



# Do afroalpine plants differ from other alpine plants by their leaf functional traits?

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Manuscript received: 27.04.2023

Review completed: 09.06.2023

Accepted for publication: 14.06.2023

Published online: 16.06.2023

Electronic Appendix: [http://www.geobotanica.ru/bp/2023\\_12\\_02/BP\\_2023\\_12\\_2\\_onipchenko\\_e\\_suppl.xlsx](http://www.geobotanica.ru/bp/2023_12_02/BP_2023_12_2_onipchenko_e_suppl.xlsx)

## ABSTRACT

Afroalpine plants develop under specific climate with great daily fluctuations and weak seasonal dynamics of temperature. Do leaf functional traits of the plants in Mt. Kenya differ from those of temperate plants in NW Caucasus? To answer this question, we conducted a comparative study at the Teleki valley (4000–4500 m a.s.l.), Mt. Kenya, Kenya, and Teberda national park (2600–2900 m a.s.l.), the Caucasus, Russia. We measured leaf area, fresh and dry mass, C, N, P,  $\delta^{13}\text{C}$ ,  $\delta^{15}\text{N}$  and derivative traits (specific leaf area – SLA, leaf dry matter content – LDMC, C:N and N:P ratios) for 48 species at the Teleki valley, and the same traits, except for the  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ , for 141 species in the Teberda national park. The CSR-strategies scores were calculated. We applied the Principal Component Analysis to reveal the main patterns of trait variation. Leaf dry mass of Mt. Kenya alpine plants ranged from 0.27 mg (*Sagina afroalpina*) to 14.0 g (*Dendrosenecio keniodendron*). Leaf area, mass and LDMC of alpine plants in both regions did not differ significantly. The SLA of Mt. Kenya's plants varied about 20-fold: from 2.6 mm<sup>2</sup> mg<sup>-1</sup> (*Festuca pilgeri*) to 39.8 mm<sup>2</sup> mg<sup>-1</sup> (*Cineraria deltoidea*), and Caucasian plants had higher SLA. N and P leaf concentrations were higher, but C lower in Caucasian plants than in Kenyan. Leaf N:P ratio was similar for both regions, while C:N ratio was higher in Kenyan plants. Species of “rosette” trees (*Dendrosenecio* spp.) differed from other species by size characteristics (maximal leaf dry mass and area were in *Dendrosenecio keniodendron*), as well as correspondingly higher investment to mechanical tissues (high C:N ratio, low SLA). By the other functional traits, “rosette” trees were similar to many other alpine plants. Thus, afroalpine plants of Mt. Kenya are close to temperate alpine plants by some leaf functional traits, but possess higher stress-tolerance.

**Keywords:** afroalpine, plant functional traits, CSR-strategies, Kenya, Caucasus, leaf area, specific leaf area, plant nutrient content

## РЕЗЮМЕ

**Онипченко В.Г., Кипкеев А.М., Копылова Н.А., Ниага Дж.М., Елумеева Т.Г., Дудова К.В., Ахметжанова А.А., Тиунов А.В., Карпукхин М.М., Макаров М.И. Отличаются ли афро-альпийские растения по своим функциональным признакам от других альпийских растений? Афро-альпийские растения развиваются в условиях специфического климата с большими суточными флуктуациями и слабой сезонной динамикой температуры. Отличаются ли функциональные признаки листьев растений с горы Кения от признаков растений умеренного климата на северо-западном Кавказе? Чтобы ответить на этот вопрос, мы провели сравнительное исследование в долине Телеки (4000–4500 м н.у.м.), гора Кения, Кения, и в Тебердинском национальном парке (2600–2900 м н.у.м.), Кавказ, Россия. Мы измерили площадь листа, влажную и сухую массу, C, N, P,  $\delta^{13}\text{C}$ ,  $\delta^{15}\text{N}$  и расчетные величины (удельная листовая поверхность – УЛП, содержание сухого вещества – ССВ, отношения C:N и N:P) для 48 видов в долине Телеки и те же самые признаки, кроме  $\delta^{13}\text{C}$  и  $\delta^{15}\text{N}$ , для 141 вида в Тебердинском национальном парке. Также были рассчитан вклад CSR-стратегий. Чтобы выявить основные закономерности изменчивости признаков, мы провели анализ главных компонент. Масса сухого листа альпийских растений с горы Кения варьировалась от 0,27 мг (*Sagina afroalpina*) до 14,0 г (*Dendrosenecio keniodendron*). Площадь листа, масса и ССВ альпийских растений в обоих регионах значимо не различались. У растений с г. Кения УЛП варьировалось почти в 20 раз: от 2,6 мм<sup>2</sup> мг<sup>-1</sup> (*Festuca pilgeri*) до 39,8 мм<sup>2</sup> мг<sup>-1</sup> (*Cineraria deltoidea*), при этом у растений Кавказа УЛП была выше. У кавказских растений содержание N и P в листьях было выше, а содержание C ниже, чем в кенийских. Отношение N:P было сходно в обоих регионах, тогда как отношение C:N было выше у растений из Кении. Виды «розеточных деревьев» (*Dendrosenecio* spp.) отличались от других видов размерными характеристиками (максимальная площадь и масса сухого листа отмечены у *Dendrosenecio keniodendron*), а также соответствующим высоким вкладом в механические ткани (высокое отношение C:N, низкая УЛП). По остальным функциональным признакам «розеточные деревья» были схожи со многими другими альпийскими растениями. Таким образом, по ряду функциональных признаков листьев афро-альпийские растения с г. Кения близки ко многим другим альпийским растениям умеренной зоны, но обладают большей стресс-толерантностью.**

