

Adaptation of *Asparagus munitus* to karst adversity and its effects on soil

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Abstract

In this study, *Asparagus munitus* was planted in karst rocky desertification (KRD) areas and arable land (AL) to explore the changes in plant adaptability to KRD environments and effects on KRD soils. Results showed *A. munitus* exhibited shrinkage in KRD habitats, evidenced by increased number and length of stems, branch length, and other agronomic traits; significantly elevated antioxidant enzyme and osmoregulator content in leafy shoots; and increased polysaccharide content in tuberous roots. Correlation and principal component analyses of plant agronomic traits revealed strong correlations among indicators except basal stems, with leaf shoot length and root diameter as the first and second principal components, respectively. Soil physical properties and nutrient contents showed KRD soil pH, water content, porosity, and nutrient content markedly changed after *A. munitus* planting, overall positively developing. This study reveals partial adaptive strategies of *A. munitus* to KRD habitats and ameliorative effects of planting *A. munitus* on KRD soils, providing theoretical bases for *A. munitus* cultivation and KRD soil improvement.

Introduction

According to the latest karst rocky desertification (KRD) survey, China's KRD area was 7.22 million hm² in 2021^[1]. KRD severely limits human land use due to poor nutrient storage, severe temporary drought, and poor ecological stability^[2]. Studies have shown a correlation between poverty and the KRD environment^[3, 4]. To address ecological and economic issues, controlling KRD is urgently needed for environmental protection and poverty eradication.

Asparagus cochinchinensis (Lour.) Merr. is a perennial herb; its tuberous roots have long been used in traditional Chinese medicine and was included in the 2020 Chinese Pharmacopoeia^[5]. Currently, *Asparagus munitus* Wang et S.C. Chen (*A. munitus*), *Asparagus lycopodineus* (Baker.) Wang et. Tang (*A. lycopodineus*) and *Asparagus subscandens* Wang et S.C. Chen (*A. subscandens*) have been artificially domesticated^[6]. Although only *A. cochinchinensis* is officially recognized, the other three *Asparagus* species are more widely cultivated due to *A. cochinchinensis*'s low yield and their similar medicinal composition.

With *Asparagus* development and utilization, there are great market prospects in pharmacology^[7–10] and health foods^[11]. *A. munitus*'s wide distribution indicates strong environmental adaptability^[12]. Several studies have shown that herbaceous plants undergo better carbon sequestration than woody plants^[13], and their well-developed root systems are able to fix the topsoil layer and prevent soil erosion^[14]. The effects of planting *Asparagus* on soil physicochemical properties and nutrients have been studied^[15], but few studies exist on *Asparagus* planting in karst soil and its interaction.

This study compared *A. munitus* changes in KRD and arable land (AL) to predict survival strategies in KRD. It also tested whether *A. munitus* could improve KRD soil conditions, providing a basis for its cultivation and KRD control and new ideas for medicinal plant development.

Results

A. munitus under KRD conditions shows a decreasing trend

The results revealed significant differences ($p < 0.05$) in stem number, stem length, middle lateral branch length and leaf length between the EG and CK plants of *A. munitus* (Table 1). No significant differences were observed for the other indicators. LSD indicated no significant difference in below-ground biomass, however CK averaged approximately one-third higher than EG, EG tubers tended to be shorter but greater in diameter (Fig. 2A, B). Overall, EG growth was inhibited, especially above ground, and was weaker than that in the CK treatment.

Table 1
Agronomic traits of *A. munitus* plants grown in different regionsa and b indicate significant differences at the 0.05 level ($p < 0.05$); A and B indicate significant differences at the 0.01 level ($p < 0.01$). The values are the means $\pm$ standard deviations

Trait	Unit	Control check	Experiment group
Number of stems	each	5.33 $\pm$ 0.82 A	3.67 $\pm$ 0.52 B
Basal stem thickness	mm	3.05 $\pm$ 0.46 a	2.98 $\pm$ 0.53 a
Stems length	cm	141.66 $\pm$ 16.8 a	114.05 $\pm$ 21.0 b
Lateral branch length	cm	21.97 $\pm$ 2.84 A	16.85 $\pm$ 1.88 B
Leafy shoot length	mm	6.76 $\pm$ 0.87 A	5.18 $\pm$ 0.61 B
Above-ground biomass	g	42.30 $\pm$ 10.19 a	34.88 $\pm$ 6.64 a
Underground biomass	g	245.53 $\pm$ 62.67 a	186.76 $\pm$ 30.11 a

