

SPATIAL PATTERN FORMATION AND INTRASPECIFIC COMPETITION OF *ANABASIS APHYLLA* L. POPULATION IN THE DILUVIAL FAN OF JUNGGAR BASIN, NW CHINA

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Abstract

Using conventional nearest neighbour analysis and Ripley's *L*-function, the goal of this study was to analyze spatial patterns of *Anabasis aphylla* plants in order to investigate underlying competitive processes that shape the population spatial structure from diluvial fan in Junggar Basin, NW China. We found that the spatial patterns of all growth stages were aggregated in the three study plots, and seedling and juvenile plants were more aggregated than expected by chance. Positive associations among growth stages of *A. aphylla* population were found at a small scale while negative associations of seedling and juvenile relative to adult plants were shown at a larger scale. The processes such as dispersal, seedling establishment, environmental heterogeneity, plant interactions and disturbance may have acted individually or in concert with other processes to produce the aggregated patterns and competitive relationship. Moreover, these findings suggested that the aggregated distribution and the competitive interaction between *A. aphylla* plants in the diluvial fan reflected not only in mortality, but also in decreased performance (smaller canopy) that was an important characteristic of drought-enduring plant, thus preventing a regular distribution pattern.

Key words: Spatial pattern, Intraspecific competition, *Anabasis aphylla*, Junggar basin.

Introduction

Spatial patterns of plants are important characteristics of vegetation, and can play a significant role in ecological processes including competitive coexistence and disturbance dynamics, and can have impacts that scale up to ecosystem-level processes (Arévalo & Fernández-Palacio, 2003; Tian *et al.*, 2013). Processes that structure plant communities still be a primary focus of plant ecological research (Armas & Pugnaire, 2005; Mokeny *et al.*, 2008). In general, abiotic and biotic factors may influence the distribution of species, and thus potentially control their abundance and promote coexistence (Zhang *et al.*, 2010). Many species also exhibited ecological habitat preferences, although species numbers and associations are different among sites (Nanami *et al.*, 2011).

Analysis of the spatial pattern indicates whether the distribution of the plants is random, aggregated, or regular by comparing the distribution with the pattern of plants under a null model (Schleicher *et al.*, 2011). In general, researchers infer the presence of competition by assessing the aggregated or regular distribution of trees (Wiegand & Moloney, 2004). Regular patterns have been historically viewed as the result of intense competition for limited resources, such as available water or soil resources (Skarpe, 1991; Rayburn *et al.*, 2011). Thus, apparently regular patterns among plants are often observed (Prentice & Werger, 1985; Max & Johan, 2008; Nanami *et al.*, 2011). Furthermore, more regular spatial patterns have often been reported with an increase in plant size in monospecific stands (Zhang *et al.*, 2010; Khan *et al.*, 2013). Stoll & Bergius (2005) suggested regular patterns result from a Turing-like instability while Sonia *et al.* (2010) revealed that bistability and regular pattern formation are linked in their model and indicate that the system is along a discontinuous transition to desertification when regular vegetation

patterns occur. An aggregated distribution is caused by regenerating strategies such as seed dispersal (Camarero *et al.*, 2000; Schurr *et al.*, 2004; Wang *et al.*, 2013; Chu *et al.*, 2014), soil moisture conditions, and spatial heterogeneity (Turner & Franz, 1985; Duncan, 1991; Schenk *et al.*, 2003; Perry *et al.*, 2009), as well as disturbances (Pelissier, 1998; Hou *et al.*, 2004; Wu & Yang, 2013).

Generally speaking, younger and smaller individuals tended to be aggregated, but the high rates of mortality through increased competition as plants increased in size caused individuals to die, and the existence of such competition was inferred from a positive correlation of plant size and nearest neighbour distance (Lee *et al.*, 2012). Density-dependent mortality usually results in a regular pattern, and it occurs when a resource that plants may utilize is limited. Intense competition may bring about the mortality of aggregated plants, resulting in a regular spacing of plants in accordance with the honeycomb rippling model (Wiegand & Moloney, 2004). In addition, random patterns may be a direct result of ecological processes such as habitat heterogeneity (Tirado & Pugnaire, 2003), or may emerge temporarily when aggregated patterns shift to regular patterns because of density dependent mortality (Prentice & Werger, 1985). However, the relative intensity of intraspecific competition could spatially fluctuate, particularly in plant communities where partitioning of establishment sites occur and population structures are aggregated (Nishimura *et al.*, 2002; Enoki, 2003).

