Soil Environ. 39(2): 194-203, 2020
DOI:10.25252/SE/2020/162314
Online ISSN: 2075-1141
Print ISSN: 2074-9546

Distribution of plant species and the rock particle size in subnival habitats of the Central Great Caucasus

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[Received:** August 01, 2020* ***Accepted:** October 24, 2020* ***Published Online:** November 28, 2020**]

Abstract

Subnival habitats of the Central Caucasus represent typical rocky environments with very sparse soil cover and patchy vegetation. We studied how spatial distribution of plant species in a subnival habitat (alpine-nival ecotone) depends on the size of rock particles. We described the distribution patterns of plants and rock particles of various sizes, and examined the possible links between these patterns using correlation analysis and multivariate tests. We found that the largest size class (20-60 cm) was in a strong negative correlation with smaller classes (0.2-0.6 cm, 0.6-2 cm and 2-6 cm), but correlation was insignificant among the largest fragments (6-20 cm) and the soil patches. The CCA included 31 species (frequency >10) and the goodness-of-fit of the obtained ordination was assessed by permutation test. The CCA ordination revealed several species with a clear preference for soils (Carex tristis and Sibbaldia parviflora), while other species preferred mid-sized (20-60 cm) rock particles (Tephroseris karjaginii, Ziziphora puschkinii, Festuca supina, Minuartia inamoena and Saxifraga juniperifolia). Further, Senecio sosnowskyi and Ziziphora subnivalis tended to colonize large (6-20 cm) rock fragments. Overall, our results show a clear differential preference of species for certain sizes of rock particles that conforms well to the patchy pattern of vegetation typical for subnival habitats: many species that prefer a fine grained substratum might clump together at such fine-grained spots and form the patches of associated plants provided there are facilitative interactions among them; the species that prefer coarser-grained substrata might establish as solitary plants outside of the patches.

Keywords: Rock particle size, soil formation, plant species distribution, primary succession, rocky environments, rock colonising plants

Introduction

Rocky environments usually represent extreme habitats with very sparse soil cover, characterized by low annual average cumulative temperature, large temperature differences between day and night, intense ultraviolet radiation, and strong winds – a good example is the subnival zone (alpine nival ecotone) in high mountains (Nagy and Grabherr, 2009; Egli and Poulenard, 2016). This type of habitat is characterised by patchy open vegetation and abundant bare substratum mainly represented as skeletal soils of frost-shattered rock fragments (Nakhutsrishvili, 2003). Plants that colonise rocky environments can contribute to rock fragmentation and soil formation (Bashan *et al*., 2002; 2006; Carrick *et al*., 2013; Estrada-Medina *et al*, 2013), and provide a suitable system for studying ecological phenomena such as colonization, plant succession and rock weathering (Guisan and Rahbeck, 2011). Currently, because glaciers are retreating owing to the ongoing climate warming, most of the research on plant-rock interactions in high mountains is rather focused on the revegetation of glacier forelands see Malanson *et al.* (2020) for the latest contribution.

Climatic gradients in mountains are steep and provide perfect settings for studying changes in species composition over relatively short distances (Lomolino, 2001). Species diversity is an important property of communities because it is often related to their functioning and potential for change (Hooper *et al.*, 2005; Gamfeldt and Hillebrand, 2008). In sunbibval-nival belts, the patchy vegetation is formed mostly by growth forms adapted to the harsh conditions of

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high elevations: cushions, prostrate plants, etc. (Körner and Larcher, 1988; Körner 2003, 2011). Our general goal was to study the local distribution of plant species across rock particles of various size. Rock fragmentation is an important initial stage of soil formation (Lavelle and Spain, 2001; Föllmi *et al*., 2009), and guidelines have already been worked out for quantitative description of rock particle size (Jahn *et al.*, 2006). In general, the studies carried out in mountains point to the importance of soil processes (Körner, 2011; Zanini *et al.,* 2015; Baruck *et al.*, 2016), yet reports on the relationships between rock particle size and plant distribution over rocky habitats are very few (if any). This is surprising, because the size of rock particles can substantially influence the colonising ability of plants: processes such as germination and root formation might greatly depend on whether the substratum is fine- or coarse-grained. We hypothesised that most of species would be associated with soil patches in the subnival belt, the list of species analyzed in our study is given in Table 2 and less species would be able to colonise bare, mainly fine-grained substratum. Accordingly, our expectation was that vegetation would be more abundant on soils and fine-grained substrata even though the species might exhibit measurable differences in their preference for substrata of certain grains.