Biochemical responses of A. munitus leafy shoots to KRD

The stomatal density in the EG treatment was significantly greater than that in the CK treatment (Fig. 3), averaging 471.26 mm⁻². Compared to those in the CK treatment, the photosynthetic pigment content in the EG treatment was markedly lower; however, the carotenoid-to-chlorophyll ratio differed highly significantly between the groups (Table 2). Similarly, the leaf SOD, POD, and CAT activities in the EG treatment were 1.4, 1.6 and 1.7 times greater than those in the CK treatment, respectively. Osmoregulatory substances showed similar increasing trends in the EG compared to the CK. These results suggest that *A. munitus* individuals experience some degree of stress under KRD conditions.

Table 2

Biochemical indicators of plants in different environments. A and B indicate significant differences at the 0.01 level ($p < 0.01$). The values are the means $\pm$ standard deviations. FW: fresh weight

Trait	Unit	Control check	Experiment group
Stomata density	Pcs/mm ²	375.43 $\pm$ 45.92 B	471.26 $\pm$ 103.52 A
Chlorophyll a	mg/g FW	1.81 $\pm$ 0.03 A	1.43 $\pm$ 0.04 B
Chlorophyll b	mg/g FW	0.72 $\pm$ 0.058 A	0.52 $\pm$ 0.033 B
Carotenoid	mg/g FW	0.41 $\pm$ 0.002 A	0.37 $\pm$ 0.004 B
Carotenoids/chlorophyll	$\times 10^{-2}$	16.27 $\pm$ 0.12 B	18.83 $\pm$ 0.49 A

The medicinal components of *A. munitus* are not affected by KRD

Total saponins, polysaccharides and total amino acids are the main medicinal components of *A. munitus* tubers. The results showed that the polysaccharide content was significantly greater ($p < 0.05$) in the EG tubers than in the CK tubers, while no significant differences were observed for the other components (Fig. 4). These findings indicate that *A. munitus* plants can accumulate medicinal components normally when planted in KRD areas, which is even slightly higher than what is observed in the CK treatment.

Correlation analysis and principal component analysis of agronomic traits in *A. munitus* Correlation analysis revealed strong associations between most agronomic traits, except for basal stem thickness, which was less correlated with the other indicators (Fig. 5). After removing the basal stem thickness, the remaining traits were subjected to principal component analysis. The first two principal components had eigenvalues above 1 (5.248 and 1.424) and accounted for 83.400% of the total variance (Table 3). Thus, these two components represent the majority of the information from the eight agronomic traits. Leafy shoot length and tuber diameter had the highest eigenvector values for the first and second principal components (Table 4). Therefore, the principal components included leafy shoot length and tuber diameter.

Table 3
Principal component analysis of the agronomic traits of *A. munitus*

Components	Eigenvalue	Contribution rate	Cumulative contribution rate
1	5.248	65.594	65.594
2	1.424	17.806	83.400
3	0.513	6.411	89.811
4	0.343	4.289	94.100
5	0.258	3.221	97.320
6	0.119	1.485	98.806
7	0.077	0.968	99.773
8	0.018	0.227	100.000

Table 4
Principal component analysis eigenvectors and contributions of agronomic traits

Agronomic trait	Eigenvector	
	Principal Component 1	Principal Component 2
Number of stems	0.867	-0.198
Stems length	0.782	0.321
Lateral branch length	0.851	0.160
Leafy shoot length	0.976	-0.010
Above-ground biomass	0.793	0.540
Underground biomass	0.951	0.083
Tuber length	0.821	-0.228
Tuber diameter	-0.025	0.951

Table 5

Effect of *A. munitus* planting on the physical properties of KRD soils. a and b indicate significant differences at the 0.05 level ($p < 0.05$); A and B indicate significant differences at the 0.01 level ($p < 0.01$). The values are the means $\pm$ standard

Trait	Unit	Soil control	Soil near <i>A. munitus</i>
pH		7.37 $\pm$ 0.05 A	7.21 $\pm$ 0.06 B
soil water content	%	24.50 $\pm$ 1.10 B	30.76 $\pm$ 0.97 A
soil bulk density	%	0.93 $\pm$ 0.02 b	1.02 $\pm$ 0.04 a
soil total porosity	%	59.81 $\pm$ 4.24 B	62.15 $\pm$ 0.92 A
soil capillary porosity	%	54.83 $\pm$ 1.48 b	58.78 $\pm$ 0.89 a
soil noncapillary porosity	%	2.64 $\pm$ 0.21 B	3.37 $\pm$ 0.12 A