At present, many ecologists worked intensively to seek the deterministic processes explaining the spatial patterns of species, for example by looking for the particular adaptations of each species to biotic and abiotic factors (Hardy & Sonké, 2004), and most of the research is mainly focused on tropical forests (Condit *et al.*, 2002). It would be important to extend the research to other species (Chave, 2004). Yet the spatial patterns and

the intraspecific associations of plants and the competitive mechanisms among plants have not been reported in harsh diluvial fan, while such studies have been recently conducted in some psammophyte of Junggar Basin (e.g., Liu *et al.*, 2008; Song *et al.*, 2010; Chu *et al.*, 2014).

The objectives of this study were to analyze the spatial patterns and the intraspecific competition of *Anabasis aphylla* in three typical slope positions of diluvial fan in Junggar Basin, NW China, to determine the formation explaining the spatial patterns of *A. aphylla* population using the *L*-function, and to detect the intraspecific associations of *A. aphylla* population by means of the null model of random labeling and nearest neighbour analysis to understand the plant population structure and function maintenance in arid area.

Materials and Methods

Study species: The species selected for this study was *A. aphylla* that is a representative plant in Junggar Basin diluvial fans. It is a chenopodiaceous subshrub mainly distributing in Xinjiang, northwest of China, and has high capability to endure salt-alkali, resist drought and prevent sand from drifting, which is important to exploit and utilize drought alkali terra, and to improve the environment (Huang, 1991; Chu *et al.*, 2009). The decoction of the leaves contains high percentages of antimicrobial components like alkaloids and steroids (Chu *et al.*, 2009). Therefore, it is also a medicinal plant used against plant diseases and insect pests.

Study site: Study site was located at the diluvial fan spanning an elevation range of 258–279 m on the southern edge of Junggar Basin in Xinjiang (45°22'43.4"N, 84°50'32.5"E). The mean temperature varies from 5 to 9°C, minimum winter temperatures vary from –30 to –41°C and maximum summer temperatures 30–40°C. Snowmelt at the end of winter, together with the rainfall, amounts to an annual precipitation of 100–150 mm. Annual potential evaporation is > 2000 mm.

Three study plots (named P1, P2 and P3, respectively) were established at three slope positions of diluvial fan facing north in summer 2009 (Table 1). Each plot has an area of 1 ha (100×100m) in horizontal distance. The plot P1 is located at the upper slope position spanning a slope range of 15–30°, and the topography is steep. The plot P2 sites at the middle slope position with a slope range of 7–15° and encompasses more irregular ground surfaces. The plot P3 is situated at the lower slope position and the slope ranges from 0° to 7°. In the study site, there are mainly *A. aphylla*,

Reaumuria soongorica, *Haloxylon ammodendron*, *Nitraria roborowskii*, *Tamarix ramosissima*. *A. aphylla* plants were more than 75% of the total population. Field observation showed that most of them have resistance to draught and tolerance to barren traits.

Data collection: Each plot was divided into 400 contiguous 5×5 m quadrates, as the basic unit of vegetation survey, using the DQL-1 forest compass (Harbin Optical Instrument Factory, China). All woody plants, including living plants and dead standing plants, were investigated. The species names, relative location of each individual, height, crown width (the greatest diameter of the vertical projection of the crown in two directions, i.e., north-south or east-west), microhabitat (e.g., soil surface, depression patch) were recorded.

Classification of growth stages: Since spatial patterns at each growth stages suggest the past process of regeneration (Nanami *et al.*, 2011), we classified *A. aphylla* plants based on reproductive ability, into adults (> 25 cm height), juveniles (10 < height ≤ 25 cm) and seedlings (≤ 10 cm height) in the diluvial fan.