**Ключевые слова:** афро-альпийские растения, функциональные признаки, CSR-стратегии, Кения, Кавказ, площадь листа, удельная листовая поверхность, содержание элементов минерального питания

Structural and chemical leaf functional traits change consistently with climate, and temperature is one of the most important factors (Joswig et al. 2022). Global temperature gradient corresponds with latitudinal and altitudinal gradients. Often traits change in the same direction with elevation and from equator to polar regions; it is mostly linked with the decrease of mean annual temperature. For example, with the increase of latitude and often of elevation, there is an increase in leaf N and P contents (Körner 2003, Reich & Oleksyn 2004, Han et al. 2005, Song et al. 2012, Kichenin 2013, Yang et al. 2015, Dvorský et al. 2016, but see Craine & Li 2003 and Zhao et al. 2014 for opposite elevation gradient of N and P), and decrease in leaf size (Körner 2003, Kichenin et al. 2013, Wright et al. 2017) and their carbon content (Bloom et al. 2016, Doležal et al. 2016), though some exceptions are also reported (Zhao et al. 2014). Changes in other functional traits are not so consistent and have opposite tendencies in different studies. These traits are leaf C:N ratio (Zhao et al. 2014, Yang et al. 2015; Callis-Deuehl et al. 2017) and N:P ratio (De Long et al. 2016, Reich & Oleksyn 2004, Han et al. 2005, Fischer et al. 2013, Zhao et al. 2014) and leaf dry matter content (Körner et al. 1989, Halloy & Mark 1996, Kichenin et al. 2013, Doležal 2016). Specific leaf area (SLA) usually decreases with elevation (Körner et al. 1989, Prock & Körner 1996, Callis-Deuehl et al. 2017), but shows different directions along the latitudinal gradient (De Frenne et al. 2013, Hulshof et al. 2013). The opposite tendencies are shown for heavy isotope content ( $\delta^{13}\text{C}$ ,  $\delta^{15}\text{N}$ ).  $\delta^{13}\text{C}$  usually increases with elevation (Zhu et al. 2010, Zhou et al. 2011, Dvorský et al. 2016, but see Körner 2011) due to decrease in atmospheric pressure, and  $\delta^{15}\text{N}$  decreases (Huber et al. 2007, Laiolo et al. 2015, Zhou et al. 2016).

The changes in contribution of Grime's CSR-strategies (Grime 1979), estimated by leaf functional traits (Pierce et al. 2017) along latitudinal and altitudinal gradients in alpine communities are poorly investigated. Only the enhancement of stress-tolerance associated traits with elevation have been reported (Grime 2001, Pierce et al. 2007, de Bello et al. 2013).

Functional traits of tropical alpine plants are not well studied. While some information are available for south American paramo (Andes) (Körner et al. 1989, Cabrera & Duivenvoorden 2020, Cruz & Lasso 2021), but functional traits of afroalpine plants are poorly studied (Kattge et al. 2011, 2020).

Climate of equatorial tropical high mountains is very peculiar. Here generally low mean daily temperatures combine with almost no seasonality (except of alternation of more or less wet seasons) and high diurnal amplitude of temperatures, which can decrease below 0°C at night throughout the year (Hemp 2006, Anthelme & Dangles 2012). Tropical high mountains are very specific by their composition of plant life forms. Under such conditions “rosette” trees (*Dendrosenecio*, *Lobelia* spp.) with the height of 3–5 m and rather big leaves prevail (Rehder et al. 1988, Mizuno & Fujita 2014, Zhou et al. 2018), but many herbaceous alpine plants are present as well. Afroalpine regions are of rather low floristic richness due to relatively low age and isolation of separate mountain areas (Onipchenko et al. 2020b).

We made a case study of leaf functional traits in two regions – afroalpine area on Mt. Kenya (tropical equatorial, Kenya) and alpine area in Teberda (temperate zone, the Northwest Caucasus, Russia). We hypothesize that: (1) Differences in leaf trait values between the two alpine regions correspond to global latitudinal gradient, i.e. leaves of afroalpine plants are larger, poorer in N and P, but have smaller SLA than leaves from temperate alpine areas. (2) Specific life forms (“rosette” trees) differ by leaf traits from alpine herbaceous plants.

## MATERIAL AND METHODS

We studied morphological (size – mass and area, specific leaf area [SLA]) and chemical (dry matter content [LDMC], C, N and P content,  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values) leaf traits of afroalpine plant species in the upper part of Teleki valley (western macroslope of Mount Kenya) and temperate alpine plant species in Teberda National Park (the Northwest Caucasus).

### Study site

The studied Teleki valley is close to equator (00°10'S 37°18'E). Mount Kenya is of volcanic origin, and the maximal uplift occurred ca. 2.6 mln years ago (Gehrke & Linder 2014). Rocks of the volcanic massif consist of basalt, phonolite, kenytes, agglomerates, trachyte and syenite (Mahaney 1990, Bhatt 1991). Alpine soils are structureless, with a lot of stones, carbon content in fine fraction is 7–10 % and pH of 4.9–5.1 (Coe 1967). Two mixed soil samples (0–10 cm) of Mt. Kenya were studied within typical *Dendrosenecio* plots of the studied site (M. Zobel, personal communication) at 4195 m above sea level at south slope, 25° steepness. They had total soil C about 14 %, total soil N 0.77–0.93 %, Mehlich III extractable P 25–55 mg/kg, K 568–584 mg/kg, Ca 2400–3400 mg/kg, Mg 357–360 mg/kg.

The annual mean temperature at 4191 m a.s.l. is 1.7°C (Coe 1967). At Mount Kenya there are two wet seasons and two dry seasons as a result of the monsoon. From mid-March to June and from October to December the mountain receives approximately a 5/6th of the annual precipitation (900–2500 mm per year) (Hedberg 1964, Coe 1967).