Table 6

Effect of *A. munitus* planting on the soil nutrient content of KRD soils. a and b indicate significant differences at the 0.05 level ($p < 0.05$), and A and B indicate significant differences at the 0.01 level ($p < 0.01$). The values are the means $\pm$ standard deviations

Trait	Unit	Soil control	Soil near <i>A. munitus</i>
Soil organic matter	%	5.80 $\pm$ 0.23 B	8.09 $\pm$ 0.40 A
Total nitrogen	g/kg	3.15 $\pm$ 0.17 B	4.04 $\pm$ 0.21 A
Total phosphorus	g/kg	0.85 $\pm$ 0.04 a	0.72 $\pm$ 0.05 b
Total potassium	g/kg	12.82 $\pm$ 0.12 a	11.07 $\pm$ 0.54 b
Alkali-hydro nitrogen	g/kg	243.87 $\pm$ 10.04 B	317.72 $\pm$ 13.14 A
Available phosphorus	mg/kg	6.26 $\pm$ 0.75 A	2.32 $\pm$ 0.19 B
Available potassium	mg/kg	119.33 $\pm$ 10.02 a	94.33 $\pm$ 6.43 b

A. munitus Planting Changes the Soil Physical Properties in the KRD Area

The KRD test site was weakly alkaline. Planting *A. munitus* significantly reduced the SA pH by 0.16 units on average compared to that in SC ($p < 0.01$). Additionally, SA had an extremely significantly higher SWC versus SC ($p < 0.01$), at more than 31%. SBD, SP, SCP and SNP all differed significantly between SA and SC to varying degrees. These results demonstrated that *A. munitus* strongly affects the basic physical properties of KRD soils.

Planting *A. munitus* altered the KRD soil nutrient content

The KRD soil nutrient levels varied according to fertility grade. SOM and TN were enriched (Class I), AK was moderate (Class III), and AP was depleted (Class IV), indicating that the site was relatively deficient

in P and K. Planting *A. munitus* significantly increased SOM, TN and AN in SA versus SC ($p < 0.05$). TP and AP differed significantly between SA and SC, with SC having 2.7 times greater AP. TK and AK were also significantly greater in the SC treatment than in the SA treatment ($p < 0.05$). Taken together, these findings demonstrated that *A. munitus* planting depletes soil P and K, especially P. Overall, *A. munitus* decreased the KRD soil pH but increased the SWC, SBD, SP, SOM, TN and AN while decreasing P and K. These data indicate that planting *A. munitus* significantly alters basic physicochemical properties of KRD soil, largely in beneficial ways.

Discussion

Adaptation of *A. munitus* to KRD habitats

To adapt to the harsh conditions of KRD habitats, plants exhibit a range of altered morphological and physiological characteristics^[16]. *A. munitus* exhibited shortened stems, branches, and leaves and a reduced aboveground biomass in KRD areas, indicating an overall "shrinkage" phenotype. This finding aligns with that of other KRD-adapted plant species^[17] and may be linked to the seasonal drought commonly experienced in these areas^[18]. The significantly greater stomatal density observed in the EG mirrors similar adaptive increases under drought conditions reported in *Berberis poiretii*^[19]. By reducing the number of leafy shoots and the aboveground light-exposed area while increasing stomatal transpiration per unit area, *A. munitus* may be minimizing water loss and heat damage. This shrinkage strategy could aid survival in the water-limited KRD habitats. Compared to those in the CK treatment, plants in the EG treatment had significantly lower total chlorophyll but a greater carotenoid-to-chlorophyll ratio. This finding aligns with that of other karst species under drought stress^[20] and may be attributed to the photoprotective role of carotenoids in addition to their functions in light absorption and energy transfer^[21]. Such adaptations enable the plants to thrive in the challenging KRD environment.

The results of the antioxidant enzyme activity and osmoregulatory substance content analyses showed that plants were subjected to a certain degree of adverse stress in the KRD habitat^[22]. Tests of the medicinal properties of the harvested tubers showed that the polysaccharide content in the EG treatment was significantly higher than that in the CK treatment, which could be related to the physiological functions of polysaccharides^[22–24]. Correlation analysis and principal component analysis of the agronomic traits of *A. munitus* revealed strong correlations among most agronomic indicators except for basal stems. These results could be simplified into two principal components, leafy shoot length and tuber diameter, which was similar to the results of a previous study^[25], suggesting that the belowground portion of *A. munitus* may play a more vital role in the plant's growth and development.

