Relationship between Root Branching Number and Link Length of Potentilla acaulis in Alpine Degraded Grassland: Postprint

Authors: Zhang Weitao, Zhao Chengzhang, Song Qinghua, Wang Jiwei, Wang Jianliang, Yao Wenxiu, Li Qun

Date: 2018-01-09T00:00:00+00:00

Abstract

Root branching number and connection length influence the spatial distribution and resource acquisition of plant root systems, and the trade-off relationship between them contributes to a deeper understanding of the ecological adaptability of plant root architecture. On the northern slope of the Qilian Mountains in alpine degraded grasslands, four degradation gradient plots were established: non-degraded (T1), lightly degraded (T2), moderately degraded (T3), and heavily degraded (T4). The relationship between root branching number and connection length of *Potentilla acaulis* was studied using a combination of whole-root excavation and Win-RHIZO root analyzer. The results showed that with intensifying degradation of natural grasslands, the density, height, coverage, aboveground biomass of grassland communities, and soil water content gradually decreased, while soil compaction continuously increased; the density, height, coverage, aboveground and belowground biomass, root-to-shoot ratio, and root connection length of *P. acaulis* populations gradually increased, while branching number showed an opposite trend. The correlation between root branching number and connection length of *P. acaulis* differed among different degraded grasslands ($P < 0.05$), with an extremely significant negative correlation in non-degraded (T1) and heavily degraded (T4) grasslands ($P < 0.01$), and a significant negative correlation in lightly degraded (T2) and moderately degraded (T3) grasslands ($P < 0.05$). With degradation of natural grasslands, *P. acaulis* adopted an architectural construction pattern of decreasing root branching number and increasing root connection length, reflecting the trade-off mechanism of biomass allocation among different plant functional traits.

Full Text

Trade-off Between Root Forks and Link Length of *Potentilla acaulis* in Degraded Alpine Grassland

ZHANG Weitao, ZHAO Chengzhang*, SONG Qinghua, WANG Jiwei, WANG Jianliang, YAO Wenxiu, LI Qun

College of Geography and Environmental Science, Northwest Normal University; Research Center of Wetland Resources Protection and Industrial Development Engineering of Gansu Province, Lanzhou 730070, China

Abstract

Root forks and link length influence the spatial distribution and resource acquisition of plant root systems. The trade-off between these two architectural traits plays a significant role in the ecological adaptation of root architecture. This study was conducted in the Machangtan grassland on the northern slope of the Qilian Mountains in northwestern China (38°47 22.1 –38°52 11.4 N, 99°45 11.7 –99°57 41.2 E), where the altitude ranges from 2610 to 2632 m, mean annual temperature varies between 1-2°C, annual precipitation is 270-350 mm, the climate is continental and vertically variable, soils are primarily mountain chestnut soils, and the dominant native vegetation consists mainly of perennial grasses and forbs. In August 2014, we established four degradation gradient plots (non-degraded (T1), lightly degraded (T2), moderately degraded (T3), and heavily degraded (T4)) with six replicates each, recording plant density, height, coverage, and species composition in 1 m × 1 m quadrats. Soil compaction was measured at 0-10 cm, 10-20 cm, and 20-30 cm depths using an SC-900 Soil Compaction Meter (five replicates per quadrat), with the average compaction across the 0-30 cm profile representing the degradation gradient. Based on detailed community studies and grassland stocking rates from 2004-2013, we defined the gradients as: no degradation (>90%), light degradation (98%-115%), moderate degradation (120%-131%), and heavy degradation (135%-156%). Whole root systems were excavated from 30 cm × 30 cm × 50 cm soil cores (240 total across all gradients), sieved (bore diameter = 0.25 mm), cleaned in a nearby river, and scanned using Win-RHIZO to measure root forks and link length. Biomass was determined after oven-drying at 105°C for 12 hours, and soil moisture was measured by oven-drying at 84°C for 24 hours.

As natural grassland degradation intensified, aboveground biomass and soil water content gradually decreased while soil compaction increased. Conversely, grassland community density, *P. acaulis* population density, above- and belowground biomass, root-shoot ratio, and root link length increased. The correlation between root forks and link length in *P. acaulis* varied among degradation levels: a highly significant negative correlation ($P < 0.01$) was found in non-degraded and heavily degraded grasslands, while a significant negative correlation ($P < 0.05$) occurred in lightly and moderately degraded grasslands. With increasing grassland degradation, *P. acaulis* adopted a root architecture strategy of decreasing root forks while increasing link length, reflecting a trade-off mechanism in biomass allocation among different functional traits.