Spatial pattern analysis: Spatial patterns of plants within a population was analyzed using Ripley's *K(r)* function (Ripley, 1977). A square root transformation of *K(r)* suggested by Ripley (1977) is easier to interpret: $L(r) = [K(r)/p]^{1/2} - r$. A value of $L(r) = 0$ indicates that the spatial pattern at a distance is random. Values of $L(r) > 0$ indicate aggregated distributions, while values of $L(r) < 0$ indicate regular distributions. Spatial associations between the populations were analyzed using the bivariate function $L_{12}(r)$, a transformation of function $K_{12}(r)$ (Wiegand & Moloney, 2004): $L_{12}(r) = [K_{12}(r)/p]^{1/2} - r$. The function $K_{12}(r)$ is a generalization of the function *K(r)* to a bivariate point process. A value of $L_{12}(r) = 0$ indicates that the two growth stages are spatially independent, values of $L_{12}(r) > 0$ indicate a positive association (attraction) and values of $L_{12}(r) < 0$ indicate a negative association (repulsion).

In this study, our null hypothesis was the complete spatial randomness (CSR) for an analysis of the univariate spatial pattern of plants (Wiegand & Moloney, 2004; Getzin *et al.*, 2008), because the spatial distributions of *A. Aphylla* plants in the three plots seem to be affected significantly by the habitat heterogeneity (e.g., soil surface, depression patch). To account for the fact that bigger size plants were established before smaller plants developed, we used a null model which incorporates antecedent conditions (Wiegand & Moloney, 2004) to analyze the spatial associations between the growth stages.

Table 1. Population feature of *A. aphylla* in the three plots of diluvial fan.

Plot#	Location	Vegetation coverage (%)	Mean canopy diameter ± SE (cm)	Living plants (individual/hm ²)	Dead standing plants (individual/hm ²)
P1	Upper slope	5.17	38.15 ± 16.17	2971	1938
P2	Middle slope	13.95	28.19 ± 11.33	10237	2882
P3	Lower slope	18.04	55.84 ± 23.12	4926	1592

The random labeling is the appropriate null model in testing for spatial segregation of adult and dead plants (Wiegand & Moloney, 2004). $L_{12}(r)$ was calculated over an area corresponding to the minimum bounding box of each population. Results were given as $L_{12}(r)-L_{11}(r)$, which represents the dispersion pattern of adults to dead plants relative to the dispersion of all plants within the joint population.

In addition, the intensity of spatial patterns or spatial associations is defined as the magnitude of the deviation from randomness or independence (Rebertus *et al.*, 1989). All analyses were conducted in the Programita software package (Wiegand & Moloney, 2004). Ninety-nine Monte Carlo simulations were used to generate 99% confidence envelopes.

Nearest neighbour analysis: For each plot, we examined whether plants were directly competing with their nearest neighbouring plants. If this is valid, then the mean distance to the nearest neighbouring trees should be smaller for smaller plants than for larger ones (Pillay *et al.*, 2012). We investigated the relationship between the sum of the distances to the four nearest neighbours, and the sum of the canopy diameters of the target plant and its four nearest neighbours. Significant positive slopes indicate competition between individuals (Shackleton, 2002). We also examined the relationship between the coefficient of variation in the nearest neighbour distances and canopy diameter, to determine whether larger plants were more evenly spaced than smaller plants, indicating density dependent mortality. These analyses were carried out using regression in Origin (version 7.5).

Results

Distribution patterns of *A. aphylla* population: The univariate spatial analysis of *A. Aphylla* plants revealed that all growth stages pattern of the three plots with heterogeneous intensity displayed aggregated spatial distributions (Fig. 1a-i). In plot P1 and P3, strongly aggregated distribution of seedlings was respectively observed at 1-31 and 1-33 m (Fig. 1a, g), while other spatial pattern were > 50 m at aggregated scales (Fig. 1b, c, h, i). In plots P2, the spatial aggregation of seedlings, juveniles and adults was detected at 1-32, 1-28, and 1-35 m, respectively (Fig. 1d-f). For seedlings, the aggregation intensity of the three plots respectively reached a maximum of $L(r)$ 17.89 at $r = 6$ m, 4.49 at $r = 7$ m and 3.94 at $r = 2$ m (Fig. 1a, d, g), it respectively reached a maximum of 3.47 at $r = 35$ m, 0.78 at $r = 6$ m and 3.30 at $r = 21$ for juveniles, and it reached a maximum 0.60 at $r = 10$ m in plot 2, while at $r > 50$ m in plot P1 and P3 for adults. These results showed that the aggregation intensity of *A. aphylla* individuals decreased progressively with increasing the growth stages and the scale for the maximum degree of aggregation increased gradually. At the small scale, the order of aggregation intensity of all growth stages was seedlings > juveniles > adults.