We tested our hypothesis in the subnival zone habitats of the Central Caucasus (slopes of Mt. Kazbegi and Mt. Tetnuldi), which occur above the elevation of 3000m (Nakhutsrishvili, 2013; Gigauri *et al.*, 2013, 2014; Nakhutsrishvili and Abdaladze, 2017a). We sampled rock particles and vegetation in the subnival zone habitats and examined the dependence of plant species distribution on rock particle size using methods of multivariate analysis.

Materials and Methods

Study sites

Our study sites were set on the slopes of two prominent mountains of the Central Great Caucasus: Mt. Kazbegi (42°39′46.87″N; 44°33′12.87″E) and Mt. Tetnuldi (43°01′49.9″N, 42°55′36.0″E), which are the major eastern and western landmarks of the Central Great Caucasus, respectively (Figure 1). These sites have a pronounced vertical vegetation zonation (Zazanashvili *et al.,* 2000). The topography is characterized by high sharp-ridge bare rocky ranges divided by large depressions and narrow ravines of erosive and tectonic origin. The climate is humid with cold and short summers and long severe winters (Figure 3). Morning frosts are frequent during summers. Weather can change dramatically several times during the day (Nakhutsrishvili *et al.,* 2005; Abdaladze *et al.,* 2015; Nakhutsrishvili and Abdaladze, 2017b). Alpine meadows form a continuous cover up to ca. 3000 m a.s.l., at higher elevations the vegetation becomes patchy representing scattered plant micro-groups on rocks, scree and among moraines (Kikvidze, 1993; Körner, 2003; Körner and Paulsen, 2017; Nakhutsrishvili and Abdaladze, 2017a; 2017b). Form the patches typically contain both alpine and subnival species, as well as those showing a wider altitudinal range (Kikvidze, 1993). On the whole, the species composition is poor, in comparison with that of alpine meadow communities (Nakhutsrishvili and Gagnidze, 1999; Gigauri *et al*., 2013, 2014, 2016). (Table 1). Soils are represented by a weak cover of leptosols (Urushadze *et al*., 2015; Kunchulia *et al.*, 2018).

Sampling design and data collection

There were two study areas: one on the slopes of Mt. Kazbegi and another on those of Mt. Tetnuldi. At each sampling site, we established sampling plots on slopes of opposite aspects (N-S), at elevations of 3000 and 3100 m a.s.l. Overall there were eight plots (two elevations, two aspects, two sampling areas) of approximately 200 m^2 each. Within each plot we randomly established 20 sampling quadrats of one m × one m size. The distance between the quadrats was at least four-five m see also (Jolokhava *et al.*, 2020).

Elevation and slope aspects were determined using a GPS device (Etrex *Summit* ™, Garmin, Switzerland). Slope angle (inclination) was measured by compass-clinometer (Recta DP 6™, Switzerland).

Soil surface fragmentation was assessed within each of the 1 m^2 quadrats according to the six size classes: 0.2-0.6 cm; 0.6-2 cm; 2-6 cm; 6-20cm; 20-60 cm. we assessed with a Guidelines for Soil Descriptions, classification of coarse surface fragments (FAO, 2006). It should be noted that we have added the soil as a sixth component. We estimated the percent share of each size class to quantify coarse surface fragments. Additionally, we used more than 300 photographs of the substrate surface to assess size classes of coarse fragments (including all 1 m^2 quadrates).