Flora of the Mt. Kenya alpine area is relatively poor (Hedberg 1964) due to isolated restricted area of high mountain as well as  $\alpha$ -diversity of alpine communities (Onipchenko et al. 2020b). We collected 48 species growing at the altitude of 4000–4500 m, above the treeline on different mesorelief forms (bottom of valleys, slopes, ridges). The studied species represented near all available species of the area which can be collected during field trip. The list of studied species included dominants as well as relatively rare plants (Appendix S1). These plants belonged to three types of communities described in Zhou et al. (2018): upper part of Heath zone (4000–4200 m, typical species *Alchemilla argyrophylla*, *Erica arborea*), Afro-alpine zone (3400–4800 m, *Carduus keniensis*, *Dendrosenecio keniendendron*, *Dendrosenecio keniensis*, *Lobelia telekii*), and Nival zone (4400–5000 m, *Arabis alpina*, *Senecio purtschelleri*, *Valeriana kilimandscharica*). All nomenclature is given according POWO (2023).

The study area in the NW Caucasus is located in the Teberda National Park (Karachaevo-Cherkessian Republic,

the Northwestern Caucasus, Russia) in the alpine belt of the mountains near Mt. Malaya Khatipara (43°27'N 41°41'E). The climate of the alpine belt here is a mountain climate of the temperate zone. The mean annual temperature is about -1.2°C and the mean annual precipitation is about 1400 mm (see Onipchenko 2004 for detailed description). Soils are Umbric Leptosols (Malysheva et al. 2004). The range of nutrient concentrations for alpine soils of studied siliceous area of Teberda national park includes measured values for the Mt. Kenya (Onipchenko 2004). So there are no principal differences in alpine soil between the studied regions.

We collected 141 species of the most common plants at elevation range 2600–2900 m above sea level. They build more than 90 % aboveground biomass in most widespread alpine plant communities of the area (Onipchenko 2004). Few results for 75 Caucasian plant leaf traits and strategies were published earlier (Onipchenko et al. 2020a).

### Field and laboratory methods

Plant functional traits on Mt. Kenya were studied according to recommended protocols (Cornelissen et al. 2003, Pérez-Harguindeguy et al. 2013). We collected 12 leaf samples per species, each sample had either one leaf or 2–5 leaves from a single plant in case of small leaves (*Erica* etc.). We selected mature leaves from different individuals without signs of herbivore or plant pathogen damages. Leaves were placed in plastic bags with water and kept in fridge (+3° – +5°C) for 1–3 days for full water saturation. Water saturated leaves were weighted and scanned to estimate leaf area. Then they were dried in a drying oven (80° for 24 hours) and weighted to determine dry mass. Specific leaf area and LDMC were calculated using these data.

We used five samples per species to measure C, N and P content. For P content determination plant samples were decomposed with a mixture of HNO<sub>3</sub> and H<sub>2</sub>O<sub>2</sub> (7:1) in a Milestone ETHOS D microwave oven. Phosphorus concentration was measured using an optical emission spectrometer with inductively coupled plasma (ICP-OES). Total C, N and natural <sup>13</sup>C, <sup>15</sup>N abundance of plant samples were determined by dry combustion using a Thermo Flash 1112 elemental analyzer coupled with a Thermo Delta V Plus continuous-flow isotope ratio mass spectrometer in the joint usage center of the A.N. Severtsov Institute of Ecology and Evolution RAS, Moscow. <sup>13</sup>C and <sup>15</sup>N abundance were expressed in the conventional δ-notation (in ‰) relative to international standards (PDB and atmospheric N<sub>2</sub> for <sup>13</sup>C and <sup>15</sup>N, respectively). We used mean values of functional traits for each species.

Leaf traits of alpine plants in the Caucasus were studied by the authors using the same methods, except δ<sup>13</sup>C and δ<sup>15</sup>N, which were not determined for the Caucasian plants. The Caucasian data were earlier included into TRY data base (Kattge et al. 2020).

### Statistics and strategies

To calculate relative contribution of Grime's CSR strategies we used StrateFy calculator (Pierce et al. 2017) based on three leaf functional traits: wet and dry mass and leaf area.

To reveal trait variation of Mt. Kenya and Caucasus plants we ran principal component ordination (PCA) in the vegan package in R (Oksanen et al. 2020). Prior to the ordination, the leaf traits were transformed to comply with normality assumptions. Leaf area was standardized by maximum value and the square root was calculated, LDMC was logit-transformed, and SLA was log-transformed (Pierce et al. 2017). The C, N and P content as well as C:N and N:P ratios were log-transformed. Leaf fresh mass and dry mass were not included in the PCA ordination due to their strong correlation with leaf area and collinearity along all main ordination axes. Spearman's correlation coefficients of traits were calculated with the three first ordination axes.

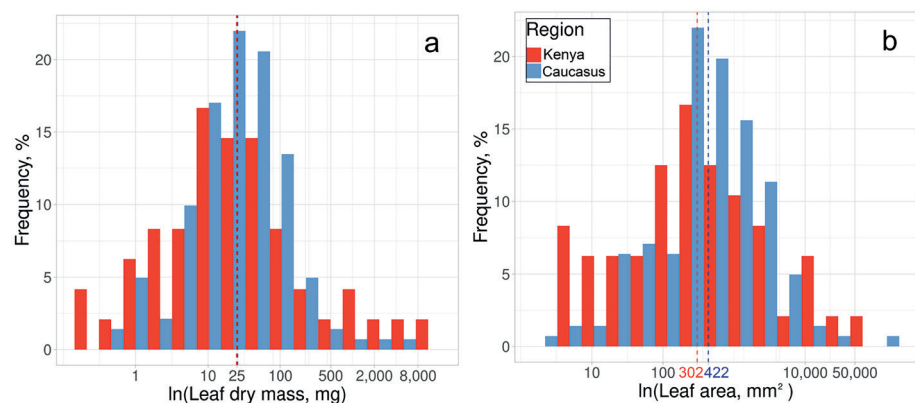
Median values of traits and strategies for Mt. Kenya and Caucasian plants were compared by non-parametric Mann–Whitney U test and descriptive statistics (mean, standard error, interquartile range, median, minimum and maximum) of trait's values were calculated.

