Effects of Population Density on Revegetation of *Artemisia sphaerocephala* and Soil Traits in a Desert Ecosystem

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Abstract: Soil desertification is a serious problem in arid northwestern China that threatens ecological sustainability. *Artemisia sphaerocephala*, a dominant shrub species, play an important role in the conservation of water and the restoration of soil in the desert ecosystem. However, the poor establishment of *A. sphaerocephala* often limits plant revegetation, and the optimal population density for sustainable growth is largely unknown. Here, we determined key soil properties and plant growth characteristics associated with different population densities of *A. sphaerocephala* (including from 1.1, 2.1, 3.1, 3.9 to 5.3 plants per m²) in the resource-limited Alashan desert of northwestern China. The results showed that plant population density was the primary factor determining the revegetation of *A. sphaerocephala*, followed by soil water availability. Soil N, P and K content, and soil fractal dimensions also contributed to the vegetation and productivity. Soil nutrients were mostly accumulated in the topsoil layers, coincidental with the root distribution pattern in which 57% to 82% of total roots were distributed in the top 20 cm soil layer. The concentrations of soil nutrients in higher population densities (3.9 to 5.3 plants per m²) were greater than those in lower population densities (1.1 to 2.1 plants per m²), suggesting that *A. sphaerocephala* may have the ability to promote nutrient cycling in the desert ecosystem. We conclude that the optimal population density for the best growth of revegetated *A. sphaerocephala* was 3 plants per m².

Keywords: desertification; population density; plant growth; soil traits; *Artemisia sphaerocephala*

1. Introduction

Many arid and semiarid areas on the planet have been experiencing certain degrees of desertification due to frequent droughts associated with climate change [1]. A typical example is rapidly evolving desertification in arid northwestern China [2]. Various practices have been implemented to minimize desertification, but the effectiveness is usually low, and the results vary with different ecosystems [3]. Because of the interaction between vegetation growth and soil, the physical and chemical properties of the soil will change with the evolution of vegetation [4]. As an important component of the terrestrial ecosystem, soil C, N, P and other nutrient elements are not only the nutrient sources for plant growth and development but also the material basis for plant survival [5], affecting the composition, development and stability of plant community [6]. Soil moisture plays an important role in the Soil–Plant–Atmosphere Continuum (SPAC), especially in desert areas where rainfall is scarce, and determines the growth and survival of regional vegetation [7]. The introduction of shrubs will break the balance and stability of the original ecosystem, change the function and service of the ecosystem, and have an important impact on soil moisture and physical properties [8,9]. Shrubs will enhance the landscape heterogeneity of time and space,
change the surface soil resources (water, carbon, nitrogen, etc.) and make these resources gathered at the bottom of the brush, produce a “fertile island effect” [10], change the spatial distribution of soil moisture and the flow direction [11], while the positive feedback leads to soil resources allocation again, also accelerated the thickets of an irreversible process [12].

*Artemisia sphaerocephala* (sagebrush) is a perennial subshrub, widely distributed in the desert and semi-desert areas of northwest China. It is a pioneer plant species on mobile dunes [13]. The branches and leaves are favored by many domestic animals, such as Bactrian camels [14], because the plants have a high nutrition value, rich in linoleic acid, vitamin E and other flavor substances. Additionally, it has reported medicinal uses [15]. Ecologically, *A. sphaerocephala* plays an important role in sand fixation, water conservation, and the maintenance of ecological balance in desert ecosystems [16]. Studies have been conducted to determine *A. sphaerocephala* adaptation and the effects on plant morphology [17], population structure [18] and the responses to soil nutrients [19]. Differences in plant population density affect plant growth and thus affect plant growth, meanwhile, plants also affect soil properties. However, little has been researched regarding the relationships between plant densities and productivity and about to with concerning soil properties for cultivated *A. sphaerocephala* populations. Therefore, the objectives of this study were to: (i) assess the plant growth characteristics among different population densities in a desert area, (ii) evaluate the soil properties in various soil layers about to with concerning plant population, and (iii) determine the correlation of soil parameters and plant growth characteristics. We hypothesized that soil properties play a major role in plant growth characteristics, while the plants could increase their productivity by changing the plants’ density. These findings can be useful to maintain the sustainability of natural desert ecosystems.