Within each plot (1 m^2), all plant species were recorded and their abundance was measured by the frequency of occurrence of countable shoots in the patches (Kent, 2011). We also quantified the density of vegetation patches by counting the number of patches per 1 m^2 plot (Figure 2). Vascular plant species were identified according to Key to Higher Plants of Georgia (Ketskhoveli, 1964; 1969) and verified through comparison with herbarium specimens stored at the Stephantsminda Alpine Ecology Institute of Ilia State University and the National Herbarium of Georgia

Table 1: Environmental conditions and vegetation patches distribution along elevation gradient (3000-4000 m a.s.l.) in the Central Great Caucasus (Kikvidze, 1993; Zazanashvili *et al*., 2000; Nakhutsrishvili *et al*., 2005; Gagnidze *et al*., 2006; Abdaladze *et al*., 2015; Nakhutsrishvili and Abdaladze, 2017a, b)

Vertical zone	Elevation gradient	Topography	Climate	Substrate	Vegetation
Subnival	3000-3700 (m a.s.l.)	High sharp-ridge bare rocky ranges, large depressions and narrow ravines of erosive and tectonic origin	Humid cold, Strong diurnal variability	Rocks and scree among moraines	Patches of herbaceous vegetation, prostrate and cushion plants
Nival	3700-4000 (m a.s.l.)		Extremely cold		Solitary plants

Figure 1: Location of our study areas: Mt. Kazbegi and Mt. Tetnuldi, the major eastern and western landmarks of the Central Great Caucasus

Table 2: Correlation matrix of alpine-nival ecotone rock fragment size classes in the central Caucasus. Numbers below the empty diagonal indicate correlation coefficients, above the diagonal are the corresponding p-values

	Soil	0.2-0.6 cm	0.6-2 cm	2-6 cm	6-20 cm	Size-5
Soil		0.02	<0.0001	<0.0001	0.07	0.17
0.2-0.6cm	0.18		<0.0001	0.0013	0.003	<0.0001
0.6-2cm	-0.18	0.48		<0.0001	0.028	<0.0001
2-6cm	-0.31	0.25	0.4223		0.44	<0.0001
6-20cm	-0.31	-0.23	-0.17	-0.06183		0.11
20-60cm	-0.14	-0.63	-0.67	-0.58	-0.13	

located at the Institute of Botany of Ilia State University. Plant species names followed the Nomenclatural Checklist of Georgian Flora (Gagnidze, 2005) and International Plant Names Index (IPNI) resources.

Data analyses

We processed climatic data on monthly precipitation and average monthly temperatures of the western (Svaneti) and eastern (Kazbegi) parts of the Central Great Caucasus (Meteoblue,https://content.meteoblue.com/en/content/view/full/2559) from 1985 to 2019 inclusive. We assessed the similarity of climate at two sampling sites (Mt. Tetnuldi vs. Mt. Kazbegi) by monthly values of mean temperature and precipitation (Hubálek and Horáková, 1988). We did not transform data for measuring Euclidean distances but used a non-parametric statistical test ANOSIM (Clarke, 1993).

Figure 2: Typical subnival habitat with scree substratum and plant patches

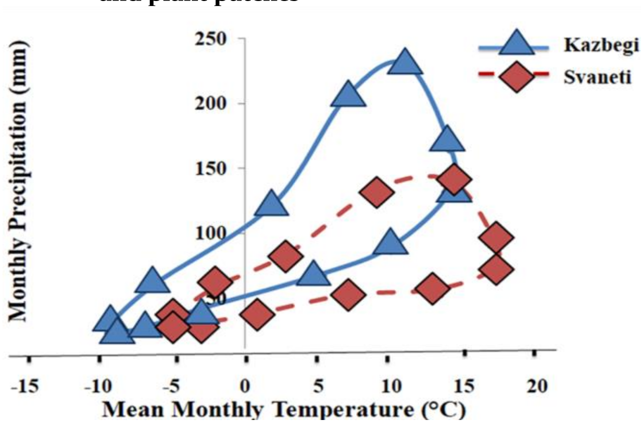

Figure 3: Climagrams of at Kazbegi and Tetnuldi alpine-nival ecotone based on the last 30 years of observation (Source: Meteoblue, https://www.meteoblue.com)