### RESULTS

Leaf dry mass of Mt. Kenya alpine plants ranged from 0.27 mg (*Sagina afroalpina*) to 14.0 g (*Dendrosenecio keniodendron*). Distribution was log-normal, and the mean (546±314 mg, Mean±SE) was considerably higher than median (25 mg), with coefficient of variation (CV) of 398 % (Fig. 1a). The similar pattern was observed for leaf area: minimal size was 3.8 mm<sup>2</sup> (*Erica filago*), maximal size was 702 cm<sup>2</sup> (*Dendrosenecio keniodendron*), mean size was 35.6±16.2 cm<sup>2</sup>, median – 302 cm<sup>2</sup>, CV – 315 % (Fig. 1b).

Distributions of size traits (area and mass) of alpine plant leaves of Mt. Kenya and the Caucasus had a similar medians and did not differ significantly (Mann-Whitney U test p>0.05).

Leaf dry matter content varied among Mt. Kenya alpine plants more than ten-fold: from 5.3 % (succulent *Sedum ruwenzoriense*) to 61.1 % (*Festuca pilgeri*). The trait distribution between species was normal with similar mean (26.5 %) and median (23.6 %) values and relatively low CV (43 %).

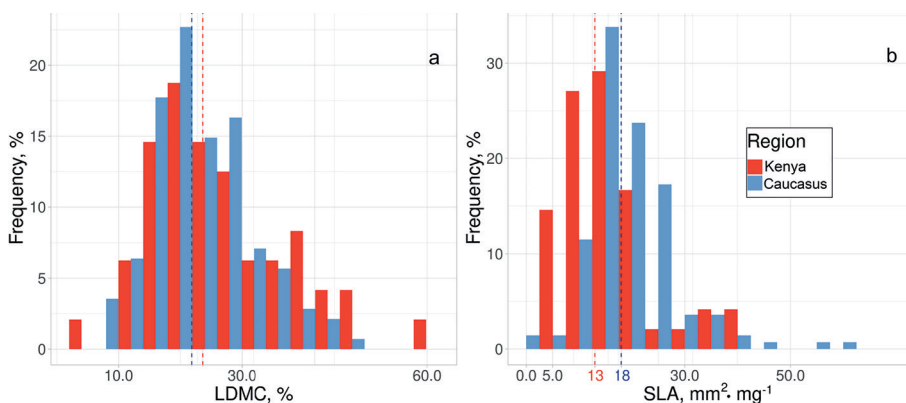


**Figure 1** Frequency distribution of leaf dry mass (a) and leaf area (b) of Kenyan (n=48, red) and Caucasian (n=141, blue) alpine plant species. Dotted lines show median values. P-values of Mann-Whitney U-test are 0.52 and 0.17 for leaf mass and area correspondingly (not significant)

There were no significant differences in LDMC between median values for alpine plants in Mt. Kenya and the Caucasus (Mann-Whitney U-test,  $p=0.084$ , Fig. 2a).

Specific leaf area for Mt. Kenya's alpine plants varied about 20-fold: from  $2.6 \text{ mm}^2\cdot\text{mg}^{-1}$  (*Festuca pilgeri*) to  $39.8 \text{ mm}^2\cdot\text{mg}^{-1}$  (*Cineraria deltoidea*). Species with lower SLA are more frequent, median is slightly less than mean ( $13.0$  and  $15.2 \text{ mm}^2\cdot\text{mg}^{-1}$  correspondingly). Caucasian plants had significantly higher SLA than Kenyan, but the distributions are similar with longer right tails (small number of high values) (Fig. 2b).

Leaf C content slightly varied among species (min  $40.5\%$  in *Arabis alpina*, max  $57.2\%$  in *Erica filago*, mean  $46.5\pm 0.5\%$ )



**Figure 2** Frequency distribution of leaf dry matter content (a) and specific leaf area (b) of Kenyan ( $n=48$ , red) and Caucasian ( $n=141$ , blue) alpine plant species. Dotted lines show median values.  $P$ -values of Mann-Whitney U-test are  $0.084$  and  $<0.001$  for LDMC and SLA correspondingly

(Fig. 3c). Leaf N content varied from  $0.71\%$  (*Festuca pilgeri*) to  $3.84\%$  (*Cardamine obliqua*). Species with lower N were more frequent, median was slightly less than mean ( $1.93\%$  and  $2.04\%$  correspondingly). Leaf P varied from  $0.06\%$  (*Erica arborea*) to  $0.39\%$  (*Heracleum elgonense*) with mean  $0.175\pm 0.010\%$ . N and P leaf concentrations were significantly higher, but C lower for Caucasian plants in comparison with Kenyan. Leaf N:P ratio was similar for both regions in contrast to C:N ratio, which was higher for Kenyan plants (Table 1).

The  $\delta^{13}\text{C}$  values varied from  $-30.8\%$  (*Cineraria deltoidea*) to  $-24.9\%$  (*Ranunculus oreophytus*) with mean and median values of  $-27.2\%$  and  $-27.1\%$  respectively. The  $\delta^{15}\text{N}$  values were very variable with minimum of  $-5.8\%$  in *Alchemilla johnstonii* and maximum of  $+7.8\%$  in *Pentameris minor*. Here mean value ( $-0.7\%$ ) was higher than median ( $-1.0\%$ ).

