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ORIGINAL ARTICLE

The partitioning patterns of nutrients between pods and seeds of *Zanthoxylum* fruits impacted by environmental factors

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Abstract The nutritive quality in plant organs is related to the different partitioning patterns of nutrient resources among the organs under various environmental conditions. This study examined the relationship between the nutritive quality of pods and seeds in *Zanthoxylum* and environmental factors, such as temperature and preciptation by using numerous samples collected from Southwest China to the East China of Shandong peninsula. The increasing accumulations of N, P and C in seeds implied that the nutritive quality in seeds was higher at the regions with relative higher mean annual temperature (MAT) and mean annual precipitation (MAP), while that in pods was on the contrary. By contrast, pod nutritive content was relatively high, but seed nutritive content was relatively low at the regions with relative high MAT and MAP. In addition, C:N ratio in pods was significantly and negatively correlated with MAT and MAP, while that in seed was significantly and positively correlated with MAT and MAP. The partitioning patterns of N-compounds between pods and seeds reflected different nitrogen translocations in the plant organs under various climate condition. The N:P ratios were negatively correlated with MAP, implying a higher proportional allocation of P to seeds than that of N in the areas with a relative high MAP. Therefore, the strategies to assess pod nutritional quality should be taken into account for nutritive translocation under various environmental conditions.

Keywords Partitioning pattern · Nutritional quality · C:N ratio · *Zanthoxylum* fruits · Mean annual temperature · Mean annual precipitation

1 Introduction

The recycling of nutrients is essential for production of seeds that contain high contents of storage compounds such as protein, lipid and starch (Bennett et al. 2011). The relocation requires high seed vigor with rapid and high germination across a wide range of environmental conditions to optimize crop establishment and productivity (Correia and Martins-Loução 1997). The pod becomes a resource sink of storing remobilized nitrogen (N), phosphate (P) and carbon (C) for utilization upon seed germination during the anthesis stage (Schiltz et al. 2005). The mobilization of post-anthesis C and N from plant organs or tissues and their remobilization by seeds directly affects the content of C, N and protein in seeds (Buchner et al. 2015). The germination percentages is often higher when more nutrients are transferred from pods to seeds, because germination percentages increases with seed mass, seed C and N contents, and seed N:P (Vergutz et al. 2012; Royer et al. 2013). Seed N content determine the germination efficiency and survival of young seedlings (Masclaux-Daubresse et al. 2010).

The seed nutrient contents are affected by various environmental conditions, including temperature, precipitation and soil nutrient contents (Carón et al. 2014). Particularly, precipitation and temperature affect organ nutrient contents and nutrient allocation among plant

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organs by changing contents of nutrients associated with plant metabolin (Zhang et al. 2012). Therefore, examining the relation between plant species especially seeds and meteorological conditions across geographical spaces can facilitate our understanding of the relative role and impacting of environmental conditions on variations of nutrient contents and its stoichiometry in pods and seeds (De Frenne et al. 2013; Carón et al. 2014). Based on the important role of nutrient conservation, we hypothesized that the pod and seed exhibit different partitioning patterns across geographical spaces, if the pod and seed nutrient contents change with meteorological conditions in the opposite direction.

The pod walls act as a nutrient source of seed development (Bennett et al. 2011; Yoneyama et al. 2016), During which increasing nutrients are transported from pods to seeds. e.g., the pods of oilseed rape could mobilize 80% of the total shoot N to seeds upon harvest (Bennett et al. 2011); the pods of pea could mobilize 20% of the N accumulated in seeds (Schiltz et al. 2005). These data suggest that N retention in pods and other vegetative parts might attenuate N accumulation in seeds (Yoneyama et al. 2016).

