

THE EFFECTS OF HABITAT DEGRADATION ON PHENOLOGY AND REPRODUCTION OF SOME SPECIES OF GENUS *PRIMULA* L.

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Abstract

Habitat degradation can significantly affect plant reproductive success. Genus *Primula* (Primulaceae; Primrose) depend on temperature and relative humidity of environmental factors. Some species of genus *Primula* flower before the forest starts leafing. Other species grow in subalpine and alpine meadows. The elevation range of studied habitats of *Primula* species in the Greater and East Caucasus is between 400 to 3000 meters: *P. woronowii* Losinsk. Grows in oak-hornbeam forests (400-1000 m); *P. macrocalyx* Bunge - in beech forest (900-1700 m); *P. auriculata* L. in subalpine wet meadows (1800-2300 m); *P. cordifolia* Rupr. in subalpine meadows (1800-2300 m). *P. amoena* M. Bieb. grows in two different habitats: subalpine birch forest (1800-2300 m) and subalpine and alpine meadows (2300-2800 m); *P. algida* Adams occurs in subalpine and alpine meadows (2300-3000 m). Seed production of two species (*P. amoena* and *P. woronowii*) were determined. We have calculated sky exposure. As a result reproductive effort of early flowering forest species of *Primula* shows close correlation to microclimatic conditions determined by sky exposition. In case of *P. woronowii* the limit index of sky exposition is 5%, below which the species does not develop flowers. Global climate change can cause shifts in "spring index" in forests and will change duration of phenological phases of *Primula* in shadow habitat. This will influence reproductive success of the species and determine the chances of its survival and propagation.

Key words: *Primula*; Habitat degradation; Sky exposition; Phenological phases; Plant reproduction.

Introduction

From the territory of Georgia (South Caucasus) 22 species of the genus *Primula* (Primulaceae) are reported. Ten of them are endemic for the Caucasus ecoregion and two species (*Primula abchasica* and *P. saguramica*) are endemic to Georgia. All these species grow in different habitats from 0 to 3000 m above sea-level, from sea shore to alpine meadows (Nakhustrishvili, 2013). In the Caucasus Mountains several *Primula* species grow in different habitats. In the paper special attention is paid to plants of highlands and arctic zone, where vegetative season is very short and plant has very little time for the seed production.

The phenology of plants' flowering phases get a special attention in terms of global climate change as it appear to be an important indicator of adaptation of plants, dependent on temperature changes (Molau, 1993; Körner, 2008; Khanduri *et al.*, 2008; Gordo & Sanz, 2010; Wolkovich *et al.*, 2012, Gigauri *et al.*, 2016). It is known that climatic changes have influence on plant phenological rhythms, especially on the reproduction phenophases (Shakarishvili & Osishvili, 2013, Li *et al.*, 2020). Additionally it is known (Akhalkatsi & Wagner, 1996, 1997) that rhythm of flowering phenology is directly connected with structural peculiarities of reproductive organs. But, unfortunately, very few researches have been conducted in this direction.

Climate change is expected to shift the phenology of understory vegetation, especially timing of flowering of early spring species. This in turn will affect quantitative and qualitative indicators of seed development determining reproductive success and long-term survival of these species.

The sky exposition is determined by microtopography, and by the thickness of canopy and coverage of existing plant stories. It has a great

importance for the formation of microclimate of the forest floor and, correspondingly, for the growth and development of ground plant cover (Théry, 2001; Tabari *et al.*, 2005). The measurement of sky exposition means not only investigating lighting, which reaches to the plant, but also many other factors like humidity and temperature which also affect the density of vegetation coverage. This parameter can affect the development and functioning of the plant both positively and negatively as plants adapted to diverse sunlight conditions from shadowed places to full sunlight. However, many plants possess the ability of adaptation to combat the destructive action of excess light (Larcher, 2003).

In addition to large-scale climate changes, local degradation of habitat caused by human impact can also have negative influence upon the vitality and fertility of species. Habitat fragmentation considerably affects reproductive success of the plant and ultimately may become the reason of losing biodiversity (Goddard *et al.*, 2010; Newman *et al.*, 2013).

We have chosen species of the genus *Primula* (Primulaceae; Primrose) as plant indicators of climate change and habitat degradation. Species of the genus *Primula* grow in different conditions and have strictly defined requirements to specific habitat (Whale, 1983; 1984). So, we should suppose that every species of primrose is adapted to environmental conditions, typical for its habitat, the main factors of which are lighting and humidity of site.

The aim of our study is to determine the changes in duration of phenological phases, which may be due to the changes of environmental factors in different habitats with individuals of the same species. As a result we would be able to define adaptation amplitude of every separate species to concrete habitat and define the chance of its survival in changeable environment. It is especially important for rare and endangered species, as well as for

plants growing in habitats sensitive to climate, such as areas with excess humidity, arid regions and highlands.