Spatial associations of *A. aphylla* population: In plot P1, P2 and P3, positive associations of seedlings relative to juveniles were found at 1-2, 1-12 and 1-13 m (Fig. 2a, d,

g), seedlings relative to adults were found at 1-15, 1-9 and 1-34 m (Fig. 2b, e, h), and juveniles relative to adults were at 1-50, 1-21 and 1-38 m, respectively (Fig. 2c, f, i). Positive associations among growth stages of *A. aphylla* population were found on a small scale while negative associations of seedlings and juveniles relative to adults were shown at middle or larger scale (Fig. 2).

Random labeling analysis of dead standing and adult plants: In the three plots, the random labeling analysis show a negative association between dead standing plants and adult *A. aphylla* subshrubs at the scale 1-24, 1-32 and 1-18 m, respectively (Fig. 3a, b, c). The association intensity of three plots respectively reached a maximum of $L_{21}(r)-L_{22}(r)$ value -0.53 at $r = 12$ m, -1.17 at $r = 9$ m and -0.35 at $r = 7$ m (Fig. 3a, b, c), and the order of association intensity and scale was plot P2 > plot P1 > plot P3.

Nearest neighbour analysis: Significant negative correlations between the sum of the distances to four nearest neighbours and the sum of the canopy diameters of the target plant and its four nearest neighbours were noted for two out of three plots ($r = -0.405, -0.601; p < 0.05$; Fig. 4b, c). Meanwhile, one plot shows no significant negative relationship between neighbours distance and canopy diameter ($r = -0.114, p > 0.05$; Fig. 4a).

Discussion

A. aphylla plants can live for about thirty years in the harsh arid area (Chu *et al.*, 2009), which suggests that the spatial structure of *A. aphylla* population may reflect processes compounded over long periods of time. We found that different growth stages of *A. aphylla* population in the three slope positions showed significantly aggregated distributions at different scales, and seedlings were more likely to follow aggregated distribution than those big ones. In addition, positive associations among growth stages of *A. aphylla* population were found on a small scale while negative associations of seedling and juvenile relative to adult plants were shown in the middle and larger scale. The distribution patterns and spatial associations observed in this study of *A. aphylla* population may be the result of multiple ecological processes.

One possibility was that the patterns are a consequence of biotic process such as vegetative reproduction or limited seed dispersal (Ludwig & Reynolds, 1988). *A. aphylla* renewal mainly relies on seeds, and there was a significant positive correlation between the number of seedlings and that of the adult plants in a small scale, which meant that the seed trapping effect of existing vegetation plays an important role in the maintenance of the aggregated structure. *A. aphylla* seeds were spread over a long distance under the action of wind, while collected together by the breeze and snowmelt in a suitable microhabitat such as small depressions, water erosion ditch. The diffusion-collection dispersal mode of *A. aphylla* seeds leads to plant spatial associations similar to intraspecific relationship caused by facilitative interactions. In addition, seeds dispersal is often spatially restricted, which results in intraspecific aggregation (Nathan & Muller-Landau, 2000; Schleicher *et al.*, 2011). Therefore, seed dispersal may also be the cause of aggregated spatial distributions of *A. aphylla* population.

