Postprint: Response of Root, Stem, and Leaf Non-structural Carbon and C:N:P Stoichiometric Characteristics to Drought in Zygophyllum xanthoxylum

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Abstract

By selecting three typical Zygophyllum xanthoxylum communities in the Alxa region as research subjects, we investigated the ecological stoichiometric characteristics and variations in non-structural carbohydrates (NSCs) among different organs (roots, stems, leaves) of Z. xanthoxylum, aiming to deepen understanding of its survival strategies and better serve ecological restoration of desert ecosystems. The results showed that the contents of soluble sugar (SS), starch (ST), and NSCs in stems and leaves of Z. xanthoxylum decreased significantly with intensifying drought. In roots, SS and NSCs showed no significant differences among the three plots, while ST first decreased and then increased, with ST content in Plot3 being 19.3% and 31.2% higher than in Plot1 and Plot2, respectively. Drought significantly decreased N and P contents in roots, stems, and leaves of Z. xanthoxylum, and significantly increased C:N and C:P ratios in these organs, with leaf N:P < 14. In Plot1, SS, SS:ST ratio, and NSCs content among organs of Z. xanthoxylum exhibited the pattern leaf > root > stem, while ST content showed stem > root > leaf; in Plot2 and Plot3, SS, ST, and NSCs contents among organs all showed root > stem > leaf. Across the three plots, leaves had higher N and P contents but lower C:N and C:P ratios compared to stems and roots. Relationships between NSCs and C:N:P stoichiometry indicated that N content was positively correlated with SS in roots, stems, and leaves, while leaf N content was negatively correlated with root ST. These results suggest that stems and roots of Z. xanthoxylum may function as "nutrient reservoirs" , and that Z. xanthoxylum alleviates the effects of water deficit on N-limited growth by enhancing N and P use efficiency. Z. xanthoxylum adapts to drought by regulating the accumulation and allocation of NSCs among organs, employing a strategy of converting ST to SS in roots to adjust osmotic potential; and with intensifying drought, it allocates more carbohydrate investment to roots for storage as ST, with N being the key element influencing the conversion between ST and SS and ST storage in roots of Z. xanthoxylum.

Full Text

Responses of Non-structural Carbohydrates and C:N:P Stoichiometry in Roots, Stems, and Leaves of Zygophyllum xanthoxylon to Drought

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Abstract: In arid ecosystems, high temperatures and low rainfall result in reduced carbon fixation. Non-structural carbohydrates (NSCs) (including soluble sugars and starch) represent the products of plant photosynthesis and are mainly involved in the balance between C acquisition and expenditure in life processes. NSCs also reflect the amount of plant carbohydrates that can be used to resist adverse environmental conditions. The C:N:P stoichiometry of plants is associated with important ecological processes, such as an organism' s ability to adapt to environmental stresses. Leaf N is the basis of chlorophyll formation for direct use in photosynthesis. Plant P is indispensable for the transportation of photosynthetic products. Thus, the C:N:P variations in plants are directly affected by the rate of photosynthesis. Leaf N concentration has been found to be positively correlated with NSC fixation ability, and P has been identified as the key element of plant metabolism. Accordingly, photosynthetic capacity and NSC synthesis are not only affected by leaf N concentration but also closely related to P concentration. Therefore, it is important to study the relationship between NSCs and C:N:P stoichiometry in *Zygophyllum xanthoxylon* to improve our understanding of its survival and growth strategies to xeric conditions.