Chinese prickly ash (*Zanthoxylum bungeanum*) is a multipurpose horticultural plant that benefit local farmers in many regions in China, where cereal productivity is very low. The pods (pericarps) from *Zanthoxylum* fruits are used as seasoning for cooking and as components of traditional medicine in China; the seeds are used to feed livestock. However, the nutritional quality of pods and seeds of *Zanthoxylum* fruits in Chinese prickly ash varied with regions, with the underlying reasons remaining unclear. The nutritional quality is important for consumers, and their perception of quality is based on sensory characteristics. The quality of fruit crops can often be attributed to environmental factors, and greatly changes with regions and seasons (Montanaro et al. 2012; Kollas et al. 2012). For example, the environmental factors have been reported to control N and C resource allocation to seeds and the crop yield was documented to negatively correlated with nutritional quality (Chardon et al. 2014). Besides, an abiotic environmental condition can influence the stoichiometric characteristic and nutrient allocation to plant tissue/organ (Yu et al. 2017). Chinese prickly ash should have a specific nutrient composition, C:N ratio and partitioning patterns under environmental conditions because of a consequence of its particular metabolism, physiology and morphology linked to its optimal functioning (Sardans and Peñuelas 2014). The aim of present study was to assess the translocation of nutrient contents and stoichiometry in plant organs to determine if variability of nutrient contents in Chinese prickly ash would be impacted by changes in environmental conditions.

2 Materials and methods

2.1 Studying site

The study areas were widely located in a transitional zone from Southwest China to East China (Shandong peninsula). Southern China and eastern China are mainly dominated by a southwest monsoon from the Indian Ocean and a southeast monsoon from the Pacific Ocean, which produce high rainfall during summer. There is generally a higher MAP or a higher MAT in Southwest China with subtropical climate than in central and eastern China with temperate climate (Table 1). The Southwest China is typically characterized by karst geometry with overpopulated villages and extremely fragile environment but (Liu 2007; Li et al. 2013), leading to Chinese prickly ash growing widely in this areas. Leaf fall in Chinese prickly ash grown on temperate areas occurred from autumn to winter, but leaf fall in Chinese prickly ash grown on subtropical areas lasted from winter to next spring.

The samples collected from Huajiang (HJ), with relatively high MAT and MAP, in turn Zunyi (ZY), Chongqing (CQ), Pingdingshan (PD), Zoucheng (ZC) to Laiwu (LW) (Table 1). The sampling sites were located in areas in which soils developed in mixed terrain, except for those at HJ, which were developed from limestone. The soil types were clay–sandy or sandy–clay loam in HJ, ZY and CQ sites. The Chinese prickly ash in these areas had fine roots more shallowly and widely rooted in the top 1–5 cm. While soil types were sandy–clay loam or sandy loam in PD, ZC and LW sites, where relatively deep roots were expected. The parameters for sampling sites and collected sample numbers are listed in Table 1. The climatic data, including MAT and MAP, obtained from local meteorological observation station. Soil samples were collected from 0 to 15 cm in six replicated plots for each soil sample around canopy and analyzed for available nutrients. Chemical fertilizer was not added to all the sampling soils at the collecting sampling year. Seed-pod samples were collected in late July for the HJ, ZY and CQ with relative higher MAT, while they were collected in early August for PD, ZC and LW with relative lower MAT, which time is just farmer's harvesting time for obtaining condiment of pods. Delay or advance of the harvesting time the seeds were not automatically separated from pods when drying the fruits.

2.2 Laboratory analysis

Plant samples for laboratory analysis were dried for 48 h at 60 °C, then ground with a mortar and pestle, after which total C and N were determined using a CHNS autoanalyzer (PE 2400-ll, Norwalk, CT, USA). The P of the plant was