Keywords: *Potentilla acaulis*; root forks; link length; root architecture; trade-off; northern slope of Qilian Mountains

---

1. Study Area and Plot Description

The northern slope of the Qilian Mountains lies at the northern edge of the Tibetan Plateau and the southern side of the Hexi Corridor, where specific natural conditions have created extensive desert steppe (1900-2450 m), alpine steppe (2450-2800 m), and meadow steppe (2800-3800 m) dominated by xeric and mesic herbs and shrubs. The study site was located in Machangtan grassland, Sunan Yugur Autonomous County, Gansu Province (38°47 22.1 –38°52 11.0 N, 99°45 11.7 –99°57 41.2 E) at an elevation of 2705-2726 m. The region has a pronounced continental and mountain vertical climate, with a mean annual temperature of 0.5-1.7°C, annual precipitation of 270-350 mm, annual evaporation of 1480-1620 mm, and a frost-free period of 80 days. Soils are primarily mountain chestnut soils, and the ecosystem is fragile. Dominant plant species include *Stipa krylovii*, *Artemisia frigida*, *Poa pratensis*, *Agropyron cristatum*, *Melica przevalskyi*, *Oxytropis kansuensis*, *Heteropappus altaicus*, *Stellera chamaejasme*, and *Thermopsis lanceolata*.

2. Community Survey and Plant Sampling

Based on long-term observations of natural grassland succession and plant ecological adaptation on the Qilian Mountains' northern slope by Zhao et al. [22], we conducted community and root surveys in mid-August 2014. Test plots were selected from fenced pastures on north-facing slopes used for winter-spring grazing with free grazing from June to November. According to grazing history and management, four fenced pastures of 80.5-100 hm^2 were chosen representing different degradation levels: non-degraded (T1), lightly degraded (T2), moderately degraded (T3), and heavily degraded (T4). Plot selection was based on community surveys, the growth status of the constructive species *Stipa krylovii*, and stocking rates (calculated as A/B × 100%, where A is the actual average livestock carrying capacity and B is the theoretical carrying capacity for the same period). Within each degradation gradient, representative 10 m × 10 m areas with uniform *P. acaulis* growth were selected based on average population height, coverage, and density.

Table 1 shows the main characteristics of the sample plots. Different lowercase letters after data in the same column indicate significant differences among degradation gradients ($P < 0.05$). T1: no degradation; T2: light degradation; T3: moderate degradation; T4: heavy degradation.

The field sampling procedure was as follows: For community surveys, we used 1 m × 1 m quadrats to measure and record density, height, and coverage of all plants, documenting all species present. All plants in each quadrat were clipped at ground level, numbered, and returned to the laboratory. Soil compaction was measured at 0-10 cm, 10-20 cm, and 20-30 cm depths in each survey quadrat using an SC-900 compaction meter, with the average of all quadrats representing the plot’ s soil compaction.

3. Laboratory Measurements

Within each plot, *P. acaulis* plants were sampled by randomly establishing 30 cm × 30 cm quadrats. Soil cores (30 cm × 30 cm × 50 cm) were excavated with intact aboveground plants. Debris such as gravel was removed near a river, and plants were separated from soil by rinsing. A total of 240 cores were collected across all degradation gradients. *P. acaulis* whole plants were selected and sieved (bore diameter = 0.25 mm). Above- and belowground parts were separated and placed in numbered ziplock bags for laboratory analysis.

For soil sampling, an auger (diameter = 4 cm) was used to collect soil at 10 cm intervals from 0-50 cm depth in each plot. All fresh soil samples were cleared of visible stones, plant roots, and litter, then placed in numbered aluminum boxes for laboratory analysis.

In the laboratory, *P. acaulis* roots were carefully brushed and spread in a root scanner tray with a small amount of water. Root systems were scanned using Win-RHIZO (Pro 2009a, Regent Instruments, Quebec, Canada) and stored as image files on computer to obtain root forks per unit length and average link length. Finally, above- and belowground parts were placed in envelopes, oven-dried at 105°C for 12 hours, and weighed with an electronic balance (0.0001 g precision) to calculate biomass. Soil moisture content was determined by oven-drying at 84°C for 24 hours and measuring weight loss.