2. Materials and Methods
2.1. Site Description

The experiment was conducted at a site near the Tengger Desert (105°31′E, 39°07′N) on the Alashan Plateau with an elevation of 1400 m. The soil at the experimental site was a typical saline-alkaline desert, and the average soil pH is between 8.85 and 9.00. The nutrients in the bare sand soil (0–10 cm layer) we measured in 1996 before sown *A. sphaerocephala* are shown in Table 1. This region has a typical arid desert climate with an average annual temperature of 8.1 °C, and ≥10 °C annual cumulative temperature of 3000 °C–3400 °C. The site is extremely arid, with 60 to 160 mm of annual precipitation occurring mainly from July to September, while annual evaporation is approximately 2300 to 2800 mm [20].

| Total N (%) | Available N (mg/kg) | Total P (%) | Available P (mg/kg) | Total K (%) | Organic Matter (%) | pH |
|------------|---------------------|------------|---------------------|------------|-------------------|----|
| 0.010 ± 0.008 | 80.28 ± 1.37 | 0.017 ± 0.001 | 2.18 ± 0.10 | 1.912 ± 0.032 | 0.058 ± 0.006 | 8.97 ± 0.19 |

*A. sphaerocephala* was sown through aerial seeding in 1996 to control mobile dunes. The plant establishment of *A. sphaerocephala* populations has been reported to be varied widely because of the unevenness of aerial seeding, seed germination rate and other factors such as differences in microhabitat conditions. As a result, the growth and reproduction of the established plants displayed significant differences. 20 years after the establishment (i.e., in 2015), the population density is mostly less than 6 plants per m².

2.2. Treatments and Plant Growth Characteristics

In 2015, three blocks (50 × 200 m per block) were established as replicates in the aerial seeding region with similar slope gradients and aspects. In each of the three blocks, five population density gradients of *A. sphaerocephala* were established. Averaged across the three blocks, the five densities were 1.1, 2.1, 3.1, 3.9, and 5.3 plants per m², respectively,
with each density in each replicate being 30 m × 30 m in size. These five population densities were designated as T1, T2, T3, T4, and T5, respectively. In each density, five 4 × 4 m quadrats were randomly chosen and 11 individual A. sphaerocephala plants were taken from each quadrat for various measurements. Plant height and crown width (long axis crown diameter) were measured using a ruler, and the number of the reproductive shoots (with a head) and vegetative shoots were counted. Seed yield and the dry weights of the reproductive and vegetative shoots were determined, and the total aboveground biomass was calculated. Roots in the 0–20, 20–40, 40–60, 60–80, and 80–100 cm soil layers were dug out, for each of the five depths, soaked in water (in plastic containers), and brought to the laboratory, washed and rinsed thoroughly. They were then dried with paper towels, oven-dried to a constant weight at 50 °C and weighed for dry mass.

2.3. Soil Sampling and Analysis

Gravimetric soil water content (SWC) on 14 June, 16 July and 15 August was measured by collecting two soil cores from each soil layer using a stainless-steel cutting ring (100 cm³) in 0–20, 20–40, 40–60, 60–80 and 80–100 cm depths in each density gradient, and then were oven dried at 105 °C for 8 h to a constant weight. Subsamples of the soil cores in the 0–10, 10–20, and 20–30 cm depths collected on the August sampling date were taken for the analysis of soil chemical properties. These subsamples were air-dried and passed through a 2-mm sieve. Soil pH was measured with water: soil ratio = 1:1 suspension (PHS-3C, Leici, Shanghai, China). Total soil nitrogen and available nitrogen were analyzed using the Kjeldahl method [21]. Total phosphorus concentration was analyzed using the alkaline oxidation method and available phosphorus was analyzed using the sodium bicarbonate method, Total potassium concentration was analyzed with flame spectrometry, and soil organic matter was measured using the dichromatic oxidation titration method [22].