Table 1 Sampling location and environmental parameters

Sampling sites	Huajiang (HJ, n = 22)	Zunyi (ZY, n = 22)	Chongqing (CQ, n = 8)	Pingdingshan (PD, n = 10)	Zoucheng (ZC, n = 12)	Laiwu (LW, n = 13)
Location	From 25°38′N to 25°41′N; From 105°38′E to 105°41′E	From 27°48′N to 27°57′N; From 107°14′E to 107°16′E	From 29°10′N to 29°14′N; From 106°11′E to 106°18′E	From 33°56′N to 33°59′N From 112°46′E to 112°49′E	From 35°20′N to 35°25′N; From 117°00′E to 117°20′E	From 36°06′N to 36°26′N; From 117°29′E to 117°39′E
MAT (°C)	18.4	15.6	18.2	15.0	14.1	13.4
MAP (mm)	1200	1160	1035	730	780	710
AE (m)	780	830	210	360	160	270

MAT mean annual temperature, *MAP* mean annual precipitation, *AE* average elevation

n number of samples

digested using nitric-perchloric acid and analyzed by the vanadomolybdate colorimetric method. The total soil P was determined after combustion of 1 g soil for 2 h at 550 °C followed by digestion with 6 M HCl. For soluble sugar determination, 0.25 g of air dried material was extracted four times with distilled water at 75 °C, modified from the method of Chinnasamy and Bal (2003) whereby water was used instead of 80% of ethanol and the water temperate was 75 °C rather than boiling. After each extraction, samples were filtered, and the filtrates were used to determine soluble sugar colorimetrically through the anthrone reaction (Piao and Liu 2011).

2.3 Statistical analysis

Statistical analysis was conducted using the SPSS 12.0 software (SPSS Science, Chicago, USA). The difference in nutrient content between the pod and seed, i.e., pod nutrient content minus seed nutrient content, as expressed by N(pod-seed), P(pod-seed), indicate the deviation of seed from pod. That means lower value of N(pod-seed) or P(pod-seed) implied that relatively high contents of N or P allocated from pods to seeds. The different significances of mean values of nutrient contents between pods and seeds were determined by a *t* test, while Pearson correlation coefficients were performed to assess relationships between each plant organs and soil parameter, and linear regression was used to assess relationships between plant organ and soil parameters. For all statistical analyses, differences were considered significant at $P < 0.05$.

3 Results

The soil pH value varied from 4.39 to 8.26. The average soil pH was 7.18 ± 0.97 for all samples (n = 87). The soil organic C ranged from 0.41 mol·kg^{-1} to 7.69 mol·kg^{-1} with an average of 1.88 ± 1.13 mol·kg^{-1}. The soil N varied from 0.05 to 0.59 mol·kg^{-1} with an average of 0.16 ± 0.09 mol·kg^{-1}. The averaged soil total P content was 25.8 ± 12.5 mmol·kg^{-1} ranged from 8.07 to 54.6 mmol·kg^{-1} in all sampling soils. Soil N was negatively correlated with seed N ($r = -0.241$, $P < 0.05$, n = 87), while not significantly, but positively, correlated with pod N ($r = 0.109$). The soil P was negatively, but not significantly, correlated with seed P ($r = -0.169$), while significantly and positively related with pod P ($r = 0.342$, $P < 0.01$). Table 2 shows that nutritive contents in pods, including N, P and C, were significantly lower than these in seeds in the areas (PD, ZC and LW) with relatively low MAT. While pod nutritive contents were significantly high than seed in the areas (HJ, ZY and CQ) with relatively high MAT, although soil nutritive contents were higher in HJ,

Table 2 Nitrogen, phosphorus and carbon contents in pods and seeds of Chinese prickly ash (mean ± standard deviation)

