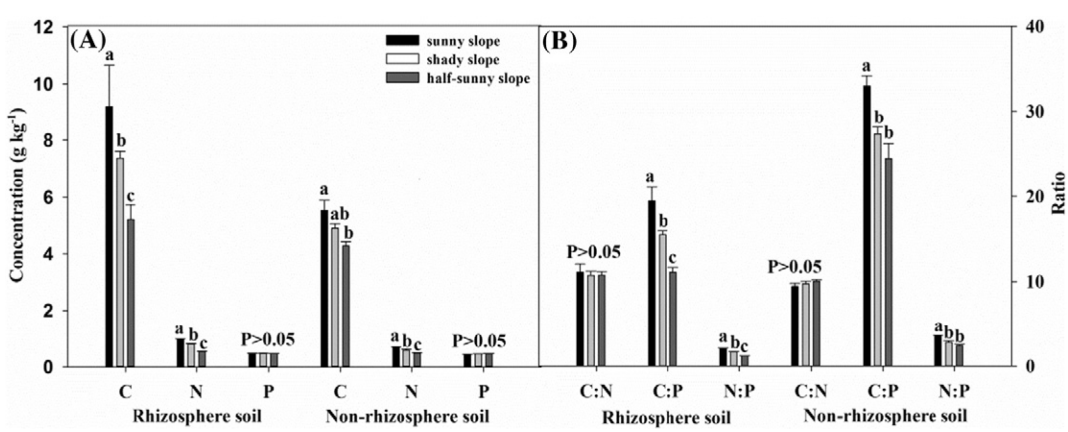

Fig. 5. Effects of slope aspect on soil C, N and P concentrations, and their stoichiometric ratios of C:N, C:P, and N:P of rhizosphere and non-rhizosphere soil. Error bars are SE ($n = 3$). Different letters above bars indicate significantly different at $P = 0.05$.