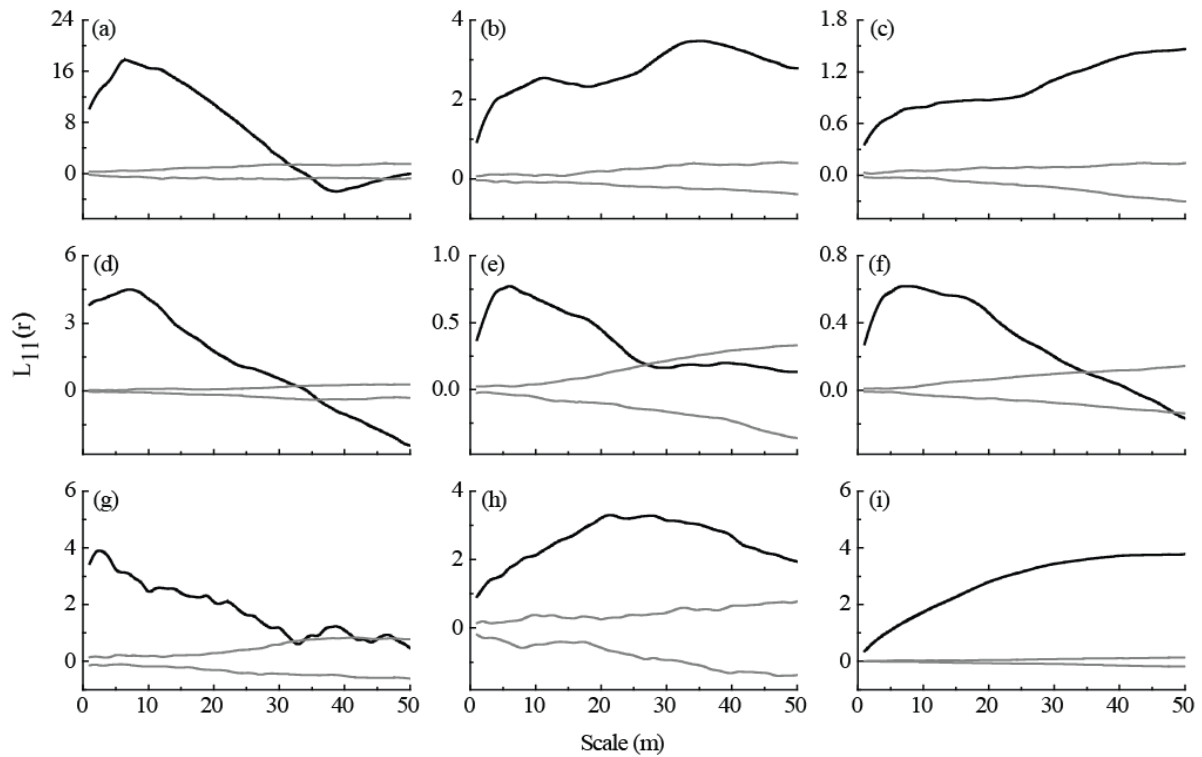


Fig. 1. The univariate L -Function statistic $L(r)$ at different scales r . (a) seedling in P1 plot, (b) juveniles in P1 plot, (c) adults in plot P1, (d) seedlings in plot P2, (e) juveniles in plot P2, (f) adults in plot P2, (g) seedlings in plot P3, (h) juveniles in plot P3, (i) adults in plot P3.