Furthermore, soil particle-size distribution was measured using a Laser Particle Size Analyzer (Mastersizer 2000, Malvern, UK) and the USDA classification system [23] was employed to classify the particle sizes into 7 groups to calculate soil fractal dimensions with Equation (1):

\[(R/R_{max})^{3-D} = W (r < R)/W_0\]  

(1)

where \(W (r < R)\) is the mass of soil particles with a radius smaller than soil particle size \((R)\), \(W_0\) is the total mass of particles with a radius less than \(R_{max}\), which is the upper size limit for fractal behavior, and \(D\) is a fractal dimension. Linear regression was used to fit Equation (1) on a log-log treatment to the experimental data. The value of the regression line slope was \(3 - D\), thus, the value of \(D\) was calculated by subtracting the slope from 3.

2.4. Statistical Analysis

Principal component analysis (PCA) is an analytical method for handling multivariate data effectively in ecological studies [24]. 29 variables were used for the PCA analysis, including soil nutrition, soil physicochemical properties and plant growth parameters, etc. Soil nutrition factors included total and available nitrogen, total and available phosphorus, total potassium and organic matter in the 0–10, 10–20, and 20–30 cm depths; soil physicochemical properties included soil fractal dimension in the 0–20 and 20–40 cm depths, and pH in the 0–10, 10–20, and 20–30 cm depths; gravimetric soil water content included the data of the 0–20 and 20–40 cm depths in June, July and August. These data constructed a matrix \(X (29,30)\). Before the PCA analysis, all the data was normalized and used Euclidean distance to ensure uniformity. These dimensional data were used to construct the new matrix \(X' (29,30)\).

The plant characteristics (seed yield, plant growth parameters) were compared among the five density gradients using a one-way ANOVA. For the analysis of soil-related properties (soil water content, soil physicochemical properties), a two-way ANOVA was employed in which the population density and the soil depths were considered as the two independent factors. Multiple comparisons were made using Tukey’s test and the confidence level was set at 95% [25]. All descriptive statistical parameters were carried out using
EXCEL 2019. The significance test was calculated by SPSS 21.0 software (SPSS for Windows, Chicago, IL, USA). All figures were plotted by OriginPro 2018 (OriginLab Corporation, Northampton, MA, USA).

3. Results
3.1. Plant Growth

Population density had a significant effect on plant vegetative growth (Figure 1a–d), reproductive characteristics (Figure 1e,f) and rooting profiles (Figure 2). All the key plant growth parameters varied among the different population densities, with the exception of plant height which did not differ among population densities (Figure 1a). Crown width decreased with the increase of population density. Compared with T1 density, crown width of T3 and T5 decreased by 19.8% and 58.1%, respectively (Figure 1b). Additionally, seed yield per plant decreased with the increase of population density (Figure 1d). The ANOVA showed that seed yields of plants in T1, T2 and T3 densities were significantly higher than those in T4 and T5. Compared with T1 density, seed yields of T5 decreased by 81%. Aboveground biomass per plant followed a trend similar to the seed yield (Figure 1c).

![Figure 1](image-url)

**Figure 1.** The box treatments of plant growth characteristics include height (a), crown width (b), aboveground biomass (c), seed yield (d), number and weight of reproductive shoot (e,f), and number and weight of vegetative shoot (g,h). The different letters within each panel denote significant differences ($p < 0.05$) among the five population densities. Abbreviations T1, T2, T3, T4, and T5 represent, respectively, the population density of 1.1, 2.1, 3.1, 3.9, and 5.3 seedlings per m$^2$. The same applies to the figures below.
Figure 2. Root biomass and the proportion of biomass in the different soil layers across the 0–100 cm profile. The different letters within a depth layer denote significant differences (\( p < 0.05 \)) among the five population densities (\( n = 6 \)).

The average number of vegetative shoots per plant in T3 was greatest among the density gradients, whereas the weight of vegetative shoots per individual plant in T1, T2, and T3 densities was significantly greater than that in T4 (Figure 1g,h). Overall, the number of vegetative shoots per plant in T3 density was the largest, whereas the weight of vegetative shoots was the smallest in T3 (with a few exceptions). The number and weight of reproductive shoots per plant decreased with the increase in population density. Plants in T1 and T2 densities had the greatest number and weight of reproductive shoots per plant and plants in T5 had the least (Figure 1e,f). Compared with T1 density, the number and weight of reproductive shoots per plant in T3 and T5 decreased by 45.2%, 88.1% and 79.7%, 95.2%, respectively. There was a different response between the number of reproductive shoots per plant and the weight per plant. For example, there was no difference in the number of reproductive shoots per plant between T2 and T3 densities, but the weight of shoot per plant differed significantly between the two density gradients.