Samples were collected from three dominant communities of *Z. xanthoxylon* across Ningxia and Inner Mongolia Provinces in northwestern China that differed in mean annual relative air moisture (Plot 1 > Plot 2 > Plot 3). Plant and soil samples were collected during the growing season (August) of 2014. Soluble sugars and starch are commonly studied NSCs. Plant samples were divided into leaves, stems, and roots to analyze the concentrations of starch (ST), soluble sugar (SS), C, N, and P. The concentrations of SS, ST, and NSCs in stems and leaves decreased from Plot 1 to Plot 3. N and P concentrations decreased, whereas C:N and C:P ratios increased with increasing xeric conditions in roots, stems, and leaves. N:P ratios in leaves were all below 13, lower than the critical ratio of 14 in all three plots, suggesting that N is the limiting factor for the growth of *Z. xanthoxylon* in xeric environments. Variations were inconsistent in NSCs and C:N:P stoichiometry among the organs. N and P concentrations in leaves were higher than those in stems and roots, while C:N and C:P ratios in leaves were lower than those in stems and roots in three plots. The correlation of C:N:P stoichiometry with NSCs showed that N concentrations positively correlated with SS concentrations in roots, stems, and leaves, whereas N concentrations in leaves negatively correlated with ST in roots. Stems and roots may act as nutrient sinks, and *Z. xanthoxylon* may alleviate water deficit-caused N limitation by increasing N and P use efficiency. *Z. xanthoxylon* adapted to drought by regulating the accumulation and distribution of NSCs among organs. Osmotic potential is regulated by conversions between ST and SS in the root system; more carbohydrates were allocated to roots and stored as ST with enhancing drought stress. N is the key factor in the transformation of ST to SS and ST storage in the root system.

Keywords: non-structural carbohydrates; C:N:P ratios; organ relevance; adaptive strategy to xeric conditions

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Introduction

As global drought intensifies, plants in desert ecosystems live at the margins of water limitation. Water deficit affects the allocation of carbohydrates among plant organs, altering their growth, survival strategies, and drought adaptation capacity. In arid ecosystems, high temperatures and low rainfall lead to slow carbon fixation, low biogeochemical cycling, and low primary productivity. Elemental C:N:P stoichiometry is crucial for plant metabolic processes, photosynthetic product transport, and photosynthetic apparatus development, making it indispensable for plant growth. Studies have shown that C:N:P stoichiometry can characterize plant survival strategies. Therefore, investigating how C:N:P ratios and NSCs change with intensifying drought and examining their correlations can help understand how desert plants cope with climate change.

Non-structural carbohydrates (NSCs), composed of soluble sugars (SS) and starch (ST), reflect plant carbon supply status and can indicate plant resistance to drought and recovery capacity. The nutrient allocation patterns among leaves, stems, and roots reflect a plant' s ability to acquire, transport, and store nutrients. Research indicates that stems and roots are not only structural components but also key organs for nutrient absorption, transport, accumulation, and storage. However, due to sampling difficulties and labor costs, most studies on shrub N:P stoichiometry have focused on leaves, often based on controlled indoor experiments. Although leaves are critical photosynthetic organs, leaf-level C:N:P composition cannot fully represent the whole plant. Therefore, to comprehensively understand carbohydrate and nutrient allocation and storage patterns in desert plants and their growth strategies for adapting to arid habitats, it is essential to investigate the nutritional status and carbohydrate accumulation and distribution in both leaves and storage organs (stems and roots).

In recent years, plant mortality in the Alxa Plateau has been largely drought-related, affecting not only carbon balance but also ecosystem services. *Zygophyllum xanthoxylon*, a dicotyledonous perennial shrub, is drought- and barren-tolerant and dominates desert and semi-desert vegetation. Previous studies have examined seasonal variations in leaf C:N:P stoichiometry and changes during leaf development, but these were limited to leaf-level analyses and failed to connect multiple sample sites to analyze survival and growth strategies of this dominant desert species. This study investigates C:N:P stoichiometry and NSC changes across roots, stems, and leaves of *Z. xanthoxylon* from different sites to deepen understanding of its survival strategies and inform ecological restoration of desert ecosystems.

1.1 Study Area Overview

The Alxa Plateau (37°24' ~42°47' N, 97°10' ~106°53' E) lies in western Inner Mongolia, covering approximately 25$\times10^{4}$ km^2. The region is arid with low rainfall (40–200 mm annually) and mean annual temperatures of 5.8–8.8°C. Most areas are desert with vegetation coverage of 15%–30%. Soil type is gray-brown desert soil. Vegetation includes four subtypes: typical desert vegetation, steppe desert, desert steppe, and psammophytic vegetation, showing obvious zonal distribution. Dominant plants are xerophytic shrubs such as *Zygophyllum xanthoxylon*, *Kalidium foliatum*, and *Peganum harmala*.