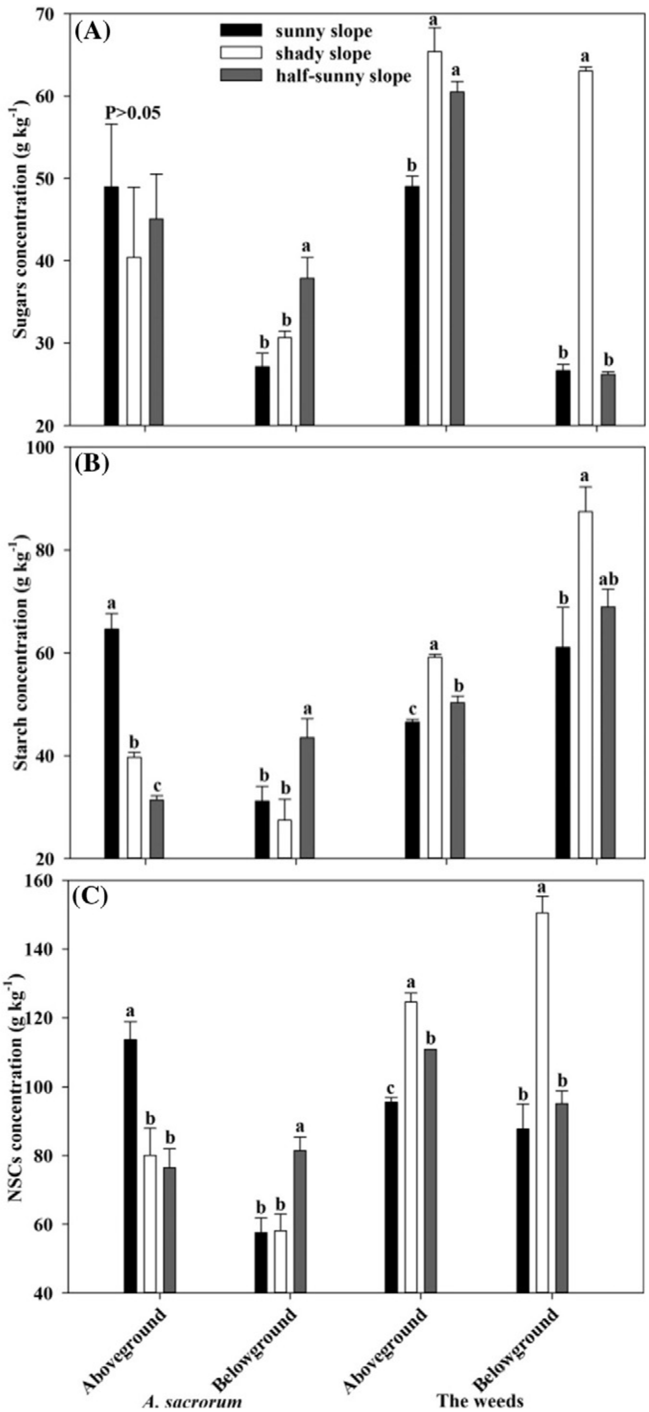

Fig. 6. Effects of slope aspect on plant soluble-sugar, starch, and NSC concentrations. Error bars are SE (n = 3). Different letters above bars indicate significantly different at P = 0.05.

traits of *A. sacrorum* and negatively correlated with the biomasses of *A. sacrorum*, which caused the overall result (Fig. 7A). *A. sacrorum* enjoys light but is not a typical sun plant; the light compensation points of *A. sacrorum* are high, and its light saturation points are low; therefore, *A. sacrorum* is better suited to grow in half-shady and half-sunny slopes (Bu et al., 2007). By contrast, the slope and N and C concentrations of the rhizosphere soil positively correlated with the biomasses of the weeds; thus, the weeds had their maximum biomasses in the sunny slope (Fig. 7B).

The ratio of belowground to aboveground biomass of *A. sacrorum* was significantly higher in the shady slope than in the sunny slope. This finding can be attributed to the competition and changes in soil factors that could impact the ratio of belowground to aboveground biomass (Hill et al., 2006); these factors include soil water content (McConnaughay and Coleman, 1999). In the present study, the shady slope had a better soil water content because of the influence of the topographic factors. The soil water content (0–20 cm) in our study plots showed a significant positive correlation with the ratio of belowground to aboveground biomass of *A. sacrorum* ($r = 0.690$, $P < 0.05$). The plant aboveground biomass would have more temporary resources under water shortage during sunny days (Chaves et al., 2002); consequently, the sunny slope had the minimum ratio of belowground to aboveground biomass. Although several studies have shown a good relationship between belowground and aboveground parts, some suggested that the relationship between the two parts is not fixed (Chapin et al., 1993). For example, some studies found that the ratio of aboveground to belowground biomass increased with increasing soil water content (Chapin et al., 1993).

In contrast to our hypothesis, we found that slope aspect exerted no significant effect on the aboveground C:N ratio of *A. sacrorum* but significantly affected the aboveground C:N ratio of the weeds. Plants would have a high growth rate with a low C:N ratio (He et al., 2008). The minimum aboveground C:N ratio of the weeds was detected in the shady slope. Thus, the weeds in the shady slope had a high growth rate. However, the maximum aboveground biomass of the weeds appeared in the sunny slope because the shady slope had insufficient light for plant growth and the aboveground C:N ratio of the weeds showed no good correlation with the aboveground biomass of the weeds (Fig. 7B). Reich and Oleksyn (2004) found that the shady slope has higher aboveground N and P concentrations than the sunny slope (Reich and Oleksyn, 2004). This result agrees with our results. In the present study, constrained RDA analyses for the weeds showed that the C concentration in the aboveground part was unaffected by environmental factors when compared with the N and P concentrations in the aboveground part (Fig. 7B). As a result, the minimum aboveground C:N ratio of the weeds appeared in the shady slope. The C:N ratios in the aboveground part would increase by drought in semi-arid environments (Sardans et al., 2012). This deduction supported our results. Similar to the result for C:N ratio, the minimum aboveground C:P ratio of the weeds appeared in the shady slope. In addition, slope aspect significantly affected the aboveground C:P ratio of the weeds but not the aboveground C:P ratio of *A. sacrorum*. However, this finding differed from our hypothesis.