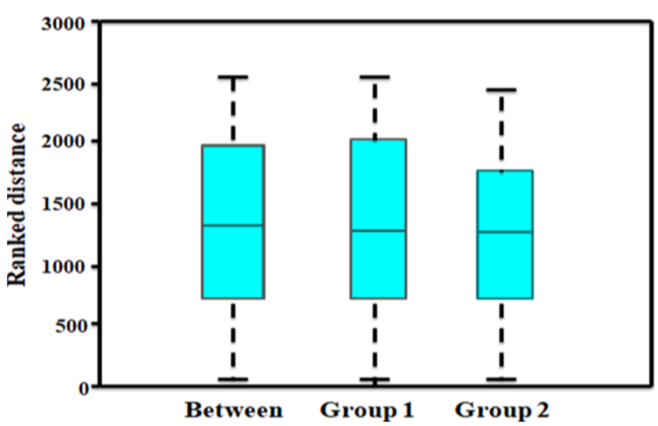

Figure 4: Box plot of ranked distance obtained in the ANOSIM test between two groups (Mt.Kazbegi, the Central Caucasus and Mt. Tetnuldi, the Greater Caucasus, 3000 to 3100 m a.s.l.). ANOSIM statistics: Mean rank within = 1284, Mean rank between = 1273, R = 0.009002, p = 0.71

Rock fragmentation was assessed by size distribution of coarse surface fragments (represented as histograms). Because the fragment size classes were compared as percent shares, the increase in one class inevitably causes decrease in other classes, which might result in significant correlations among certain size classes; to look at these relations we calculated Pearson's correlation for all possible pairs of coarse fragment size classes.

Statistical analyses

We constructed a community matrix, which included data on coarse fragment sizes and plant species occurrence and their abundance at sites. Then we employed a CCA ordination to analyze the dependence of plant species distribution on fragment size. The goodness-of-fit of the obtained ordination was assessed by permutation test (999 permutations). In the CCA, we included only frequent species (frequency of occurrence >10). We also analysed the dependence of vegetation abundance on a given size of rock fragment by Pearson's correlation. We used IBM SPSS Statistics for Windows, Version 21.0 (Heck *et al.*, 2013) and PAST 3.20 (Hammer *et al*., 2001) for the above statistical analyses.

Results

The climate (mean air temperature and annual precipitation) at two sampling areas (3000-3100 m a. s. l.) were qualitatively similar, as the climagrams for Mt. Tetnuldi and Mt. Kazbegi showed a similar shape and overlapped strongly (Figure 3). Quantitative comparison also showed insignificant differences (p = 0.71 by ANOSIM), (Figure 4). Therefore, we proceeded in our analyses on the assumption that the major climatic characteristics at Mt. Tetnuldi and Mt. Kazbegi were similar and the minor differences in them did not affect measurably the relationships between substrate coarse fragments and plant species distributions

The geographical ranges of most species on Earth are dispersal limited, and abiotic conditions are considered to be especially strong drivers of alpine plant distribution due to the tight coupling between plant physiology and the harsh climatic conditions found in alpine environments. Size distribution of coarse particles showed a prevalence of large-sized rock fragments. We included soil in this distribution because soils are formed from the finest particles and thus can represent a natural product of rock fragmentation (see Introduction). We expected that soil patches were the best habitable islands on the surface for most plant species, therefore it was important to know the share of soil among the rock fragments of various sizes. In fact, soils appeared to be the least frequent in size distribution (Figure 5), thus revealing how strikingly different can plant life conditions be in alpine-nival ecotone if compared to adjacent alpine habitats.