Root distribution across the various soil layers varied with the depth and interacted with population density (Figure 2). The distribution pattern of root dry weight showed that the largest proportion of the roots was distributed in the 0–20 cm depth and reached 57% to 82%. The absolute amount of the root biomass in the 0–20 cm depth decreased with the increase of population density gradients. In the depths below 20 cm,
there was no significant difference among density gradients except T1 density in which the root biomass was significantly larger than those in the other densities. Percent root biomass in the various soil depths differed with population densities; a smaller proportion of root biomass in T1 density resided in the 0–20 cm depth compared with the T2 density.

3.2. Soil Properties

Soil water content at various depths was measured three times during the growing season (Figure 3). The soil under T3, T4 and T5 densities contained a similar amount of water at each depth, measured in June. However, the soil water content in the 0–40 cm depth for T1 and T2 densities were significantly higher than those in the deeper soil layers. Soil water content at all the depths measured in July and August was significantly higher than those obtained in June. On the July measurement date, the soil water content in the 0–20 cm depths was significantly higher than those in the other depths.

![Figure 3](image-url)

Figure 3. Gravimetric soil water content in the different soil depths was measured in June, July and August. The different letters within a depth layer denote significant differences ($p < 0.05$) among the five population densities. The standard error of the mean for June, July and August soil water content were 0.12, 0.15 and 0.26, respectively.

However, such differences between soil depths did not show in the August measurement. On the June and July measurement dates, the soil water content in the 0–40 cm depth in T1 and T2 densities were significantly higher than those in T3, T4 and T5, whereas, on the July and August measurements, the soils in T1 and T2 densities had significantly higher water content than the other three density gradients. These interactive responses of soil water with the stage of plant growth (i.e., the different measurement dates) were related to precipitation received during the sampling period. Precipitation one month before sampling was 8.5, 31.7, and 9.4 mm, respectively, for the three sampling dates. The soil water for the June and the July sampling dates in the topsoil layers was increased by precipitation. However, there was no difference in soil water content between the topsoil and those in subsoil layers as no rainfall occurred near the sampling date in August.

Population density had a significant effect on soil nutrient content and the effect interacted with soil depth (Figure 4). Overall, soil nutrient concentrations increased with the increased population density (T1 to T5) and the concentrations in the topsoil were generally
greater than those in the subsoils. Total soil N in T1 and T2 densities was comparably less than those in T4 and T5 densities at each depth. For example, compared with T1 density, total N concentration in T5 increased 61.5% in the 0–10 cm soil layer (Figure 4a). Available soil N concentrations (Figure 4b) and organic concentrations (Figure 4d), however, varied largely with soil depth and were less affected by population density; the topsoil (0–10 cm layer) had greater concentrations of available nitrogen and organic matter than the subsoil (10–20, and 20–30 cm layers) for each population density (with a few exceptions). There were no differences in total K concentration in the 0–10 cm depth among the five population densities (Figure 4c), however, the K concentration in the 10–20 cm depth in T1 and T2 densities were significantly less than those in T3, T4 and T5 densities. Total P (Figure 4e) and available P (Figure 4f) concentrations in the 0–20 cm depth were significantly greater than those in the deeper layers for each population density. Increasing population density from T1 to T5 increased total P in all three depths and available P at the 0–10 cm depth.

The pH values declined significantly with the increased population density gradients (Figure 5). The pH values of soils in T3, T4, and T5 densities were significantly lower than those in T1 and T2 and decreased by 0.67%. This trend holds for all the three soil depths evaluated where no significant differences in soil pH were found between soil depths.