4. Data Processing

All raw data were processed using Microsoft Excel 2007. To normalize the data for root forks per unit length and link length for linear regression analysis, log10 transformation was applied. Statistical analysis was performed using SPSS 20.0 with one-way ANOVA. Significance level was set at $P < 0.05$. All figures were created using SigmaPlot 10.0 and Microsoft Excel 2007.

5. Results

5.1 Changes in Root Forks and Link Length Across Degradation Gradients

Root forks and link length of *P. acaulis* varied significantly among degradation gradients ($P < 0.05$). One-way ANOVA revealed that as grassland degradation increased from non-degraded (T1) to heavily degraded (T4), the average root forks per unit length gradually decreased by 65.51%, while root link length showed the opposite trend, increasing by 161.80%.

5.2 Relationship Between Root Forks and Link Length

Correlation analysis showed a significant negative relationship between root forks and link length across all degradation gradients (Pearson, $P < 0.05$). As root forks decreased along the degradation gradient, link length increased. The standardized major axis slopes of the regression equations differed significantly among gradients ($P < 0.05$). The slopes for lightly degraded (T2), moderately degraded (T3), and heavily degraded (T4) grasslands were all less than -1, while the slope for non-degraded grassland (T1) was greater than -1. The slope increased gradually from non-degraded to heavily degraded grassland, with no significant difference between light (T2) and moderate (T3) degradation ($P > 0.05$).

Figure 2 [Figure 2: see original paper] shows changes in root forks and link length of *P. acaulis* along the degradation gradient. Different lowercase letters indicate significant differences among degradation gradients ($P < 0.05$). T1: no degradation; T2: light degradation; T3: moderate degradation; T4: heavy degradation.

Figure 3 [Figure 3: see original paper] illustrates the relationship between root forks and link length of *P. acaulis* across different degraded grasslands. T1: no degradation; T2: light degradation; T3: moderate degradation; T4: heavy degradation.

5.3 Community Characteristics and Soil Physical Properties

Community density, coverage, and aboveground biomass differed significantly among degradation gradients ($P < 0.05$), decreasing from non-degraded (T1) to heavily degraded (T4) grasslands by 52.11%, 70.18%, and 43.05%, respectively. Soil moisture content and compaction also varied significantly ($P < 0.05$). Soil water content decreased by 40.44% from T1 to T4, while soil compaction increased by 123%, showing opposite trends.

Table 2 presents community characteristics and soil water content across degradation gradients. Different lowercase letters after data in the same column indicate significant differences among gradients ($P < 0.05$). T1: no degradation; T2: light degradation; T3: moderate degradation; T4: heavy degradation.

5.4 Population Characteristics of *P. acaulis*

Biological characteristics of *P. acaulis* populations varied significantly among degradation gradients (Table 3). Population density, aboveground biomass, belowground biomass, and root-shoot ratio all increased significantly ($P < 0.05$), rising by 101.00%, 86.98%, 166.10%, and 70.79%, respectively, from T1 to T4. The proportion of root biomass to total population biomass increased from 10.70% in non-degraded to 24.25% in heavily degraded grassland, a 166.67% increase.

Table 3 shows biological characteristics of *P. acaulis* across the degradation gradient. Different lowercase letters after data in the same column indicate significant differences among gradients ($P < 0.05$). T1: no degradation; T2: light degradation; T3: moderate degradation; T4: heavy degradation.

---

6. Discussion

Plants adapt to environments through a series of interconnected functional traits [23]. Within this framework, root systems possess inherent growth and response patterns that coordinate relationships between key traits such as root forks and link length under specific environmental conditions, establishing a trade-off and compensation mechanism through natural selection [25]. This study found that as grassland degradation progressed, *P. acaulis* root systems exhibited decreasing forks and increasing link length, with a clear trade-off between these traits that reflects the species' adaptive root architecture strategy in degraded grasslands.

In non-degraded grassland (T1) dominated by *Stipa krylovii*, livestock grazing and trampling were relatively weak. Community height, coverage, and biomass were high, soil moisture was adequate, and compaction was low. Here, *P. acaulis* occurred sporadically in a prostrate form, with population density, biomass, and root-shoot ratio all relatively small. Constrained by neighboring dominant species and at a competitive disadvantage, *P. acaulis* prioritized allocating more biomass to aboveground stems to increase height and leaf number [27], while constructing root systems with greater forks and smaller link length. This strategy enhanced branching intensity and clump density, allowing the species to form dense underground networks and aboveground patches through coordinated ramets, thereby improving resource use efficiency within limited space. Smaller link length shortened resource transport distances, enabling effective resource sharing among ramets and ensuring minimum survival conditions under intense competition.