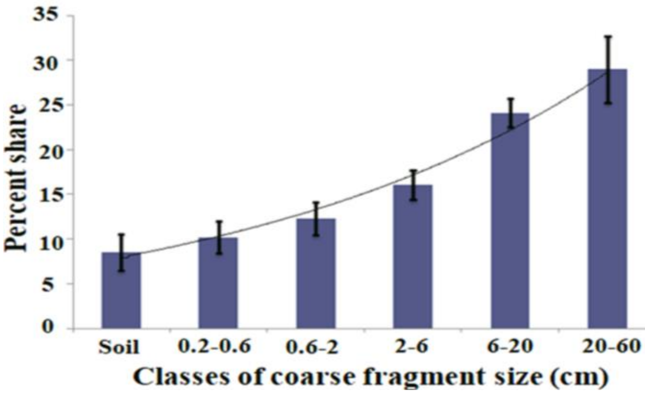

Figure 5: Size distribution of coarse surface fragments in alpine-nival ecotone areas of the Central Greater Caucasus (3000 to 3100 m a.s.l.)

Since the fragment size classes were compared as percent shares, the increase in one class should cause decrease in other classes, which might result in significant correlations among certain size classes (Table 2). We found that the largest size class (20-60 cm) was in a strong negative correlation with smaller classes (0.2-0.6 cm, 0.6-2 cm and 2-6cm), but correlation was insignificant among the largest fragments, the second largest class (6-20 cm) and the soil. Therefore, we used these three uncorrelated rock fragment classes as environmental variables for ordination analysis (Figure 6). Overall, we recorded 58 species in the quadrats (Table 3), out of which 31 species were frequent (>10) and were used in the CCA.

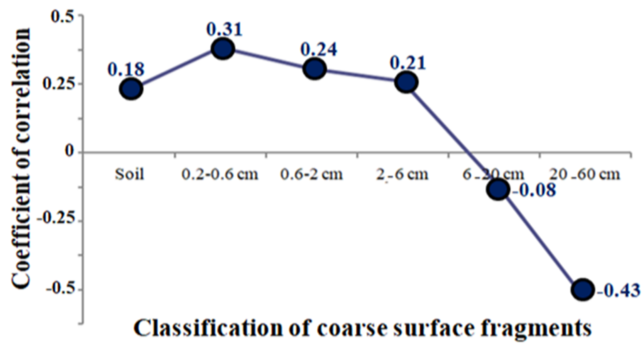

Figure 7: The Correlation between the density of vegetation and soil particle class proportions in the Central Caucasus (3000 to 3100 m a.s.l..) Numbers above the symbols show the values of correlation coefficient. Except for size class 6-20 cm, all values of correlation coefficient are significant