![Figure 4](image-url) Soil nutrient traits included Total N (a), Available N (b), Total K (c), Organic matter (d), Total P (e) and Available P (f) in the 0–10, 10–20, and 20–30 cm soil layers under the five population densities. The different letters for each line in each panel denote the significant differences (p < 0.05) among the five densities.
3.3. Soil Fractal Dimensions

The status of soil fractal dimensions with the different population densities showed that the fractal dimensions in the 0–20 cm depth in T1 and T2 densities were significantly greater than those in T3, T4, and T5 densities. In the 20–40 cm depth, however, there was no significant difference among density gradients (Figure 6).

3.4. Soil Parameters Affect Plant Growth

We used a principal component analysis (PCA) to determine the correlations between the soil parameters and plant growth characteristics. As shown in Figure 7, the first
and second axes explained 58.9% and 8.3% of the standardized variance, respectively. Furthermore, the cumulative variance explained by the first five principal components was 82.7%. The heavily weighted parameters (with loading values > 0.200) in PC1 were gravimetric soil water content (24–29), available nitrogen in the 10–20 and 20–30 cm layer (8, 14), organic matter in the 20–30 cm layer (18), soil fractal dimension in the 0–20 cm layer (19), and pH in the 10–20, and 20–30 cm layer (22–23). The heavily loaded parameters in PC2 included the total potassium in the 0–10 cm layer (5), available phosphorus in the 20–30 cm layer (16), and soil fractal dimension in the 20–40 cm layer (20).

4. Discussion

In arid and semiarid environments, the availability of resources, such as water and nutrients, often limits the development of agricultural systems. In desert agroecosystems, how to utilize the limited resources to optimize plant productivity and enhance ecosystem services becomes a major subject in ecological studies [26]. Often, a high rate of resources is added to the system with the aim of stimulating the ecosystem services [27]. However, it has been a challenge to minimize biogeochemical fixation or abiotic losses of the added resources in the desert ecosystem [28]. In the scientific literature, little information is available concerning how a plant community structure (i.e., population density) over a long period of time (for example 20 years since establishment) may function concerning soil properties in desert ecosystems. In such harsh environments, the availability of water to plant communities is unpredictable from year to year and the amount of rainfall varies within a growing season. Understanding the characteristics of available soil resources in the context of plant population density may provide insights for establishing effective strategies to manage desert ecosystems.
In the present study, the effects of different plant population densities on plant growth and soil characteristics were investigated. The principal component analysis enabled us to assess multiple factors and their relative weights in affecting plant growth. Previous research has shown that soil nutrients can affect the growth of some plant species, such as *Atriplex parryi* [29]. However, the results of this study showed that water availability was a dominant factor that affected the establishment and the revegetation of *A. sphaerocephala*. A higher density of plants will mean more plants drawing from the same available water, and hence they compete, and each plant grows less, as indicated by the total biomass per plant (aboveground biomass + belowground biomass) for T1 to T5 was 757.1, 543.0, 273.2, 189.7 and 135.3 g, respectively. Moreover, soil water availability interactively affected the availability of other soil physicochemical properties [30]. The vegetative growth of *A. sphaerocephala* in such a desert ecosystem can be restricted by low nutrient supplies because the plants would prefer rapid growth at a point in time when water is momentarily available. Nevertheless, water resource is undoubtedly the most important factor limiting the services and products of the desert-like ecosystem.

However, belowground biomass per m$^2$ increased with the increase of population density in the present study, and average aboveground biomass per m$^2$ in T2 density was greatest among the densities but had no difference ($p > 0.05$) in T1 and T3 densities, and the total biomass per m$^2$ for T1 to T5 were 832.8, 1140.4, 846.8, 739.7 and 717.2 g, respectively (data not shown), which indicated that plants can achieve higher productivity at the right density under the same available water conditions. This is very interesting because earlier studies revealed that with the decrease in available water, species richness, aboveground biomass, community coverage, foliage projective cover, and leaf area index all significantly decreased [31,32]. The reason may be that there is an optimal population density, which may provide a balance point for optimizing plant growth with a maximized use of available water and nutrients in the soil; helping maintain a stable population proliferation and plant community stabilization [30]. This optimal population has an important reference value for *A. sphaerocephala* reseeding rate on vegetation restoration in desertification grassland.