For the same species, plant stoichiometry may be different when placed in different sunlight intensities. In the present study, the shady slope had the maximum aboveground N:P ratio of *A. sacrorum*. Valladares et al. (2000) found that N:P is lower in the sun aboveground than that in the shade aboveground for the same species (Valladares et al., 2000). Biomass production declined with increasing N:P ratio in *A. sacrorum*, but the relationship between biomass and N:P ratio was weak (Fig. 7A). A similar result was reported in other research (Güsewell, 2004). The slope aspect significantly affected the aboveground N:P ratio of *A. sacrorum*. This finding supported our hypothesis because the slope aspect influenced the exposure to sunlight. Thus, the influence extent of N and P concentrations was different in the different slope aspects and would significantly change the aboveground N:P ratio of *A. sacrorum* (Fig. 7A). Consistent with the result for *A. sacrorum*, slope aspect exerted significant effects on the aboveground N:P ratio of the weeds; however, the maximum N:P ratio appeared in the half-sunny slope because the slope aspect exhibited different effects on the weeds when compared with *A. sacrorum* (Fig. 7A and B).

The plant N:P ratio can be used to indicate N or P limitation (Güsewell, 2004). Zhang et al. (2004) provided a large threshold of N:P ratio for N and P limitation in the study area; the species would be N limited when $N:P < 21$, and $N:P > 23$ may indicate P limitation, and co-limitation would occur when the ratio is between 21 and 23 (Zhang et al., 2004). Güsewell (2004) proposed that the species is easily affected by N limitation when $N:P < 10$ and by P limitation when