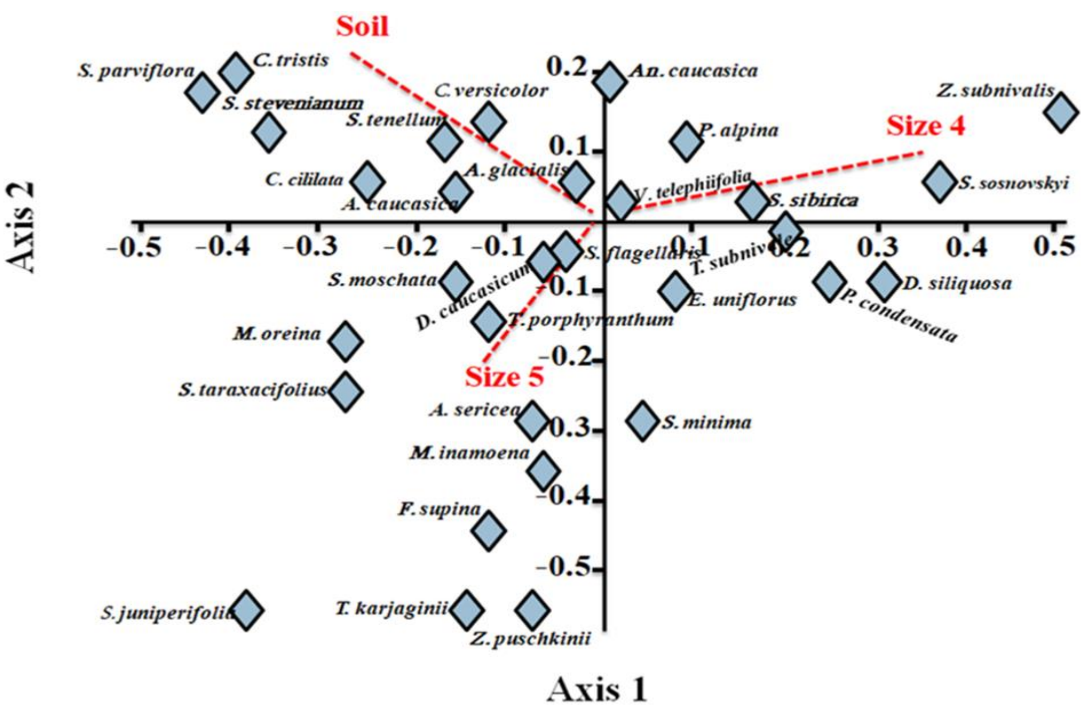

Figure 6: CCA ordination biplot of plant species distribution in alpine-nival ecotone (3000-3100 m a.s.l.) in the Central Caucasus along a gradient of rock fragment size. Species full names are given in Table 2. Size 4 and Size 5 correspond to rock fragment size class 6-20 cm and 20-60 cm, respectively

The CCA ordination appeared to be marginally significant (*p = 0.067* for the first axis). The first two axes nevertheless explained cumulatively almost the entire variation in species distributions (67.9% and 31.8% for the first and second axes, respectively). Some plant species showed a clear preference to large rock fragments or to soil; in particular, *Tephroseris karjaginii, Ziziphora puschkinii, Festuca supina, Minuartia inamoena and Saxifraga juniperifolia* tended to colonise a substrate with large fragments (20-60 cm), *Senecio sosnowskyi* and *Ziziphora subnivalis* showed certain affinity to rock fragment size of 6-20 cm, while *Carex tristis and Sibbaldia parviflora* prefered soil substratum. However, most plants concentrated in the central area of the CCA biplot probably because of not very strong preference for a certain class of rock fragments.

Rock fragment size was also important to the abundance of plants in alpine-nival ecotone (Figure 7). The density of vegetation was most strongly and negatively correlated (r = -0.43) with the largest fragment class (20-60 cm); however, the correlations with smaller fragment sizes were positive, and the highest positive correlation (r = 0.31) was observed with the finest fragment class (0.2-0.6 cm). Surprisingly, soil was not so tightly correlated with plant abundance (r = 0.18), probably because of a large proportion of species adapted to the lack of soils in alpine-nival environments (see also Table 2).

Table 3: Distribution of species abundances (countable stems) along elevation gradient (3000-3100 m a.s.l.) in alpine desert of Mt. Kazbek and Mt. Tetnuldi. Nomenclature: Sakhokia and Khutsishvili 1975; Nakhutsrishvili and Gamtsemlidzde 1984)

Species	Frequency	Typical distribution
Tripleurospermum subnivale	420	alpine-nival screes, meadows, moraines
Saxifraga sibirica	408	subalpine-subnival rocks, moraines, screes
Alopecurus glacialis	360	upper alpine meadows - subnival
Poa alpina	252	subalpine-alpine meadows
Antennaria caucasica	232	subalpine-alpine meadows
Saxifraga moschata	202	subalpine-nival rocks, stones
Sibbaldia parviflora	126	subalpine-upper alpine meadows
Erigeron uniflorus	124	alpine-subnival rock, moraines, screes
Saxifraga flagellaris	114	alpine-subnival moraines, stony places
Carex tristis	106	aubalpine-alpine meadows
Sedum tenellum	92	alpine stony places
Festuca supina	88	alpine meadows, screes
Campanula ciliata	82	upper alpine meadows
Colpodium versicolor	76	upper alpine moraines
Delphinium caucasicum	76	subnival stony areas, moraines
Senecio sosnovskyi	70	subalpine-subnival screes, moraines, meadows
Veronica telephiifolia	54	alpine screes
Taraxacum porphyranthum	40	Upper forest-alpine meadows
Alchemilla caucasica	38	alpine meadows
Minuartia oreina	38	upper forest-alpine screes, moraines
Minuartia inamoena	36	alpine screes, moraines
Scrophularia minima	30	Alpine-subnival snowbeds, screes, moraines
Draba siliquosa	26	subalpine-subnival rock, screes, bare soils
Saxifraga juniperifolia	24	subalpine-nival rocks
Tephroseris karjaginii	24	subalpine-nival meadows, screes, moraines
Ziziphora pushkinii	20	subalpine-alpine screes, stony places
Pedicularis condensata	18	upper forest-alpine meadows
Alchemilla sericea	16	upper alpine meadows - subnival
Ziziphora subnivalis	14	Alpine-subnival screes, stony places
Sedum stevenianum	12	alpine rocky and stony places
Senecio taraxacifolius	12	subalpine-subnival rocks, moraines, snowbeds
Alchemilla chlorosericea	10	upper alpine meadows
Anthemis iberica	10	alpine meadows
Potentilla gelida	10	alpine-subnival meadows, screes, moraines