Grazing is the primary external driver of grassland degradation [30], while internal factors include community structure changes and species replacement strategies, along with resulting inter- and intraspecific dependencies and competition [31]. Under long-term selective grazing, palatable grasses like *S. krylovii* became sparse and stunted, reducing vegetation cover and increasing soil evaporation. Soil compaction increased, hindering root growth and nutrient uptake. In heavily degraded grassland (T4), unpalatable and trampling-resistant *P. acaulis* reached maximum population density, biomass, and root-shoot ratio, becoming the community dominant species. Intraspecific aggregation intensified resource competition within populations. To expand soil resource acquisition, avoid unnecessary intraspecific competition, and reduce above- and belowground crowding, *P. acaulis* adopted a strategy of decreasing root forks while increasing link length. Reduced forks minimized root overlap and alleviated competition for water and nutrients, while increased link length enhanced spatial exploration, overcoming soil compaction effects and facilitating clonal expansion into areas with abundant resources. This allowed patch merging and consolidation, supporting population expansion and dominance succession.

This pattern aligns with studies on *Reaumuria soongorica* in the Hexi Corridor [34] and on *Tamarix taklamakanensis*, *Calligonum roborovskii*, and *Apocynum venetum* in the Taklamakan Desert [35]. Plant responses to disturbance fundamentally involve functional trait adjustments [36], often exhibiting trade-offs between internal and external functions that reflect important adaptive strategies [37]. As degradation progressed from non-degraded to lightly and moderately degraded grasslands, the competitive advantage of *S. krylovii* declined [40]. *P. acaulis* populations expanded through patchy distribution with increasing density, height, and root-shoot ratio. To utilize vacated niches and increase ground cover, the species selected for decreased root forks and increased link length, laying the foundation for population expansion and dominance succession. This matches findings on *P. acaulis* root architecture across degradation gradients [42].

Our results demonstrate that *P. acaulis* adapts to community environmental changes and dominant species succession by adjusting root forks and link length, revealing phenotypic plasticity mechanisms for trait trade-offs. This underscores the species' robust survival strategy and strong ecological adaptability as a final line of defense against grassland degradation. Understanding this trade-off relationship is crucial for comprehending degradation succession processes and guiding grassland restoration. Root architecture is also influenced by plant structure, soil physicochemical properties, and age [17]. Further exploration of these factors will deepen our understanding of root ecological adaptation and its regulation.

References

[1] Waisel Y, Eshel A, Kafkafi U. Plant roots: the hidden half. New York: Marcel Dekker, 1996.

[2] [Chinese reference on drip irrigation and poplar root zone soil moisture dynamics]

[3] [Chinese reference on *Stipa grandis* root architecture response to grassland degradation]

[4] Smit A L, Bengough A G, Engels C, van Noordwijk M, Pellerin S, van de Geijn S C. Root Methods: a handbook. Berlin Heidelberg: Springer, 2000.

[5] [Chinese reference on *Reaumuria soongorica* root architecture adaptation to drought]

[6] Dannowski M, Block A. Fractal geometry and root system structures of heterogeneous plant communities. Plant and Soil, 2005, 272(1/2): 61-76.

[7] Le Maire G, Nouvellon Y, Christina M, Ponzoni F J, Gonçalves J L M, Bouillet J P, Laclau J P. Tree and stand light use efficiencies over a full rotation of single- and mixed-species *Eucalyptus grandis*, *Acacia mangium* plantations. Forest Ecology and Management, 2013, 288: 31-42.

[8] Walk T C, Van Erp E, Lynch J P. Modelling applicability of fractal analysis to efficiency of soil exploration by roots. Annals of Botany, 2004, 94(1): 119-128.

[9] Schenk H J, Jackson R B. Rooting depths, lateral root spreads and below-ground/above-ground allometries of plants in water-limited ecosystems. Journal of Ecology, 2002, 90(3): 480-494.

[10] Winter S R, Unger P W. Irrigated wheat grazing and tillage effects on subsequent dryland grain sorghum production. Agronomy Journal, 2001, 93(3): 504-510.