Planting *A. munitus* to improve KRD soil conditions

The results of the study revealed that the planting of *A. munitus* significantly reduced the soil pH and augmented the SWC, providing a favorable environment for plant survival. However, the SBD was greater

in the SA treatment group than in the control group, unlike previous findings ^[26]. This may be due to the high gravel and stone contents at the sampling site affecting the results. SP, SCP and SNP were significantly greater in SA than in SC, which was potentially related to root growth or increased SOM improving soil structure and looseness ^[27]. SOM, TN and AN were significantly higher in SA than in SC. SOM is central to soil fertility and vegetation recovery ^[28, 29]. Related studies have shown that N limits early-mid-stage karst ecosystem recovery ^[30]. Fern rhizosphere soils have lower AP than non-rhizosphere soils ^[31], but the difference here was greater. This could be because of the already low substrate P concentration coupled with the high P demand during *A. munitus* growth. Similarly, low soil P in *A. munitus* habitats was previously observed ^[12], suggesting that P depletion is linked to high P requirements and needs further verification. Overall, *A. munitus* decreased the KRD soil pH but increased the SWC, SBD, SP, SOM, TN and AN while decreasing P and K. The data indicate that planting *A. munitus* significantly alters the basic physical and nutritional properties of KRD soil, largely in beneficial ways.

The results of the study revealed that the planting of *A. munitus* significantly reduced the soil pH and augmented the SWC, providing a favorable environment for plant survival. However, an unexpected outcome was noted in the SBD, which was more pronounced in the treatment group with *A. munitus* (SA) than in the control group, deviating from the findings of Peng et al ^[26]. This anomaly could be attributed to the high concentration of gravel and stones at the sampling site, which might have influenced the results. The SP, SCP, and SNP were markedly higher in SA than in the control group, which was potentially associated with enhanced root growth or improved soil structure and looseness as per Viviana et al ^[27]. The SOM, TN, and AN were significantly elevated in SA compared to SC. SOM is pivotal for soil fertility ^[28] and vegetation recovery ^[29]. Related studies have revealed that nitrogen constraints early-mid-stage karst ecosystem recovery ^[30]. Fern rhizosphere soils exhibit lower AP than non-rhizosphere soils ^[31], but the difference observed in this study was more pronounced. This could be attributed to the already low substrate P concentration coupled with the high P demand during *A. munitus* growth. Similarly, low soil P in *A. munitus* habitats was previously observed ^[12], suggesting that P depletion is linked to high P requirements and necessitates further verification. In summary, *A. munitus* reduced the KRD soil pH but increased the SWC, SBD, SP, SOM, TN, and AN while decreasing P and K. The data underscore that planting *A. munitus* significantly alters the basic physical and nutritional properties of KRD soil, predominantly in beneficial ways.

Conclusion

In conclusion, this experiment initially confirmed that *A. munitus* could thrive in the KRD environment. This was evident from the morphological changes and physio-chemical reactions that occurred in the plant and its surrounding environment. After planting *A. munitus*, the physical and chemical properties of KRD soil changed, with increased soil water holding capacity and overall fertility, making it more suitable for other plants. Planting *A. munitus* in KRD areas not only brings economic benefits but also improves KRD soil conditions and ecological value. This lays a good foundation for KRD management and sustainable development in karst areas.

Materials and methods

Test site and plant materials

The test area is located at the experimental base (26°25'54"N, 106°40'53"E) of Guizhou University, Huaxi District, Guiyang City, Guizhou Province, China. This area features a karst plateau landform with a humid subtropical monsoon climate, an average elevation of 1178 m, an average annual temperature of 20.21°C, and an average annual precipitation of 1,318.90 mm. The vegetation is mainly natural secondary forest. The germplasm resources of *A. munitus* were sourced from the Planting Base of *Asparagus* in Xingren Town of Qiandongnan (in Guizhou Province, China), and were identified by Prof. Zhang Mingsheng of Guizhou University. The plants were sampled on April 20, 2023 (Fig. 1).

The effect of karst environments on *A. Munitus*.

Measurement of agronomic traits

A. munitus plants were randomly selected from the KRD habitat as the experimental group (EG), and plants from the AL habitat as the control (CK). The number of plant stems, basal stem thickness (mm), stem length (cm), lateral branch length (cm), foliage branch length (mm), tuber length (cm) and diameter (cm) were measured. an electronic balance was used for biomass measurements (the dry parts and sediment attached to the plants were removed, and the plants were subsequently dried in an electric oven at 60°C until the weight was constant).