The contributions of CSR-strategies strongly varied, however stress-tolerance on average prevailed ( $55.7\%$ ) and ranged from  $0\%$  in *Arabis alpina* and *Crepis dianthoseris* to  $100\%$  in *Agrostis trachyphylla* and *Erica arborea*. Ruderal strategy was less expressed with mean contribution value  $23.1\%$  and ranged from  $0\%$  (for example, in *Alchemilla argrophylla* or *Festuca pilgeri*) to  $83.7\%$  in *Arabis alpina*. Competitive

**Table 1.** Comparison of leaf functional traits between Mt. Kenyan ( $n=48$ ) and Caucasian ( $n=141$ ) alpine plant species. LDMC – leaf dry matter content, SLA – specific leaf area. SE – standard error, IQR - Interquartile range.  $P$ -values are obtained from non-parametric Mann-Whitney U-test.

Trait	Region	Mean	SE	IQR	Median	Min	Max	$p$ -value
<b>Chemical traits</b>								
Carbon, %	Kenya	46.47	0.48	3.01	46.1	40.5	57.2	0.006
	Caucasus	45.37	0.16	1.93	45.2	38.0	52.6	
Nitrogen, %	Kenya	2.04	0.10	0.71	1.9	0.71	3.84	$<0.001$
	Caucasus	2.70	0.07	0.93	2.6	1.20	5.87	
Phosphorus, ppm	Kenya	1751	102	487	1635	596	3911	$<0.001$
	Caucasus	2333	73	1011	2207	821	5273	
C:N	Kenya	25.7	1.6	9.4	23.6	10.6	66.0	$<0.001$
	Caucasus	18.4	0.5	6.0	17.4	8.0	42.5	
N:P	Kenya	12.3	0.4	4.1	11.8	6.8	21.1	0.849
	Caucasus	12.1	0.2	2.9	11.9	5.1	23.7	
<b>Structural traits</b>								
LDMC, %	Kenya	26.5	1.6	15.8	23.6	5.24	61.1	0.084
	Caucasus	23.0	0.7	10.9	21.8	6.02	46.1	
SLA, $\text{mm}^2/\text{mg}$	Kenya	15.2	1.3	11.2	13.0	2.56	39.8	$<0.001$
	Caucasus	20.1	0.7	9.1	18.5	4.94	59.7	
<b>Size traits</b>								
Leaf area, $\text{mm}^2$	Kenya	3560	1620	1200	302	3.77	70193	0.173
	Caucasus	2525	1025	1015	422	3.00	128141	
Dry mass, mg	Kenya	546	314	81	25	0.27	14042	0.524
	Caucasus	104	37	57	25	0.30	4624	
<b>CSR strategies</b>								
C, %	Kenya	21.3	2.9	31.7	18.1	0.0	75.1	0.093
	Caucasus	25.7	1.6	26.4	23.1	0.0	87.3	
S, %	Kenya	55.7	4.4	45.8	57.0	0.0	100	$<0.001$
	Caucasus	36.8	2.5	53.2	34.6	0.0	100	
R, %	Kenya	23.1	3.6	34.2	17.2	0.0	83.7	$<0.001$
	Caucasus	37.5	1.9	32.4	35.4	0.0	99.3	

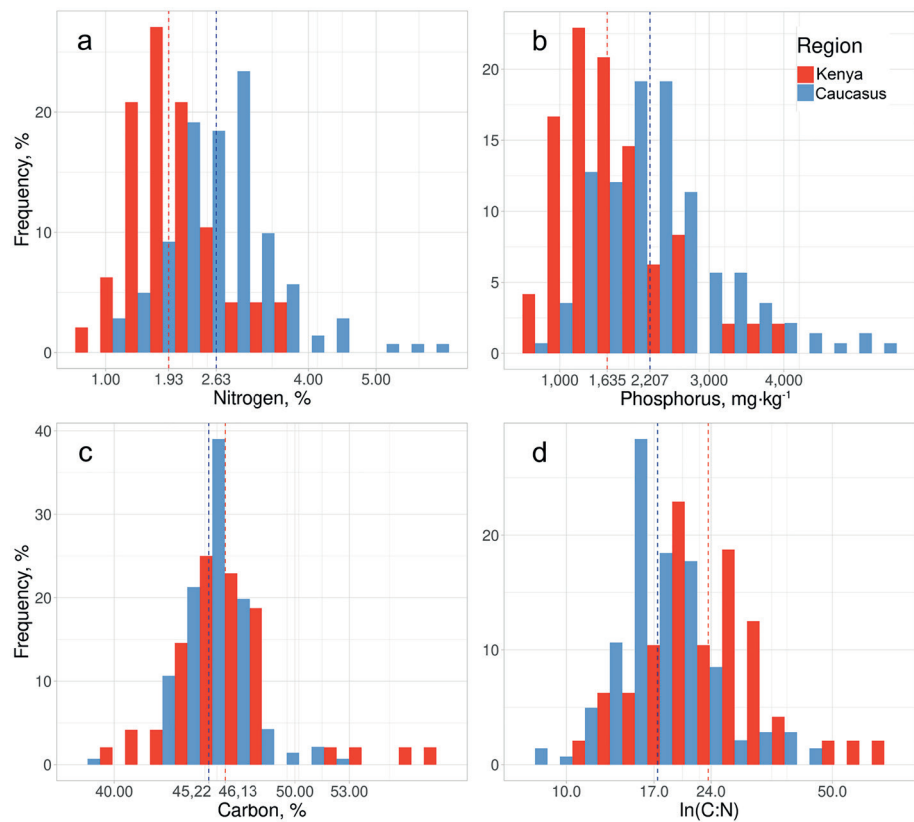
strategy on average contributed 21.3 % and ranged from 0 % (for example, in *Avenella flexuosa* or *Helichrysum brownei*) to 75.1 % in *Heracleum elgonense*. The main dominant of the afroalpine vegetation in Mt. Kenya, *Dendrosenecio keniodendron*, had C/CS strategy of 60.6 % C and 39.4 % S.