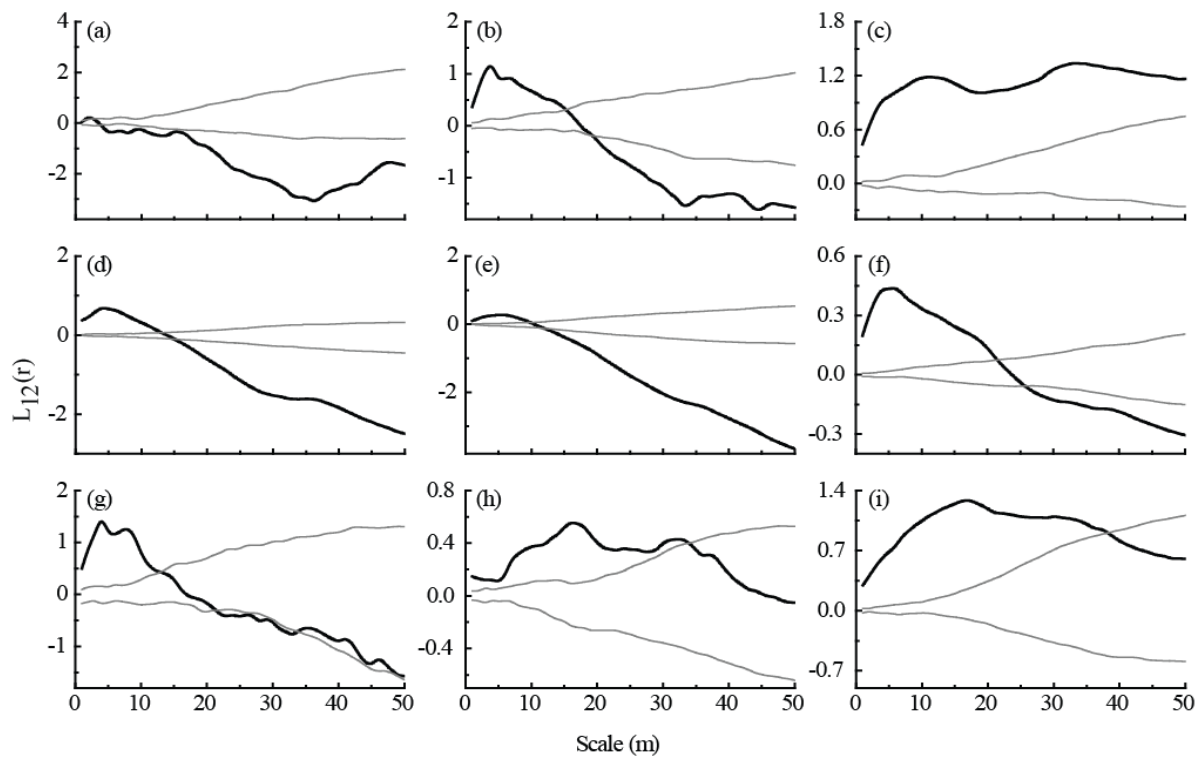


Fig. 2. The bivariate L -Function statistic test of spatial dependence between growth stages of *A. aphylla* population. (a) seedlings versus juveniles in P1 plot, (b) seedlings versus adults in P1 plot, (c) juveniles versus adults in P1 plot, (d) seedlings versus juveniles in P2 plot, (e) seedlings versus adults in P2 plot, (f) juveniles versus adults in P2 plot, (g) seedlings versus juveniles in P3 plot, (h) seedlings versus adults in P3 plot, (i) juveniles versus adults in P3 plot.

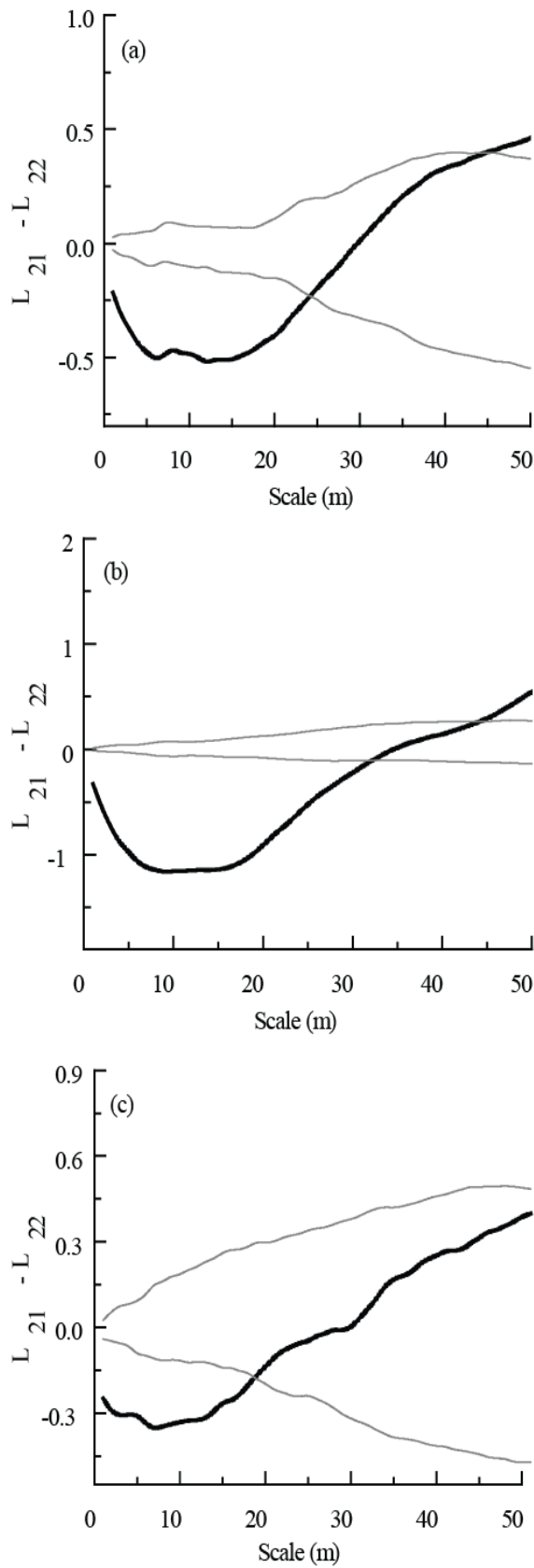


Fig. 3. Results of random labeling analysis of dead standing plants and adult *A. aphylla* subshrubs. (a) plot P1, (b) plot P2, (c) plot P3.