1.2 Experimental Design

During the growing season (August) 2014, we surveyed along national highways and selected three typical *Z. xanthoxylon* communities (Plot1, Plot2, Plot3). Plot1 is near Xiregetu in Alxa Left Banner, Plot2 is near Zhongqu Township in Alxa Left Banner, and Plot3 is in Minqin County. Straight-line distances are: Plot1-Plot2 = 129 km, Plot1-Plot3 = 254 km, and Plot2-Plot3 = 152 km. To exclude road interference, sampling sites were >10 km from highways.

Based on root distribution patterns (1–60 cm in Plot1, 1–80 cm in Plot2, 1–100 cm in Plot3), we established 10 m × 10 m quadrats at each site. Soil background values were surveyed (Table 1). Soil organic matter and nutrient content decreased significantly from surface to deep layers, following Plot1 > Plot2 > Plot3. To characterize drought intensity, we used mean annual relative humidity as an indicator, which decreased gradually from Plot1 to Plot3 (Plot1 < Plot2 < Plot3), indicating increasing drought severity.

1.3 Sample Collection and Laboratory Analysis

In each quadrat, three healthy *Z. xanthoxylon* shrubs were selected. Roots were collected at 0–60 cm (Plot1), 0–80 cm (Plot2), and 0–100 cm (Plot3) depths using root augers (2–5 mm diameter). Current-year stems and functional leaves from the middle of selected stems were sampled. All samples were washed with tap water, rinsed with deionized water, bagged, returned to the laboratory, killed at 105°C for 10 minutes, dried to constant weight at 60°C, ground, and sieved through an 80 m mesh.

Plant total C and N were measured with a Vario EL III elemental analyzer. Total P was determined using a SmartChem 200 chemical analyzer. Soluble sugars (SS) were measured by anthrone colorimetry, starch (ST) by perchloric acid method, and NSCs calculated as NSC = SS + ST. Soil samples were air-dried, sieved, and analyzed for organic matter, total N, and total P using standard methods.

1.4 Data Analysis

Differences among plots and organs were compared using ANOVA in SPSS 16.0, with Duncan' s test for multiple comparisons ($\alpha = 0.05$). Redundancy analysis (RDA) was performed in Canoco 4.5 to examine relationships between environmental factors and NSCs/C:N:P stoichiometry. Monte Carlo permutation tests assessed significance of constrained ordination models. Forward selection excluded collinear environmental variables. Soil organic matter and total N/P content were weighted averages across layers. Figures were prepared in GraphPad Prism 5.

2.1 Accumulation and Distribution of NSCs Among Organs

With intensifying drought, NSC concentrations in stems and leaves decreased significantly ($P < 0.01$). In roots, NSCs first decreased then increased, with no significant differences among plots ($P > 0.05$). SS concentrations decreased significantly in stems and leaves from Plot1 to Plot3 (by 19.3% and 31.2%, respectively), while root SS first decreased then increased, rising 43.2% in Plot3 compared to Plot1. ST concentrations decreased significantly in leaves (by 24.6%) but increased in roots (by 19.3% in Plot3 vs. Plot1). Consequently, the SS:ST ratio increased in roots (by 63.9% in Plot3) but decreased in stems and leaves (by 30.9% and 28.1%, respectively). Across all plots, SS and NSC concentrations were highest in leaves, followed by stems and roots, while ST concentrations were highest in roots and stems, with leaves lowest.