Sites($mol \cdot kg^{-1}$)	Huajiang (HJ)	Zunyi (ZY)	Chongqing (CQ)	Pingdingshan (PD)	Zhoucheng (ZC)	Laiwu (LW)
Pod N	1.49 ± 0.24	1.40 ± 0.23	1.96 ± 0.45	1.05 ± 0.26	1.15 ± 0.24	1.25 ± 0.23
Seed N	1.09 ± 0.16	0.90 ± 0.10	1.00 ± 0.06	1.66 ± 0.29	1.72 ± 0.15	1.45 ± 0.27
Pod P	0.11 ± 0.04	0.10 ± 0.03	0.10 ± 0.02	0.06 ± 0.03	0.09 ± 0.04	0.08 ± 0.02
Seed P	0.07 ± 0.01	0.07 ± 0.01	0.06 ± 0.01	0.10 ± 0.01	0.09 ± 0.01	0.09 ± 0.02
Pod C	36.9 ± 3.0	37.2 ± 2.1	34.3 ± 1.5	36.1 ± 0.5	32.0 ± 1.9	36.6 ± 1.1
Seed C	37.8 ± 5.0	38.3 ± 3.0	33.9 ± 3.4	44.1 ± 1.8	34.3 ± 2.9	43.4 ± 2.7

ZY and CQ soils than in PD, ZC and LW soils. Therefore, the correlation between the nutrient contents in plant organ and the soil nutrient contents was not consistent.

The average value of C(pod-seed) was significantly high (-0.8 ± 2.7 $mol \cdot kg^{-1}$) in the areas with relative high MAT compared with that (-5.9 ± 3.8 $mol \cdot kg^{-1}$) in the areas with relative low MAT ($P < 0.001$, Fig. 1a). The average value of P(pod-seed) in HJ, ZY and CQ areas (40 ± 34 $mmol \cdot kg^{-1}$) was significantly higher than that (-20 ± 33 $mmol \cdot kg^{-1}$) in PD, ZC and LW areas ($P < 0.001$, Fig. 1b). The average value of N(pod-seed) in the areas with relatively high MAT (0.53 ± 0.31 $mol \cdot kg^{-1}$) was significantly higher than that (-0.45 ± 0.36 $mol \cdot kg^{-1}$) in the areas with relatively low MAT ($P < 0.001$, Fig. 1c). Therefore, both pod N and P were negatively and significantly correlated with both seed N ($r = -0.336$, $P < 0.01$) and P ($r = -0.298$, $P < 0.01$), respectively. The results imply that seed N, P and C contents in the HJ, ZY and CQ areas were relatively lower than in the PD, ZC and LW areas, while pod N, P and C contents in the HJ, ZY and CQ areas were relatively high than in the PD, ZC and LW areas. The values of N(pod-seed) were significantly and positively related with P(pod-seed) (Fig. 2a), and with C (pod-seed) (Fig. 2b). The results indicate that the more amounts of both C and N mobilized from pods to seeds in the PD, ZC and LW areas were higher than in the HJ, ZY and CQ areas at the harvest time in the present study.

Both pod and seed N:P ratios were not significantly correlated with MAT, while only seed N:P ratios were negatively and significantly correlated with MAP ($r = -0.378$, $P < 0.01$), implying that the higher proportional allocation of P than N to seeds was related to increasing MAP. The average value of pod C:N ratios (21.6 ± 4.6) in HJ, ZY and CQ areas was significantly lower than that (27.6 ± 7.1) in PD, ZC and LW areas ($P < 0.001$). Pod C:N ratios increased with increasing latitude, i.e., they were negatively related with MAT (Fig. 3a), and were also negatively related to MAP. While the average value of seed C:N ratios (33.0 ± 5.9) in HJ, ZY and CQ areas was significantly higher than that (22.3 ± 4.9) in PD, ZC and LW areas ($P < 0.001$).