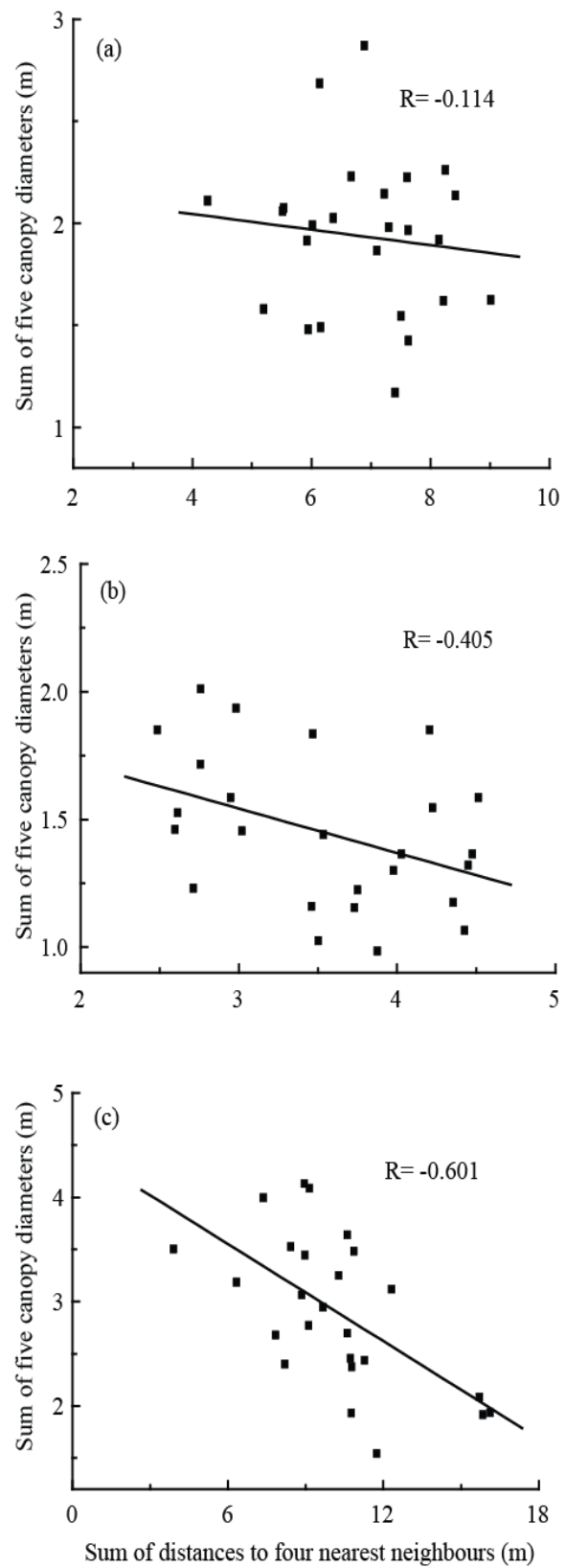


Fig. 4. Nearest neighbour analysis showing the relationship between the sum of the canopy diameters of the target tree and its four nearest neighbours and the sum of the distances to the four nearest neighbours in each of the three plots. (a) plot P1, (b) plot P2, (c) plot P3.