2.2 C:N:P Stoichiometry Among Organs

N and P concentrations decreased significantly in roots, stems, and leaves with increasing drought ($P < 0.05$). C:N and C:P ratios increased significantly ($P < 0.01$). Leaf N and P concentrations were higher than in stems and roots across all plots. For example, leaf N was 73.5% and 75.4% higher than in roots in Plot1 and Plot2, respectively. Leaf P was 61.8% and 59.7% higher than in roots in Plot1 and Plot2. Leaf C:N and C:P ratios were lower than in stems and roots. N:P ratios in leaves were below 14 in all plots (ranging 10.33–13.67), indicating

N limitation. Stem N:P ratios were higher than in roots and leaves, while root N:P ratios showed no clear pattern across plots.

2.3 Relationships Between NSCs and C:N:P Stoichiometry

Correlation analysis revealed that N concentrations were significantly positively correlated with SS concentrations in roots, stems, and leaves ($P < 0.01$). Leaf N was negatively correlated with root ST ($P < 0.05$). Leaf P was positively correlated with leaf SS ($P < 0.01$) but negatively correlated with leaf ST ($P < 0.05$). C:N and C:P ratios were negatively correlated with SS in all organs ($P < 0.01$) but positively correlated with ST in roots and stems ($P < 0.01$). These results suggest stems and roots may function as nutrient sinks.

RDA showed that environmental factors explained 79.4% of variation in C:N:P stoichiometry and NSCs (Fig. 4). Mean annual temperature was positively correlated with C:N and C:P ratios. Air humidity was positively correlated with N and P concentrations but negatively correlated with C:N and C:P ratios. Soil total N was positively correlated with N and P concentrations but negatively correlated with C:N and C:P ratios.

3.1 Drought Effects on NSCs and C:N:P Stoichiometry

NSCs, composed of SS for maintaining water potential and hydraulic conductivity and ST for energy storage, indicate plant carbon balance. Plants with high NSC concentrations survive longer in arid environments. Studies on *Pinus ponderosa* and poplar show that moderate water deficit increases SS concentrations, enhancing osmotic adjustment. Our results show that SS, ST, and NSC concentrations in stems and leaves decreased with intensifying drought, while root NSCs first decreased then increased. The significant increase in root NSCs in Plot3 may result from: (1) drought hindering conversion of NSCs to functional structural materials, causing accumulation; or (2) excessive water deficit causing cavitation that blocks transport, forcing NSCs to accumulate in roots. Thus, under mild drought, *Z. xanthoxylon* converts ST to SS in roots for osmotic adjustment; under severe drought, it allocates more carbohydrates to roots for ST storage to support future growth.

Drought environments impose dual stress of water deficit and nutrient limitation. Soil background values show that organic matter, total N, and total P decreased significantly from Plot1 to Plot3, especially in deep soil layers (Table 1). Reduced soil water content limits nutrient mobility, decreasing N and P availability. Consequently, plant N and P concentrations decreased significantly in all organs (Fig. 3). However, N and P concentrations in leaves remained higher than in stems and roots, suggesting stems and roots function as nutrient sinks. Plants invest more in roots for water absorption while reducing aboveground investment under drought, increasing root:shoot ratios. Despite drought-induced reductions in NSCs, leaves maintained higher NSC concentrations than stems and roots, as plants prioritize allocating nutrients to photosynthetic structures to maintain function under nutrient deficiency.

3.2 Organ-Level Variations in NSCs and C:N:P Stoichiometry

The allocation patterns of NSCs and nutrients among organs reflect comprehensive environmental adaptation. Although leaves are crucial for carbohydrate accumulation, leaf-level NSCs and stoichiometry cannot represent whole-plant status. Across all plots, leaf N and P concentrations were significantly higher than in stems and roots, while C:N and C:P ratios were lower. This indicates leaves are the primary "source" while roots are the primary "sink." NSCs produced in leaves are temporarily stored there but long-term storage occurs in roots and stems to meet future growth demands. The increase in root NSCs with drought reflects continuous transport from leaves to root sinks.