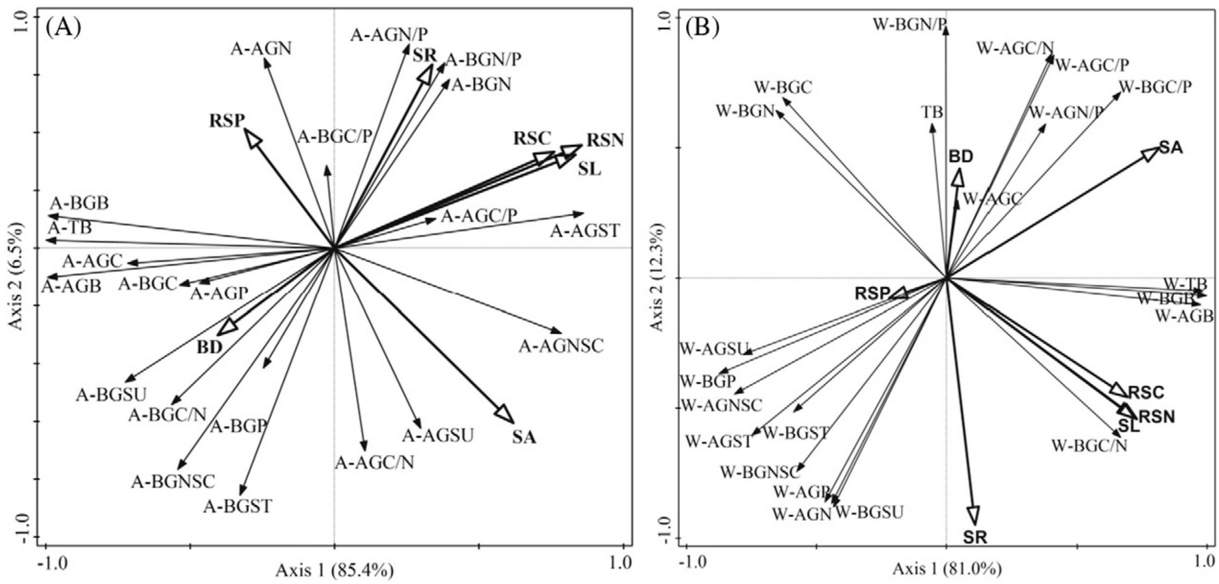

Fig. 7. Bidimensional graph from redundancy analysis to explore the relationship between plant functional trait and environmental variables. A-AGB = *A. sacrorum* aboveground biomass, A-AGSU = *A. sacrorum* aboveground soluble sugar concentrations, A-AGST = *A. sacrorum* aboveground starch concentrations, A-AGNSC = *A. sacrorum* aboveground NSC concentrations, A-AGC = *A. sacrorum* aboveground C concentration, A-AGN = *A. sacrorum* aboveground N concentration, A-AGP = *A. sacrorum* aboveground P concentration, A-AGC/N = *A. sacrorum* aboveground C:N ratio, A-AGC/P = *A. sacrorum* aboveground C:P ratio, A-AGN/P = *A. sacrorum* aboveground N:P ratio, A-BGB = *A. sacrorum* belowground biomass, A-BGSU = *A. sacrorum* belowground soluble sugar concentrations, A-BGST = *A. sacrorum* belowground starch concentrations, A-BGNSC = *A. sacrorum* belowground NSC concentrations, A-BGC = *A. sacrorum* belowground C concentration, A-BGN = *A. sacrorum* belowground N concentration, A-BGP = *A. sacrorum* belowground P concentration, A-BGC/N = *A. sacrorum* belowground C:N ratio, A-BGC/P = *A. sacrorum* belowground C:P ratio, A-BGN/P = *A. sacrorum* belowground N:P ratio, A-TB = *A. sacrorum* total biomass; W-AGB = The weeds aboveground biomass, W-AGSU = The weeds aboveground soluble sugar concentrations, W-AGST = The weeds aboveground starch concentrations, W-AGNSC = The weeds aboveground NSC concentrations, W-AGC = The weeds aboveground C concentration, W-AGN = The weeds aboveground N concentration, W-AGP = The weeds aboveground P concentration, W-AGC/N = The weeds aboveground C:N ratio, W-AGC/P = The weeds aboveground C:P ratio, W-AGN/P = The weeds aboveground N:P ratio, W-BGB = The weeds belowground biomass, W-BGSU = The weeds belowground soluble sugar concentrations, W-BGST = The weeds belowground starch concentrations, W-BGNSC = The weeds belowground NSC concentrations, W-BGC = The weeds belowground C concentration, W-BGN = The weeds belowground N concentration, W-BGP = The weeds belowground P concentration, W-BGC/N = The weeds belowground C:N ratio, A-BGC/P = The weeds belowground C:P ratio, W-BGN/P = The weeds belowground N:P ratio, W-TB = The weeds total biomass, TB = Total biomass of entire plot; SA = slope aspect, SL = slope, BD = bulk density, SR = species richness, RSC = rhizosphere soil C concentration, RSN = rhizosphere soil N concentration, RSP = rhizosphere soil P concentration.

N:P > 20; at ratios between 10 and 20, the species would be co-limited by N and P (Güsewell, 2004). Our results indicated that the growths of *A. sacrorum* and weeds were restricted by N and P, except for *A. sacrorum* in the shady slope, which was restricted by P (N:P = 20.04).

4.2. Effects of slope aspect on soil C:N:P ratio

The C:N (9.42–11.11), C:P (24.39–50.24), and N:P (2.43–4.54) ratios of the soil were close to previously reported (Liu et al., 2013) ratios of 6.9–14.9, 12.1–59.7, and 1.5–4.2, and of 10.7, 38, and 3.6 in China (Tian et al., 2010).

The C:N ratios of the rhizosphere and non-rhizosphere soils were insignificantly affected by slope aspect. This result did not agree with our hypothesis. Consistent with our hypothesis, the C:P and N:P ratios of the rhizosphere and non-rhizosphere soils were significantly affected by slope aspect. The maximum C and N concentrations of the rhizosphere and non-rhizosphere soils appeared in the sunny slope, and this finding is consistent with that of a previous study (Yimer et al., 2006) but contrary to that by Sun et al. (Sun et al., 2015). Slope aspect affects the hydrological and solar energies that consequently affect the vegetation composition, soil formation, organic matter decomposition, and soil temperature and moisture. These changes affect the decomposition rate of soil organic matter and thus cause the difference in soil C and N concentrations in different slope aspects. Our constrained RDA analyses showed that the C and N concentrations of the soil demonstrated a good correlation with the C and N concentrations of the belowground plant part (Fig. 7A and B) but a poor correlation with the P concentration of the soil. Thus, the C and N concentrations were significantly changed by the slope aspect. However, the P concentration was not significantly changed. Thus, the C:P and N:P ratios were significantly changed. In addition, the variation in C:P and N:P ratios were higher in the rhizosphere soil than in the non-rhizosphere soil. This result may be attributed to the fact that the soil nutrient was mainly derived from the decomposition of plant roots and rhizosphere microbial activity, and that the rhizosphere soil was closer to the plant root than the non-rhizosphere soil. Therefore, the C:P and N:P ratios of the rhizosphere soil largely varied.