The process of seedling establishment is a dynamic and critical stage for future spatial pattern in plant life history because seedlings are typically the most susceptible of any life stage to environmental stresses (Wilson & Witkowski, 1998; Wu & Yang, 2013). In this case, *A. aphylla* seedling plants were significantly aggregated in relation to juvenile and adult plants in most sites, with maximum aggregation almost occurring on the scale of <14 m. Interestingly, and this estimated zone of influence for the *A. aphylla* plants measured was also about 12 m (based on maximum observed at a small depression scale), indicating that seedlings of *A. aphylla* may be successfully germinating in the small depression in the diluvial fan. Patterns of seedling aggregation have been explained in terms of regeneration ecology due to the occurrence of “safe sites” (Skarpe, 1991), and have been proven to occur among a variety of species and life forms (Pillay *et al.*, 2012). In addition, plants that display an aggregated distribution may be facilitating the growth of one another (Holmgren *et al.*, 1997; Schleicher *et al.*, 2011). In this case, *A. aphylla* plants growing at high densities create “the damp islands” after the snowmelt period which favours the germination of surrounding seeds and seedling establishment. Therefore, *A. aphylla* plants facilitation has been observed in the diluvial fan environments and is regarded as a response to impulse type rainfall events in arid areas.

The plants growth environment is heterogeneous (e.g., patchy distribution of soil resources) and as a consequence seed germination or seedling survival is higher in some microhabitats (Schlesinger *et al.*, 1990; Holmgren *et al.*, 1997; Wang *et al.*, 2013) and this alone could lead to spatial aggregation of shrubs. Furthermore, biotic interaction should also be taken into account when dealing with the availability of scarce resources. In arid areas, water is the restricted resource, water budget is known to result from complex interactions between climate, soil and vegetation (Skarpe, 1991). Consequently, one very important aspect is the number of water infiltrating from runoff that rainfall forms in diluvial fans. It is fairly well established that soil surface features are of overriding influence on infiltration under prevernae climates of Junggar Basin characterized by torrential snowmelt events (Huang 1991). Soil surface displays a high level of permeability within dense vegetation patches (Joffre & Rambal, 1993), owing to microtopography catchments and biopores formed by root systems. Within *A. aphylla* population, plants experience serious water stress at the upper slopes where soils are harder than those at adjacent middle slopes and sparse vegetation going against infiltration. In the presence of a consistent slope, water is reallocated from upper slope areas to lower slope through run-off, and such a process has been related patterned vegetations. Micro topography of the soil surface is known to determine catchments condition in diluvial fan (Huang, 1991), and enhance water infiltration within a radius of about ten meters. This results in a major promotion to *A. aphylla* renewal and may also cause an increased seedling survival rate during severe drought period. Therefore, these heterogeneous patch persistence and soil

infiltration law are likely to play an important role in maintaining a small scale aggregation and intraspecific association of *A. aphylla* population.

The pattern of *A. aphylla* growth stages also revealed that three plots displayed aggregation, despite the presence of a mass of mortality. This is contrary to the result of many researchers that the spatial pattern of mature plants should be regular under drought stress (King & Woodell, 1973), indicating competitive interactions. Besides, random labeling test reveal that intraspecific competition brings about a mass of mortality at small scales. But, significant positive relationship between the coefficient of variation in the nearest neighbour distances and canopy diameter was not found in three plots, implying that spatial competition between canopies was absent. We suggested that negative neighbour interactions between *A. aphylla* plants were probably due to a masking effect caused by a small canopy of desert subshrub, and ignored underground part interactions. In arid areas, desert roots extend laterally for about 1–3 m from the main root, a typical distance for small shrubs (Schenk & Jackson, 2002). This conclusion is supported by experimental findings from the study site, which has shown that sparse planting led to a significant increase in canopy size of *A. aphylla* plants over an 8-year period. Moreover, desert plant roots have been proven to possess a self/nonself recognition mechanism (Mahall & Callaway, 1996) which may lead to the root systems competition between plants under water stress. Therefore, *A. aphylla* root competition effects might result in decreased performance in a large part, which in turn prevented formation of the regular spacing in arid areas.

In this study, each of the above-mentioned processes (dispersal, seedling establishment, environmental heterogeneity, plant interactions and disturbance) may have acted individually or jointly with other processes to produce the aggregated patterns and competitive relationship. We suggest that the effects of intraspecific competition are expressed as the underground part interactions and the dwarf performance tolerating drought stress, which continues to maintain aggregated state of population and promote cyclical succession. In addition, intraspecific competition may be essential in structuring *A. aphylla* population at a small spatial scales, while other factors such as atmospheric drought or topography may be more important at larger spatial scales.

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