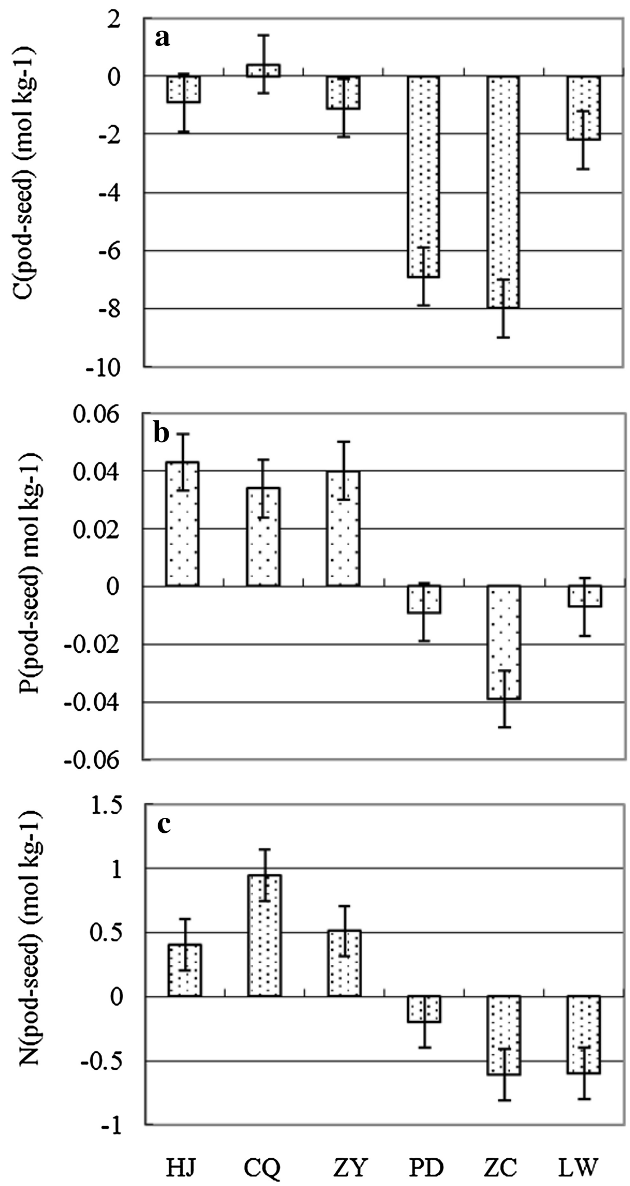

Fig. 1 The plots of the values of C(pod-seed), i.e., the differences of C between pods and seeds (**a**), the values of P(pod-seed), i.e., the differences of P between pods and seeds (**b**), and the values of N(pod-seed), i.e., the differences of N between pods and seeds (**c**), versus sampling sites, where the MAT decreased in turn from HJ to LW

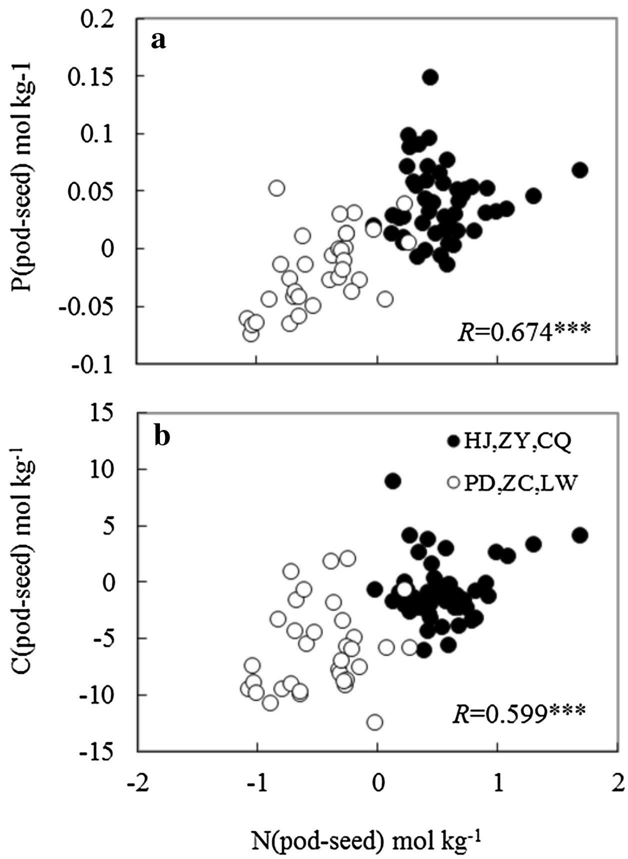

Fig. 2 The relationships of P(pod-seed) (**a**) and C(pod-seed) (**b**) with N(pod-seed), open symbols indicate the samples collected from the areas with relatively low temperature, including PD, ZC and LW; close symbols indicate the samples collected from the areas with relatively high temperature, including HJ, ZY and CQ