As a whole, Caucasian alpine plants had similar to Mt Kenya plants C impact, according to Mann-Whitney U they had significantly lower S (mean 36.8 %) and higher R (mean 37.5 %) impacts (Table 1, Fig. 4).

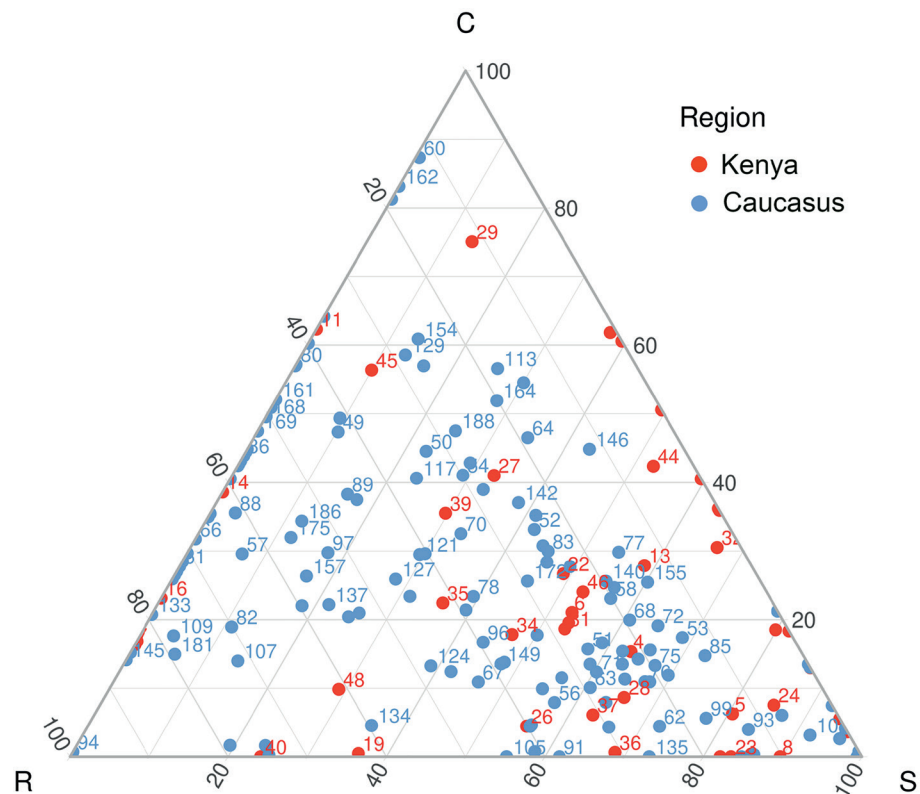
Alpine species of Mt. Kenya and the Caucasus were considerably mixed in the space of functional traits in the ordination diagram (Fig. 5). The three first PCA axes accounted for 78 % of variance (48.6, 16.5 and 12.9, respectively). We used three axes because the third axis accounts for significant variation (>10 %) and better separates plants according their leaf size traits.

In afroalpine communities, a life form of “rosette” tree is mostly represented by species of *Dendrosenecio*, as well as several species of *Lobelia*. The species of *Lobelia* do not differ from other plants by their traits (Fig. 5), but species of *Dendrosenecio* form a separate cluster in the ordination diagram. This reflects their size characteristics (among the studied afroalpine species, the maximal leaf dry mass and area are in *Dendrosenecio keniodendron*), as well as correspondingly higher investment to mechanical tissues (high C:N ratio, low SLA). By other functional traits these species do not differ considerably from many other alpine plants.

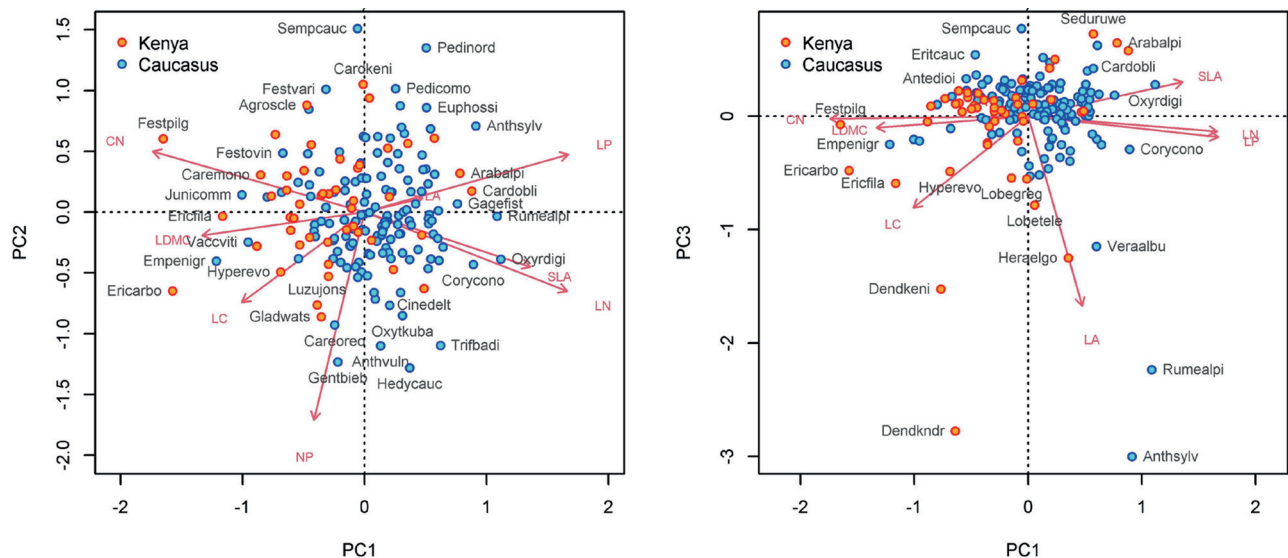
The first ordination axis was positively correlated (at  $p < 0.001$ ) with SLA, leaf N and P content and negatively with leaf C:N ratio, thus reflected “leaf economic spectrum” (Fig. 5a, b). One edge corresponded to species with S-strategy (*Festuca pilgeri*, *Erica arborea*, *Erica filago*, *Empetrum nigrum*, *Vaccinium vitis-idaea*), and