[11] [Chinese reference on grazing effects on grasslands]

[12] [Chinese reference on plant roots in northern China grasslands]

[13] [Chinese reference on morphological plasticity of stoloniferous herbs]

[14] Trachsel S, Kaeppler S M, Brown K M, Lynch J P. Shovelomics: high throughput phenotyping of maize (*Zea mays* L.) root architecture in the field. Plant and Soil, 2011, 341(1/2): 75-87.

[15] Kalliokoski T, Sievänen R, Nygren P. Tree roots as self-similar branching structures: axis differentiation and segment tapering in coarse roots of three boreal forest tree species. Trees, 2010, 24(2): 219-236.

[16] [Chinese reference on trade-off between root forks and link length of *Glycyrrhiza uralensis* on different slopes]

[17] Lynch J P. Steep, cheap and deep: an ideotype to optimize water and N acquisition by maize root systems. Annals of Botany, 2013, 112(2): 347-357.

[18] Zhao Y, Peth S, Horn R, Krümmelbein J, Ketzer B, Gao Y Z, Doerner J, Bernhofer C, Peng X H. Modeling grazing effects on coupled water and heat fluxes in Inner Mongolia grassland. Soil and Tillage Research, 2010, 109(2): 75-86.

[19] [Chinese reference on ecological adaptation of two rhizomatous plants' root architecture to typical steppe degradation]

[20] [Chinese reference on root biomass distribution in natural grasslands under different enclosure periods in the Loess Plateau]

[21] [Chinese reference on ecological adaptation of rhizomatous plant root architecture to meadow steppe grazing degradation]

[22] [Chinese reference on trade-off between leaf size and number of *P. acaulis* in degraded alpine grassland]

[23] Bernard-Verdier M, Navas M L, Vellend M, Violle C, Fayolle A, Garnier E. Community assembly along a soil depth gradient: contrasting patterns of plant trait convergence and divergence in a Mediterranean rangeland. Journal of Ecology, 2012, 100(6): 1422-1433.

[24] Jung V, Violle C, Mondy C, Hoffmann L, Muller S. Intraspecific variability and trait-based community assembly. Journal of Ecology, 2010, 98(5): 1134-1140.

[25] Fortunel C, Fine P V A, Baraloto C. Leaf, stem and root tissue strategies across 758 Neotropical tree species. Functional Ecology, 2012, 26(5): 1153-1161.

[26] Klumpp K, Fontaine S, Attard E, Le Roux X, Gleixner G, Soussana J F. Grazing triggers soil carbon loss by altering plant roots and their control on soil microbial community. Journal of Ecology, 2009, 97(5): 876-885.

[27] [Chinese reference on morphological plasticity and biomass allocation of *Artemisia frigida* and *P. acaulis* under different grazing intensities]

[28] [Chinese reference on root architecture characteristics of typical sand plants on South China coast]

[29] [Chinese reference on slope aspect differences in trade-off between root forks and link length of *Reaumuria soongorica*]

[30] Bird S B, Herrick J E, Wander M M, Murray L. Multi-scale variability in soil aggregate stability: implications for understanding and predicting semi-arid grassland degradation. Geoderma, 2007, 140(1/2): 106-118.

[31] Zhang J T. Succession analysis of plant communities in abandoned croplands in the eastern Loess Plateau of China. Journal of Arid Environments, 2005, 63(2): 458-474.

[32] [Chinese reference on spatial heterogeneity of soil seed bank of *Stellera chamaejasme* in degraded grassland based on geostatistics]

[33] [Chinese reference on review of livestock trampling effects on grasslands]

[34] [Chinese reference on morphological differences of *Stipa krylovii* populations in different habitats in central-eastern Inner Mongolia]

[35] [Chinese reference on spatial pattern and association of *Stipa krylovii* individuals in degraded grassland]

[36] [Chinese reference on root architecture adaptation of *P. acaulis* to grassland degradation]

[37] Mooney K A, Halitschke R, Kessler A, Agrawal A A. Evolutionary trade-offs in plants mediate the strength of trophic cascades. Science, 2010, 327(5973): 1642-1644.

[38] [Chinese reference on functional trait responses to grazing disturbance]

[39] [Chinese reference on patch fragmentation intensification in degraded grasslands]

[40] [Chinese reference on review of grazing livestock trampling effects]

[41] [Chinese reference on population spatial pattern and association of *Stipa krylovii* in degraded grassland]

[42] [Chinese reference on ecological adaptation of *P. acaulis* root architecture to grassland degradation]

Note: Figure translations are in progress. See original paper for figures.