Measurement of physio-biochemical indicators

The leafy shoots of *A. munitus* were randomly collected and rapidly frozen in liquid nitrogen to the laboratory. The stomata density was calculated according to the methods of Ming and Chen ^[32]. The chlorophyll content in the leafy shoots was measured according to the methods of Li ^[33]. Superoxide dismutase (SOD), peroxidase (POD), catalase (CAT), soluble sugar, and proline were determined by using a kit (Suzhou Keming Biotechnology Co., Ltd., China), and the soluble protein content was determined by the Caulmers Brilliant Blue method with reference to Li ^[33].

Measurement of medicinal components

A. munitus tubers were collected randomly from two habitats, boiled in boiling water for 10 min, peeled, and subsequently dried at 60°C and crushed. The total saponin, total amino acid and polysaccharide contents of the tubers were determined by the methods of Li et al. ^[34] and Wu Fei et al ^[35].

Measurement of soil physical properties

On several consecutive sunny afternoons, six soil samples near *A. munitus* plants (SA) in the KRD area and unplanted blank controls (SC) were collected to test physicochemical properties using methods in

"Soil Agrochemical Analysis" ^[36]. Soil pH was determined by electrode method. SA and SC soils from 0–20 cm were collected by ring knife method, and assessed for soil bulk density (SBD), soil water content (SWC), soil total porosity (SP), soil capillary porosity (SCP), and soil non-capillary porosity (SNP) using the following formulae: M (ring knife mass), M_1 (soil fresh mass), M_2 (soil saturated mass), M_3 (soil resting mass for 12 h), M_4 (soil air-dried mass), and V (ring knife volume).

$$\begin{aligned} SBD &= (M_4 - M) / V \\ SWC &= (M_1 - M_4) / (M_4 - M) \times 100 \% \\ SP &= (M_2 - M_4) / V \times 100 \% \\ SCP &= (M_3 - M_4) / V \times 100 \% \\ SNP &= (M_2 - M_3) / V \times 100 \% \end{aligned}$$

Measurement of soil nutrients

Soil organic matter (SOM) content was determined via potassium dichromate oxidation, total nitrogen (TN) via Kjeldahl method, total phosphorus (TP) via $\text{HClO}_4\text{-H}_2\text{SO}_4$, total potassium (TK) via sodium hydroxide fusion and flame photometry, alkali-hydro nitrogen (AN) via alkaline diffusion, available phosphorus (AP) via sodium bicarbonate extraction, and molybdenum antimony anti-colorimetry, and available potassium (AK) via flame photometry method ^[36]. The level of soil nutrient grade was evaluated according to the method of Hu et al ^[37].

Declarations

Author Contribution

MS Z did supervision. LT and ML designed and conducted the experiment. LT, L S, and Y H performed collection of data and laboratory analysis. LT and M L performed statistical analysis of the data. LT, GG L and HD H were involved in writing—review and editing of manuscript. All authors have read and approved the final version of manuscript.

Data Availability

The datasets used and/or analyzed during the current study are available from the Liu Tang on reasonable request.

Collection license statement for *Cremastra appendiculata*

Statement:

The plant materials used in this study have been obtained with the necessary permits or licenses, complying with all applicable laws and regulations. The plant materials have been formally identified by Professor Mingsheng Zhang at Guizhou University and are deposited in the specimen repository at Guizhou University for reference and verification.

Statement of Compliance with Endangered Species Research Policies

We hereby affirm our commitment to adhere to relevant institutional, national, and international guidelines and legislation when conducting experimental and field research on wild plants. Specifically, we pledge to comply with the IUCN Policy Statement on Research Involving Species at Risk of Extinction and the Convention on the Trade in Endangered Species of Wild Fauna and Flora.

We will respect principles of plant material collection and ensure strict adherence to ethical standards and best practices in the collection, use, and handling of plant samples. We will endeavor to minimize our impact on plant ecosystems in our research and mitigate any potential negative effects on endangered species.

We will collaborate with local and international conservation organizations to ensure that our research does not result in overexploitation, misuse, or destruction of plant species. We will promote the conservation and sustainable use of plant biodiversity to support ecosystem health and human well-being.

We solemnly pledge that our research will uphold the highest scientific standards and ethical principles to contribute positively to the protection of natural environments and biodiversity.

Declaration of interests

☐ The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

☐ The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

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