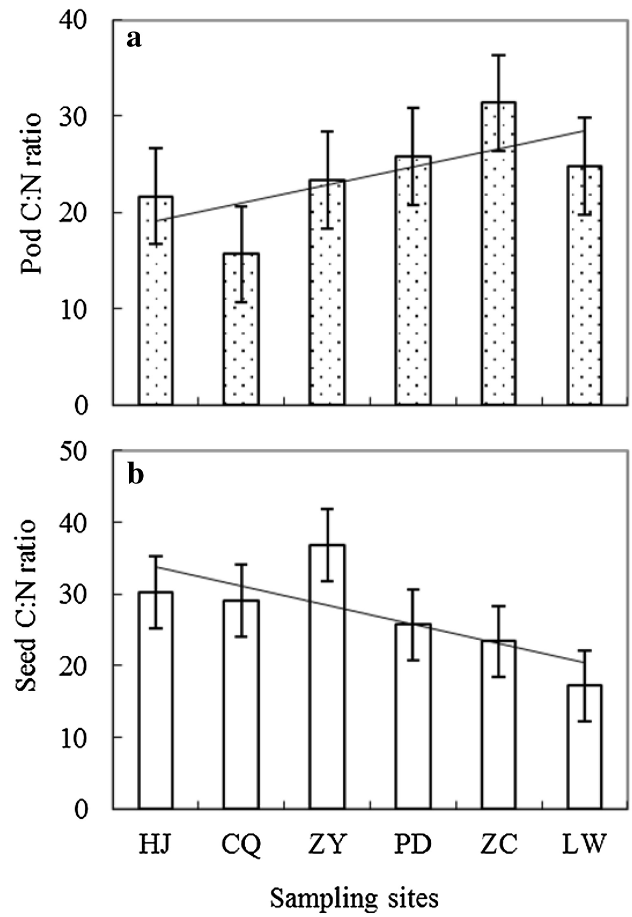

Fig. 3 The plots of pod C:N ratios (**a**) and seed C:N ratios (**b**) versus sampling sites, where latitude increased in turn from HJ to LW, therefore, MAT decreased in turn from HJ to LW

Therefore, seed C:N ratios decreased with increasing latitude, therefore, were positively correlated with MAT (Fig. 3b), and were also positively related with MAP. The results suggested that a latitudinal gradient patterns for seed C:N ratios were variable across ecosystems.

The average value of pod sugar (0.17 ± 0.06 mol·kg^{-1}) in HJ, ZY and CQ areas was significantly lower than that (0.25 ± 0.09 mol·kg^{-1}) in PD, ZC and LW areas ($P < 0.001$). Therefore, pod sugar contents decreased with increasing MAT (Fig. 4a). While the average value of seed sugar (0.04 ± 0.013 mol·kg^{-1}) in HJ, ZY and CQ areas was significantly higher than that (0.035 ± 0.008 mol·kg^{-1}) in PD, ZC and LW areas ($P < 0.05$).