Correlation analysis showed that N concentrations were positively correlated with SS across organs, while leaf N was negatively correlated with root ST. This supports that stems and roots act as nutrient sinks, supplying nutrients to leaves during growth. P is essential for photosynthetic product transport and accumulation. The positive correlation between leaf P and SS and negative correlation with ST suggests P availability affects carbohydrate transport and storage.

RDA indicated that with intensifying drought, *Z. xanthoxylon* increased investment in roots while reducing carbohydrate allocation to leaves. Root distribution deepened from 60 cm in Plot1 to 100 cm in Plot3, supporting this strategy. The higher C:N and C:P ratios in Plot3 indicate increased nutrient use efficiency under severe drought, consistent with studies on *Ulmus pumila*. By allocating more N to photosynthetic structures, plants maximize photosynthetic capacity; as water deficit intensifies, they improve N use efficiency to cope with dual water and nutrient limitations.

4 Conclusions

1. With intensifying drought, SS, ST, and NSC concentrations in stems and leaves of *Z. xanthoxylon* decreased gradually, while root NSCs first decreased then increased. The species adapts to drought by regulating NSC accumulation and distribution among organs, converting root ST to SS for osmotic adjustment and allocating more carbohydrates to roots for ST storage.

2. Drought decreased N and P concentrations in roots, stems, and leaves, while increasing C:N and C:P ratios. Leaves maintained higher N and P concentrations than stems and roots, indicating differential nutrient allocation among organs. *Z. xanthoxylon* alleviated N limitation caused by water deficit by increasing N and P use efficiency.

3. Positive correlations between N concentrations and SS across organs, and negative correlation between leaf N and root ST, suggest stems and roots

function as nutrient sinks. The species invests more carbohydrates in roots for ST storage, while N is the key element affecting ST-SS transformation and ST storage in roots.

References

[6] Azcon R, Gomez M, Tobar R. Effects of nitrogen source on growth, nutrition, photosynthetic rate and nitrogen metabolism of mycorrhizal and phosphorus fertilized plants of *Lactuca sativa* L. [J]. *New Phytologist*, 1992, 121(2): 227-234.

[10] Zhang T, Cao Y, Chen Y, et al. Non-structural carbohydrate dynamics in *Robinia pseudoacacia* saplings under three levels of continuous drought stress[J]. *Trees*, 2015, 29(6): 1837-1849.

[11] Arx G V, Arzac A, Fonti P, et al. Responses of sapwood ray parenchyma and non-structural carbohydrates of *Pinus sylvestris* to drought and long-term irrigation[J]. *Functional Ecology*, 2017, 31(7): 1371-1382.

[12] Xie H, Yu M, Cheng X. Leaf non-structural carbohydrate allocation and C:N:P stoichiometry in response to light acclimation in seedlings of two subtropical shade tolerant tree species[J]. *Plant Physiology and Biochemistry*, 2018, 124(1): 146-154.

[13] Sala A, Woodruff D R, Meinzer F C. Carbon dynamics in trees: Feast or famine[J]. *Tree Physiology*, 2012, 32(6): 764-775.

[14] Reich P B, Oleksyn J. Global patterns of plant leaf N and P in relation to temperature and latitude[J]. *Proceedings of the National Academy of Sciences of the United States of America*, 2004, 101(30): 11001-11006.

[15] Mcgroddy M E, Daufresne T, Hedin L O. Scaling of C:N:P stoichiometry in forests worldwide: Implications of terrestrial Redfield-type ratios[J]. *Ecology*, 2004, 85(5): 2390-2401.

[16] Chapin F S. The mineral nutrition of wild plants[J]. *Annual Review of Ecology and Systematics*, 1980, 11(1): 233-260.

[17] Chapin F S, Schulze E D, Mooney H A. The ecology and economics of storage in plants[J]. *Annual Review of Ecology and Systematics*, 1990, 21(1): 423-447.

[18] Li F, Hu J, Xie Y, et al. Foliar stoichiometry of carbon, nitrogen, and phosphorus in wetland sedge *Carex brevicuspis* along a small-scale elevation gradient[J]. *Ecological Indicators*, 2018, 92(9): 539-545.