Campanula biebersteiniana	8	upper alpine meadows
Carex dacica	8	alpine meadows
Jurinea filicifolia	8	upper alpine stony meadows
Myosotis alpestris	8	subalpine-alpine meadows
Silene pygmaea	8	upper forest-alpine rocks
Trifolium polyphyllum	8	alpine meadows
Veronica schistosa	8	upper alpine screes
Hieracium sp.	6	upper forest-subalpine meadows
Nardus stricta	6	subalpine-alpine meadows
Trisetum spicatum	4	alpine-subnival screes, dry meadows, moraines
Cerastium undulatifolium	4	subalpine-alpine meadows
Taraxacum stevenii	4	subalpine-alpine meadows
Viola minuta	4	alpine-subnival screes, stony places
Arenaria lychnidea	2	alpine meadows
Botrychium lunaria	2	upper forest-upper alpine
Cirsium obvallatum	2	subalpine-alpine meadows
Daphne glomerata	2	subalpine-alpine meadows, stony areas
Dryopteris oreades	2	upper forest-alpine scrubs, screes
Luzula spicata	2	subalpine-alpine meadows
Minuartia circassica	2	subalpine-alpine meadows, rocks, screes
Saxifraga cartilaginea	2	upper forest-upper alpine rocks, stones
Saxifraga scleropoda	2	alpine rocks, stony places
Veronica gentianoides	2	upper forest-alpine meadows

Discussion

There were not many studies conducted on the relations of rock particles to vegetation in general and, to our knowledge, no such work has been performed in the Caucasus. A few relevant studies can be discussed that depict a following picture: the appearance of patchy vegetation with an abundant skeleton substratum probably generated the perception of the soils of subnival habitats as “primitive”, “weakly developed” shallow soils, which on the maps of the Soviet epoch were shown as “lithogenic bare rocks” and “rock outcrops” (Kunchulia *et al*., 2018; Tielidze, 2019). In Soil Taxonomy (Soil Survey Staff, 1999), soils in lithic subgroups have hard rock within 50 cm of the surface and meet the definition of Lithosols in that they contain abundant coarse fragments and may occur on steep slopes (Bockheim, 2015). It is also important because in recent times degradation processes of mountain soils have intensified because of climate change, unsustainable land use practices (e.g. deforestation and overgrazing) and erosion, which is the biggest contributor (Tsereteli *et al*., 2011; Urushadze *et al*., 2015; Patarkalashvili, 2016). In general, because hillslope processes expose new parental rocks from time to time, soils here remain shallow (Egli and Poulenard, 2016). All these might leave an impression of a subnival habitat as a homogeneously rocky environment. However, our study shows that the rocks can be presented as particles of various sizes with a certain frequency distribution. In particular, our results show that large-sized rock fragments are most abundant and the abundance of the particles declines with their decreasing size. The finest particles are the least abundant, but there is also soil formed under vegetation patches, which covers even smaller areas than the finest particles. Our results also show that certain plants exhibited a clear preference to a certain size of rock particles. While some species *Carex tristis and Sibbaldia parviflora* prefered the substratum covered with soil, others showed affinity to rather larger-sized rock fragments (*Tephroseris karjaginii, Ziziphora puschkinii, Festuca supina, Minuartia inamoena, Saxifraga juniperifolia).* This might suggest relatively higher stress tolerance in these species; actually, there is evidence of such tolerance in *S. juniperifolia* which by some sources is a petrophite commonly occurring on (Nakhutsrishvili and Abdaladze, 2017a) this species exhibits very low but exceptionally stable rate of photosynthesis with rare depressions (Abdaladze, 1998). Intuitively, we expected that most plants would prefer soil-covered patches, but this was not the case. At this stage, our knowledge of eco-physiological peculiarities of the species mentioned above are unknown, and we can only speculate that they are very stress-tolerant species, and that some of them could contribute to biological weathering of the rocks. This obviously is a target for future research.