In desert areas, nutrient limitation may play an important role in the vegetation and productivity of a plant community. For example, N, P and Mg are found to be the major factors limiting plant growth in the Mojave Desert over K and Ca [27]. In the arid region of Australia, P is reported to be the main limiting factor, while in the Namib Desert dune sand the deficiency of the macro-nutrients N, P and K often limit plant productivity [33,34]. It is often the case that decomposition rates in desert ecosystems are slow due to lack of water, meaning that nutrients in a desert ecosystem may be recycled slowly, leading to characteristic swift and ephemeral growth [13,14]. In the present study, PCA revealed that N, P, and K all contributed to the variation in soil properties under the different population densities. Soil physical property, reflected as soil fractal dimension also contributed to the root and aboveground biomass of *A. sphaerocephala*. And the fractal dimensions in the 0–20 cm depth in T1 and T2 densities were significantly greater than those in T3, T4, and T5, while the root to aboveground biomass ratio for T1 and T2 were lower than T3, T4 and T5 with more total above- and below-ground biomass. There is a correlation between fractal dimension and soil’s physical, chemical and biological properties in arid regions [7,35].

A significant value of this study is the finding that the rooting system acts as a major response to resource limitation. The results of this experiment indicated that 57% to 82% of root biomass spread in the upper 0.2 m of soil regardless of density gradients. Some other studies also showed that the topsoil (0.2 m) layers can have more than 60% of all roots [36,37]. The distribution of roots in a soil profile can be affected by many factors, including plant species [10], plant community structure and diversity [38], as well as soil environment, such as soil water condition [39], soil texture and nutrient availability [40–42]. Additionally, plant root systems can be a discrepancy of soil traits in different depths; these discrepancies may be related to plant characteristics such as tissue stoichiometry, biomass cycling rates, above- and below-ground allocations [38], and root distributions across soil depths [33]. In the present study, the different root distribution between T1
and T2 densities indicates that the underground competition for resources may be low in these low-population densities as the individual plants tend to allot more roots in the more nutrient-rich topsoil with a shallow root distribution. In contrast, in the higher population (T4 to T5) the underground competition intensity increases where a deeper root distribution with more roots being abundantly distributed in the deeper layers. However, it is debatable whether competition to retain resources in the topsoil layers occurs in a nutrient-rich field [43,44]. In a high population, the competition for resources increases to a critical level, then the individual plants tend to distribute roots to a wider range of soil depths, a mechanism of maximizing resource capture and minimizing resource competition [45–47]. However, the competition for resources will become more important when the resource is below a critical level.

In desert regions, soil water content is primarily related to rainfall in summer and root activities [48,49]. Soil water content in the topsoil is larger than that in subsoil after a rainfall, providing the privilege for the growth of the roots in the top layers over the deeper layers. In return, root activities can serve as a primary factor to affect soil water retention and utilization in different soil depths. Ryel et al. [50] demonstrated that Artemisia tridentate could redistribute precipitation to different soil layers to conserve water; this can serve as a mechanism for prolonging water availability to the plant community during a period of drought.

5. Conclusions

The main factor limiting the vegetation and productivity of A. sphaerocephala in the Alashan desert for 20 years after seeding is soil water, whereas soil particle size distribution (reflected by soil fractal dimension) and soil N, P and K contribute to the overall ecosystem services. The interactive effect of water availability and the other soil physicochemical properties in the arid environment depends on the time scale; during the entire year, water is unquestionably the primary limiting resource, but after rainfall, nutrient supply becomes the main limitation for plant growth. The roots of A. sphaerocephala are primarily concentrated in the 0–20 cm depth where soil nutrients are typically enriched, thus, maintaining stable and nutrient-rich topsoil is crucial for plant vegetation in desert regions. With a low population of A. sphaerocephala (T1 and T2) water is sufficient to meet the need of the individual plant growth, for T2, whereas in high populations (T3, T4, and T5), the concentrations of soil nutrients are often sufficiently high due to rhizosphere activities but the competition for available soil water limits an optimal growth. Putting the three factors together—soil water, nutrient availability, and plant densities, we conclude that the population density in density T3 (about 3 seedlings per m²) may provide a balance point for optimizing plant growth with a maximized use of available nutrients in the soil; helping maintain a stable population proliferation and plant community stabilization.

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