**Figure 3** Frequency distribution of leaf nitrogen content, % (a), leaf phosphorus content, ppm (b), leaf carbon content, % (c) and C:N ratio (d) of Kenyan (n=48, red) and Caucasian (n=141, blue) alpine plant species. Dotted lines show median values. P-values of Mann-Whitney U-test are <0.001, <0.006 and <0.001 for N, P, C and C:N correspondingly



**Figure 4** Triangular Grime's ordination of alpine species strategies. C – competitors, S – stress-tolerators, R – ruderals. Numbers correspond to species numbers in the Appendix S1



**Figure 5** The PCA ordination of alpine species according to leaf functional traits: a) projection to the first and second axes, b) projection to the first and the third axes. LA – leaf area, SLA – specific leaf area, LDMC – leaf dry matter content, LN – leaf nitrogen content, LC – leaf carbon content, CN – C:N ratio, N:P – NP ratio. The names are shown only for species at the edges of axes and abbreviated by the first four characters of genus and species Latin names (Appendix S1). PC1 explains 48.6 % of variance, PC2 – 16.5 %, and PC3 – 12.9 %

the other edge included species with high SLA and leaf nutrient content both with prevail of R (*Cardamine obliqua*, *Arabis alpina*, *Oxyria digyna*) and C strategies (*Rumex alpinus*). The second ordination axis was negatively correlated with N:P ratio (Fig. 5a). N-fixing legumes grouped at higher N:P values (*Anthyllis vulneraria*, *Hedysarum caucasicum*, *Trifolium badium*, *Oxytropis kabanensis*). The third PCA axis reflected leaf size (Fig. 5b). Among the species with big leaves, “rosette” trees from Kenya (*Dendrosenecio keniensis* and *D. keniodendron*) were shifted to edge of the first axis reflecting nutrient conservative traits, while Caucasian subalpine tallherbs *Anthriscus sylvestris* and *Rumex alpinus* occupied nutrient acquisitive edge.

## DISCUSSION

Our first hypothesis was generally supported: Mt Kenya afroalpine plants differ from Caucasian alpine temperate plants according to general latitudinal gradient, their leaves have more “conservative” traits (Westoby 1998) with lower SLA, N and P contents and more C. Stress-tolerant strategy was more expressed and ruderal strategy was less expressed in afroalpine plants in comparison with temperate alpine plants.

Afroalpine species do not differ from Caucasian alpine plants by size traits (mass and area). Their mean values considerably exceed, for example, those in high alpine forb species in the Alps (leaf area 90 mm<sup>2</sup>, Körner et al. 1989) and alpine meadows of Qinghai-Tibetan plateau (240 mm<sup>2</sup>, at about 3900 m a.s.l., measured by the same methods, Elumeeva et al. 2015). Lower values in these cases are caused by the lack of relatively large leaved species in samples and the significant cattle grazing in Tibet and the Alps. On the other side, plants of Paramo (Eastern Andes, Colombia, Cruz & Lasso 2021) have smaller mean leaf area than studied afroalpine plants (2670 mm<sup>2</sup> versus 3560 mm<sup>2</sup>), may be due to lower precipitation and higher water deficit. The studied plants of Mt. Kenya and the Caucasus grow at the reserved areas without livestock grazing. It suggests that

size leaf traits of alpine plants depend on the latitudinal position of mountains at low extent.

The LDMC varied significantly among Kenya alpine plants, but median value is very similar to temperate alpine plants in the Caucasus (at elevation of 2600–2900 m a.s.l.). Observations in the other mountain systems show similar or contradictory patterns (Körner et al. 1989, Halloy & Mark 1996, Kichenin et al. 2013, Doležal et al. 2016, Dvorsky et al. 2016). So we cannot determine latitude gradient of LDMC. It seems that other factors (e.g. humidity) may be more important for this trait. For drier tropical Andes, mean LDMC is significantly higher (38.8%) than for other alpine areas (Cruz & Lasso 2021).

The other pattern is suggested for SLA. Median value of this trait for Kenya’s plants is lower than for temperate Caucasus (13 and 18 mm<sup>2</sup>·mg<sup>-1</sup> correspondingly). The last value is very close to mean value 18.9 mm<sup>2</sup>·mg<sup>-1</sup> obtained by Körner et al. (1989) for high alpine forbs in European Alps. It was shown several times that SLA decreases with elevation and latitude (Prock & Körner 1996, Hulshof et al. 2013, Callis-Deueh et al. 2017, but see De Frenne et al. 2013 for cultivated plants) and our results support this tendency. Even less mean values (11.5 mm<sup>2</sup>·mg<sup>-1</sup> – Cabrera & Duivenvoorden 2020; 6.9 mm<sup>2</sup>·mg<sup>-1</sup> – Cruz & Lasso 2021) were shown for tropical Andes. So, afroalpine plants have relatively harder leaves in comparison with temperate alpine plants.