4 Discussion

The results showed that the spatial variation of nutrient contents in pods, but not seeds, is similar to the spatial pattern of that in soil, reflecting nutrient sources supply as a major factor for nutrient transportation. Götz et al. (2007) reported that seed nutrient content depends on not only N uptake from the soil, N fixation and allocation, but also remobilization from vegetative tissues, including pod walls. Chinese prickly ash prefers nitrate (Piao et al. 2017), its N uptake from the soil is usually low, while N supply from vegetative organs is the main source to match N requirement during seed filling, similar to that in oilseed rape (Noquet et al. 2004; Malagoli et al. 2005; Coello and Martínez-Barajas 2016). Vergutz et al. (2012) concluded that there is no consistent relationship between plant nutrient mobilization and soil nutrient availability based on global data. Plants do not always show high nutrient uptake capacity in low-fertility soils (Tang et al. 2013). In this study, the results indirectly illustrated that the nutrient contents in seeds should be remobilized from various sources, including leaves, stems and pods, during seed development.

The climatic factors influence N and C resource allocation to seeds (Chardon et al. 2014). Högy et al. (2013) reported that elevated temperature affected the

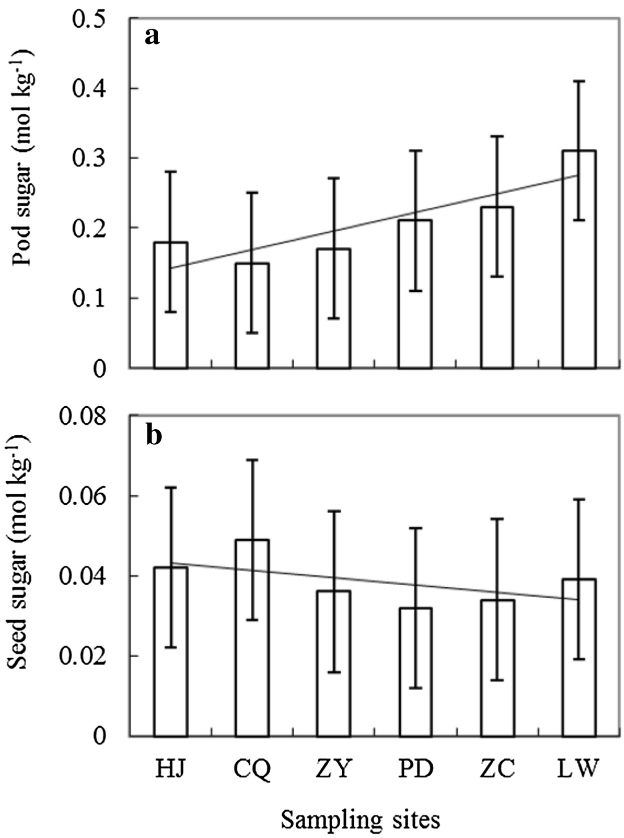

Fig. 4 The plots of pod sugar contents (**a**) and seed sugar contents (**b**) versus sampling sites, where MAT decreased in turn from HJ to LW

performance and grain quality more significantly than changes in rainfall. Rugemalila et al. (2017) reported that seed production and viability are not influenced by rainfall in *Acacia robusta* and *Acacia tortilis* species across the Serengeti rainfall gradient. A number of studies have shown that the N and P contents of whole organisms generally declines with increasing temperature (Cross et al. 2015, other references therein). Therefore, it is expected that the climatic gradient patterns for seed nutrient contents are variable across ecosystems. The relative high contents of N, P and C in seeds and the low contents of N, P and C in pods were found in the areas with relatively low temperature. Meanwhile, the relative low contents of N, P and C in seeds and the high contents of N and P compounds in pods were found at the areas with high temperature. A high temperature after anthesis could reduce seed quality in bean (Sanhewe et al. 1996), while a low temperature might enhance nutritional value of various crops (Yoon et al. 2017, other references therein). Thus, the nutrient contents in pods should be impacted significantly by temperature for Chinese prickly ash.