4.3. Effects of slope aspect on NSC concentrations

Slope aspect significantly affected the NSC concentrations of *A. sacrorum* and the weeds. This result is consistent with our hypothesis but not in accordance with the report of Li et al. (2001) that slope aspect exerts no effect on NSC concentrations (Li et al., 2001). NSCs are the product of photosynthesis; thus, topographic factors affect the level of NSC concentrations in plant (Millard et al., 2007). As a main factor affecting sunlight (Auslander et al., 2003), slope aspect naturally affects plant NSC concentrations. High NSC concentrations help plants maintain a balanced osmotic pressure (Millard et al., 2007) and cope with stress (Poorter and Kitajima, 2007). The aboveground NSC concentrations of *A. sacrorum* reached their maximum values in the sunny slope, which could help *A. sacrorum* resist sunlight. Previous studies indicated that plants store more carbon in harsh environments to improve their survival than to use them on growth (Smith and Stitt, 2007). Accordingly, we found that the NSC concentrations showed a good negative relationship to the aboveground biomass of *A. sacrorum* (Fig. 7A). In addition, high aboveground soluble sugars and starch stored in *A. sacrorum* allow *A. sacrorum* to avoid starvation when the stomata are closed to prevent dehydration during sunny days (McDowell et al., 2008). However, the maximum values of belowground soluble sugars and starch of *A. sacrorum* appear in the half-sunny slope; therefore, *A. sacrorum* in the sunny slope would use the soluble sugars and starch in the belowground first than those in the aboveground when experiencing severe events (Hartmann et al., 2013). Meanwhile, the soluble sugars and starch for *A. sacrorum* belowground in the half-sunny slope show no change under moderate drought conditions (Anderegg, 2012). Furthermore, the three major factors exerted different influences on the aboveground and belowground NSC concentrations of *A. sacrorum*; the effect on the aboveground was positive, whereas that on the belowground was negative (Fig. 7A). The reason is that *A. sacrorum* is suited to grow in the half-shaded and half-sunny slopes. Soluble sugars are a product of photosynthesis and used to meet current plant needs, and starch is the main currency of storage and used to meet future plant needs (Kozlowski and Keller, 1966). Thus, the sunny slope had the maximum aboveground ratio of soluble sugar to starch concentrations of *A. sacrorum*. The significant changed ratio of the soluble sugar to starch concentrations in *A. sacrorum* aboveground is in accordance with our hypothesis, but that in the belowground is not.

@Different from those in *A. sacrorum*, the maximum NSC concentrations in the weeds appeared in the shady slope. Slope aspect exerted a stronger effect on the weeds than on *A. sacrorum* (Fig. 7A and B). The reason is that light availability was a major factor. In this case, the weeds in the shady slope need to store more NSCs to improve their ability to cope with harsh environments (e.g., low temperature) (Li et al., 2009). Studies have found that the sugar concentrations in plants are closely related to their ability to cope with harsh environments (Ramel et al., 2009). Thus, we hypothesized that the ratio of soluble sugar to starch concentrations that had the maximum value in the shady slope would help the weeds cope with low temperature (White, 1973).

5. Conclusions

In summary, slope aspect significantly affected the biomass, aboveground N:P ratio, the C:P and N:P ratios of the rhizosphere and non-rhizosphere soil, and the NSC concentrations of *A. sacrorum* in the grassland of the Loess Plateau in China. The half-sunny slope had the maximum value of *A. sacrorum* biomass, and the shady slope had the maximum value of aboveground N:P ratio. Therefore, *A. sacrorum* was restricted by P rather than N in the shady slope. These findings would help us understand the effects of slope aspect on *A. sacrorum* in the study area. Furthermore, the ratio of belowground to aboveground biomass significantly changed in different slope aspects. The ratio of the soluble sugar to starch concentrations in *A. sacrorum* aboveground also significantly changed. These findings provide new insights into the environmental factors affecting the mechanisms driving biomass and NSC allocation in different plant species. Further field investigations on different plants should be conducted to understand the relationships between slope aspect and plant characteristics.

Acknowledgments

We thank the anonymous reviewers and the editors of the journal who provided constructive comments and suggestions on the manuscript. This work was supported by the Natural Science Foundation of China (41371510, 41371508, 41471438) and West Young Scholars Project of The Chinese Academy of Sciences (XAB2015A05).

Appendix A. Supplementary data

Supplementary data associated with this article can be found in the online version, at http://dx.doi.org/10.1016/j.catena.2016.12.024. These data include the Google map of the most important area described in this article.

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