As we expected, plant abundance was strongly negatively correlated with largest-sized particles. However, the observation that the majority of species and vegetation abundance in general appeared to be most strongly associated with the finest-grained substratum and not with soil, was somewhat unexpected. In other words, the hypothesis that soils would be the most preferable substratum was not supported and, instead, we found that plant abundance correlated most strongly with soilless but fine-grained substratum, while several species preferred rather larger-grained substratum. Again, we lack ecophysiological knowledge to satisfactorily explain this observation, however we can reasonably speculate that a sizable proportion of species found in the subnival belt are adapted to the lack of soils in subnival environments and can establish on soilless rocks. Many authors have reported that soil characteristics and topographical factors also have a significant effect on vegetation formations (Bajer, 2003; Härdtle *et al*., 2005; Xian-Li *et al*., 2008).

It was shown that the patchy vegetation pattern characteristic for subnival habitats of temperate mountains worldwide can be a result of facilitative interactions that produce spatial species associations (Kikvidze *et al.*, 2005; 2011). At the same time, it was shown that species that associate in patches are different from solitary plants that can establish outside of these patches (Butterfield *et al.*, 2013; Cavieres *et al*., 2014; Kikvidze *et al.*, 2015). Site conditions including topographic and soil characteristics as well as local climate conditions have determinant impacts on plant distribution (Davies *et al*., 2007). The differential preference of species for certain sizes of rock particles observed in our study conforms well to these patterns: many species that prefer fine-grained substratum might clump together at such fine-grained spots and form the patches of associated plants provided there are facilitative interactions among them; the species that prefer coarser-grained substrata might establish as solitary plants outside of patches.

Conclusion

Our study describes the size distribution of rock particles in subnival and nival zones of the Central Caucasus mountains, and relates it with the local patterns of plant species distribution. We found that the largest size class (20-60cm) was in a strong negative correlation with smaller classes (0.2-0.6cm, 0.6-2cm and 2-6cm), but correlation was insignificant among the largest fragments (6-20cm) and the soil patches. Multivariate ordination revealed several species with a clear preference for soils (*Carex tristis* and *Sibbaldia parviflora*), while other species preferred mid-sized (20-60cm) rock particles (*Tephroseris karjaginii*, *Ziziphora puschkinii*, *Festuca supina*, *Minuartia inamoena* and *Saxifraga juniperifolia*). Further, *Senecio sosnowskyi* and *Ziziphora subnivalis* tended to colonize large (6-20cm) rock fragments. Overall, our study demonstrates a clear differential preference of species for certain sizes of rock particles that conforms well to the patchy pattern of vegetation typical for subnival habitats: many species that prefer a fine grained substratum might clump together at such fine-grained spots and form the patches of associated plants provided there are facilitative interactions among them; the species that prefer coarser-grained substrata might establish as solitary plants outside of the patches.

Acknowledgments

We are grateful to Ilia State University for financial and technical support of the project. We would also like to especially thank Prof. Emeritus of Ilia State University George Nakhutsrishvili for providing guidance in this project. We wish to thank all our colleagues and especially, Mr. Ilia Akobia, Ms. Shorena Gadilia and Mr. Arsen Bakhia for their help during the field work and all the technicians who assisted us in handling the instruments.

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