Leaf N of afroalpine plants is lower, but C and C:N higher than those for temperate (Caucasus) alpine plants. Similar to Caucasus, mean values for N and C contents were reported for a wide set (more than 240 species) of alpine plants in European Alps (Körner et al. 2016). So we can suggest that according to their leaf traits, afroalpine plants have more “conservative” strategy (according Westoby 1998) than temperate ones. This pattern completely reflects latitudinal gradients, where often the N content increases and the C content decreases from low to high latitudes (Reich & Oleksyn 2004, Han et al. 2005, Bloom et al. 2016).

On the other hand, various changes of these traits were observed along altitudinal gradients. For example, leaf N content may either increase with elevation (Körner 2003, Song et al. 2012, Kichenin et al. 2013) or decrease (Craine & Li 2003, Zhao et al. 2014). Our data set suggests rather stronger impact of latitudinal than altitudinal patterns, possibly because the higher relative input of carbon to leaf tissues in plants of tropical mountains is linked with their long life span, roughness and low attractiveness for herbivores (Körner 2003). Leaves of Paramo's plants have much less N and P contents (1.5 % and 1100 ppm correspondingly, Cruz & Lasso 2021) even in comparison with studied afroalpine plants.

Median carbon heavy isotope content ( $\delta^{13}\text{C}$  value) in leaves of afroalpine plants was very similar to that of European alpine plants (Körner et al. 2016):  $-27\text{‰}$  and  $-28\text{‰}$  correspondingly. These values are typical for C3 plants, because both the regions contain few species with CAM photosynthesis, and the role of C4 plants, which prevail in African savannas, decreases to zero in afroalpine vegetation (Tieszen et al. 1979). A similar value of  $\delta^{13}\text{C}$  ( $-26.3\text{‰}$ ) was reported in high (elevation range 2,954–5,269 m a.s.l.) mountains of Tibet (Zhou et al. 2011). Because in C3 plants  $\delta^{13}\text{C}$  generally is an indicator of water stress and limitations in stomatal conductance (Farquhar et al. 1982) and depends on the temperatures and precipitation (Zhou et al. 2011), we suppose that in plants of humid high mountain zone, both in temperate and tropical climate, water relations and gas exchange are similar.

On the contrary,  $\delta^{15}\text{N}$  values differed considerably in tropical and temperate mountains. In our case median  $\delta^{15}\text{N}$  value was considerably higher (mean  $-1.0\text{‰}$ ), than, for example, that in the European Alps ( $-2.3\text{‰}$ , Körner et al. 2016) or  $\delta^{15}\text{N}$  for non-fixing alpine forbs in the Caucasus ( $-2.2\text{‰}$ , Makarov et al. 2014). Soil and plant  $^{15}\text{N}$ -enrichment in tropics are significantly higher than in temperate regions (Martinelli et al. 1999) due to more open and intensive nitrogen cycle. So, for this trait we can suggest important influence of latitudinal position. A range of  $\delta^{15}\text{N}$  values in our dataset (about  $13.5\text{‰}$ ) was similar to that reported for plants growing at corresponding mean annual temperatures (Craine et al. 2009).

The P content also supports the principal role of latitudinal gradient, because despite of the P increases with elevation in several mountains (Kichenin et al. 2013, Yang et al. 2015, Dvorský et al. 2016), the main global pattern is the P decrease from polar regions to the tropics (Reich & Oleksyn 2004, Han et al. 2005). We also observed on average lower P content in alpine plants of Mt. Kenya in comparison to alpine plants of the Caucasus.

General tendency for more stress-tolerance strategy of afroalpine plants was supported in ordination diagram (Fig. 5) where for the first axis plants from Mt. Kenya are mainly on the left side, but Caucasian plants on the right side. We can suggest that general stress is more important in alpine tropical area due to near every night frost. So the plants have no possibility to grow at nights (Körner 2003). It is interesting to note, that in our study the third ordination axis separates plants with large leaves (C-strategy). Similarly, C-strategy was separated from R-strategy by the third axis

of PCA ordination for Sheffield flora (Grime et al. 1997). Strategy spectrum in Paramo is much more stress-tolerant (C:S:R 24.8:73.1:2.1, Cruz & Lasso 2021). So, in general, afroalpine and Paramo plants support our hypothesis that leaves of tropical alpine plants are larger, poorer of N and P, but have lower SLA than leaves from temperate alpine areas and have more expressed stress-tolerant strategy.

In tropical high mountains often prevails the specific plant life form, "rosette" trees, or giant rosettes (Rundel et al. 1994). We obtained that only two species *Dendrosenecio* in studied afroalpine communities form a separate cluster in the ordination diagram due to their size characteristics and higher investment to mechanical tissues (high C:N ratio, low SLA), but not other traits. In temperate mountains a range of species also have rather large leaves (for example, *Anthriscus sylvestris*), but due to lower leaf life span of alpine plants in the temperate zone (Diemer et al. 1992), these plants invest less to defensive and mechanical structures, they have higher SLA and lower C:N values of leaf tissues. This partly supports our second hypothesis: the specificity of leaves of "rosette" trees is linked with their high mass and area combined with strong development of mechanical tissues, reflected in low SLA and high C:N ratio.

## CONCLUSIONS

Generally, leaf functional trait values of high mountain plants of Mt. Kenya are close to those of temperate alpine plants, but possess higher stress-tolerance, lower SLA, N and P contents, higher C and 15N.

## ACKNOWLEDGEMENTS

VO, TE, AA, KD, MM were supported by Russian Science Foundation (project 19-14-00038p).

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