[19] Lu X T, Freschet G T, Kazakou E, et al. Contrasting responses in leaf nutrient use strategies of two dominant grass species along a temperate steppe grazing exclusion chronosequence[J]. *Plant and Soil*, 2015, 387(2): 69-79.

[20] Sala A, Hoch G. Height-related growth declines in Ponderosa pine are not due to carbon limitation[J]. *Plant, Cell & Environment*, 2010, 32(1): 22-30.

[21] He M Z, Dijkstra F A, Zhang K, et al. Influence of life form, taxonomy, climate, and soil properties on shoot and root concentrations of 11 elements in herbaceous plants in a temperate desert[J]. *Plant and Soil*, 2016, 398(1): 339-350.

[22] He M Z, Zhang K, Tan H, et al. Nutrient levels within leaves, stems, and roots of the xeric species *Reaumuria soongorica* in relation to geographical, climatic, and soil conditions[J]. *Ecology and Evolution*, 2015, 5(7): 1494-1503.

[26] Ramirezbriones E, Rodriguzmacias R, Salcedoperez E, et al. Seasonal variation in non-structural carbohydrates, sucrolytic activity and secondary metabolites in deciduous and perennial *Diospyros* species sampled in Western Mexico[J]. *PloS One*, 2017, 12(10): 1-24.

[27] O' brien M J, Leuzinger S, Philipson C D, et al. Drought survival of tropical tree seedlings enhanced by non-structural carbohydrate levels[J]. *Nature Climate Change*, 2014, 4(8): 710-714.

[28] Sala A, Hoch G. Height-related growth declines in Ponderosa pine are not due to carbon limitation[J]. *Plant, Cell & Environment*, 2010, 32(1): 22-30.

[29] Zhang T, Cao Y, Chen Y, et al. Non-structural carbohydrate dynamics in *Robinia pseudoacacia* saplings under three levels of continuous drought stress[J]. *Trees*, 2015, 29(6): 1837-1849.

[32] Ai Z M, Xue S, Wang G L, et al. Responses of non-structural carbohydrates and C:N:P stoichiometry of *Bothriochloa ischaemum* to nitrogen addition on the Loess Plateau, China[J]. *Journal of Plant Growth Regulation*, 2017, 36(3): 714-722.

[34] Drenovsky R E, James J J, Richards J H. Variation in nutrient resorption by desert shrubs[J]. *Journal of Arid Environments*, 2010, 74(11): 1564-1568.

[35] He M Z, Dijkstra F A. Drought effect on plant nitrogen and phosphorus: A meta-analysis[J]. *New Phytologist*, 2014, 204(4): 924-931.

[36] Hartley A N, Bargerj B, Okin G. Dryland ecosystems[C]//Marschner P, Rengel Z. *Nutrient Cycling in Terrestrial Ecosystems.* Berlin & Heidelberg: Springer, 2007: 271-308.

[37] Sterner R W, Elser J J. *Ecological Stoichiometry: The Biology of Elements from Molecules to the Biosphere*[M]. Princeton: Princeton University Press, 2002: 357.

[38] Vitousek P. Nutrient cycling and nutrient use efficiency[J]. *American Naturalist*, 1982, 119(4): 553-572.

[40] Von A G, Archer S R, Hughes M K. Long-term functional plasticity in plant hydraulic architecture in response to supplemental moisture[J]. *Annals of Botany*, 2012, 109(6): 1091-1100.

[42] Farooq M, Hussain M, Wahid A, et al. Drought stress in plants: An overview[M]. Berlin & Heidelberg: Springer, 2012: 288.

[43] Farooq M, Wahid A, Kobayashi N, et al. Plant drought stress: Effects, mechanisms and management[J]. *Agronomy for Sustainable Development*, 2009, 29(1): 185-212.

[44] Thompson K E N, Parkinson J A, Band S R, et al. A comparative study of leaf nutrient concentrations in a regional herbaceous flora[J]. *New Phytologist*, 1997, 136(4): 679-689.