Nitrogen and phosphorous are fundamental to seed filling because they constitute the basic components of many organic molecules, such as protein (Vinod and Heuer 2012). Phosphorus allocation into seed helps maximize the survival of the seedlings in seasonally dry and nutrient-poor areas (Denton et al. 2007). An increase in MAP was reported to be related to a higher proportional allocation of P than N to seeds (Sardans and Peñuelas 2013). Similar results were obtained in this study, which reflected nutrient using strategy for Chinese prickly ash impacted by environmental condition. The plants have developed efficient remobilization of P from leaves, and that more P and N are resorbed in nutrient poor soils, resulting in higher remobilization of P than of N at a global scale (Sardans and Peñuelas 2015). The results suggested that Chinese prickly ash had efficient remobilization of nutrient for pods.

C and N cycles are strongly coupled by the stoichiometry of plant autotrophic nutrition and soil microbial processes (Soussana and Lemaire 2014). The relationship of N-compound and carbohydrate metabolism is usually expressed with the index of the carbohydrate and the total N ratio, i.e., C:N ratio (Zhang et al. 2014). The ratio of C:N of an organ is often regarded as a convenient indicator of growth and quality (Royer et al. 2013). Manipulation of precipitation only marginally resulted in reduction of barley grain amount with increasing of amino acid content. (Högy et al. 2013). The protein content is strongly correlated with decreasing C:N ratios (Truong et al. 2013; Zhang et al. 2014). Oikawa et al. (2008) reported that most proteins are degraded into mobile forms, which are resorbed and transferred to new organs upon shedding. Therefore, it could be expected that the mobilized protein to seeds increasing with decreasing MAT and MAP. Truong et al. (2013) reported that protein biosynthesis is sensitive to decreasing C:N ratios in the culture medium, and starch content increased with increasing C:N ratios. In the case of maize, an increase in the genetic potential is accompanied by a decrease in the content of proteins (about 1.5%) and an increase in that of starch (about 2%). Moles et al. (2009) suggested that plants allocate a much greater proportion of net primary productivity to reproduction in tropical regions, resulting in geographical gradient for seed mass, which is in agreement with the present study. The nutrient allocation in plant would be influenced by various environmental conditions. The temperature and precipitation would have an effect on plant physiological process, resulting in translocation of nutrient in plant organs.

It is well known that there are trade-offs between the quantity and quality of harvestable products, and any condition that improves yield may reduce the nutritive quality, such as protein contents, in seeds (Franzaring et al. 2012). Therefore, seed sugar increased with increasing temperature, implying that when seed sugar was high, seed N-compound was low at the areas with relatively low temperature. Veneklaas et al. (2012) concluded that grains with high N contents are favored because of the proteins' nutritional value, however, high P contents are not necessarily desirable in crop plants. Phosphorus remobilization into seed would help maximize the survival of the seedlings in seasonally dry and nutrient-poor environments (Denton et al. 2007). In this study, the germination percentage of seeds collected at HJ located the area with relatively high temperature and extremely low precipitation, indicating that relative low nutritive quality in seeds resulted in low germination percentage. By contrast, relative high nutritive quality in pods would produce more benefits for eating qualities, which might increase economic incoming for local farmers.

5 Conclusions

This study investigated the nutritive quality in organs of Chinese prickly ash under various environmental conditions at different regions in China. The contents of N and P compounds in seeds of Chinese prickly ash decreases as MAT increases, resulting in the relatively low pod nutrient quality in regions with relatively high MAT. The increase in the allocation of N to seeds at lower MAT and MAP should attribute to the conservation strategies of N storage especially in the areas with relatively low temperature. Our findings show that N-compounds were highly available where needed, that was, relative low temperature and precipitation, and poor soil fertility require higher seed nutritional quality, resulting in a decreasing pod nutritional quality, while increasing seed nutritional quality along a climatic gradient. The physiological process in Chinese prickly ash was significantly impacted by temperature and precipitation, resulting in the translocation of nutrients in plant organs. The results in this study demonstrated that the nutrient quality of plant organs were mainly dominated by various environmental conditions.

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Conflict of interest The authors declare no competing financial interests.

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