The main purpose of this paper is to study phenology of forest plants blooming in early spring in different environmental conditions.

The results will be important to define peculiarities of seedage of these specific species and their ability to survive, as well as effect of global warming on vegetative cover and plant reproduction, in particular.

Material and Methods

Study species: The effect of the sky exposition on phenological rhythm has been studied in 6 species in 18 study sites. Studied species are: *P. woronowii* Losinsk., which grows in the most closed oak-hornbeam forest as this species of primrose spread in Georgia; *P. macrocalyx* Bunge grows in beech forest; *P. amoena* M. Bieb. is found both in subalpine birch forest and in subalpine and alpine meadows. Two other species (*P. cordifolia* Rupr., *P. algida* Adams) grow only in subalpine and alpine meadows, and one of them (*P. auriculata* L.) is found in humid meadows in subalpine and alpine zones.

Our target species for reproduction studies are perennial herbs *P. amoena* and *P. woronowii* (Primulaceae; Primrose). They grow at different altitudes and habitats. *P. amoena* is distributed in different habitats of subalpine and alpine zones, such as meadows, among rocks near melting snow, avalanches, stony banks of river and also in the birch forests and alpine meadows at 1700-2900 m a.s.l. Generally it grows on northern slopes in soil rich of humus with good drainage, common in Caucasus area and Transcaucasia.

P. woronowii grows in the forests, ravines, up to the middle belt of mountain, sometimes reaches subalpine belt. It is widespread almost all over Georgia. This life-form can be found in various colors.

Study area: The first study region is Kakheti, Kvareli district, village Shilda, which is situated in east Georgia. The study place is Nekresi Church area (41.975°N; 45.763°E, 410-970 m a.s.l.) protected historically by religious traditions, where local Georgian population was not allowed to use natural resources near sacral place. The vegetation in this area is dominated by *Quercus iberica* Steven, *Carpinus betulus* L., *C. orientalis* Mill., *Tilia begoniifolia* Steven, *Fraxinus excelsior* L., *Cornus mas* L., *Corylus avellana* L., *Swida australis* Fisch. & C.A. Mey., *Lonicera caucasica* Pall., *Mespilus germanica* L., *Clinopodium vulgare* L., *Veronica peduncularis* M. Bieb., *Galanthus woronowii* Losinsk., *Primula woronowii* Losinsk., *Ophrys sphegodes* subsp. *caucasica* (Woronow ex Grossh.) Soo, *Epipactis persica* (Soo) Nannfeldt subsp. *persica*, *Limodorum abortivum* (L.) Sw. *Orchis purpurea* subsp. *caucasica* (Regel) B. Baumann, R. Lorenz & R. Peter.

In the first study region there is another area called "Udziro", the forest is influenced by anthropogenic impact (41.591° N 45.425° E, 400-600 m a.s.l.). Species composition in this place is: *Quercus iberica* Steven, *Carpinus betulus* L., *Tilia begoniifolia* Steven, *Cornus mas* L., *Corylus avellana* L., *Swida australis* Fisch. &

C.A. Mey., *Lonicera caucasica* Pall., *Mespilus germanica* L., *Galanthus woronowii* Losinsk., *Primula woronowii* Losinsk., *Scilla siberica* Haw., and *Cyclamen coum* subsp. *causicum* K. Koch.

The second study region of Kazbegi district (1081 km²) is situated in the north of the main Watershed Range of the Central Greater Caucasus, on the valley of the R. Tergi (42°48'N; 44°39'E) at the border with Russia. The relief of the Kazbegi region is formed by ascending, bare, sharp ridges, isolated peaks, very steep rocky slopes, narrow gorges and caves of erosion-tectonic origin (Nakhutsrishvili et al., 2005, 2006).

The first study area from Kazbegi district called "Lifu", protected by Sameba church, is situated in the subalpine birch forest zone (N42.66702 E44.62016) composed of 15-20 m tall trees. Apart from trees layer, composed mostly of birch (*Betula litwinowii*), the plant cover of the understory is about 70-75% and it is represented mostly by the following species: *Aconitum nasutum* Fisch. ex Rchb., *A. orientale* Mill., *Daphne mezereum* L., *Geranium sylvaticum* L., *Platanthera chlorantha* (Custer) Rchb., *Polygonatum verticillatum* (L.) All., *Populus tremula* L., *Primula amoena* M. Bieb., *Pyrola media* Sw., *Rubus saxatilis* L., *Sorbus caucasigena* Kom. ex Gatsch., *Swertia iberica* Fisch. & C. A. Mey., and *Veratrum lobelianum* Bernh.

As the second study area from Kazbegi district was chosen anthropologically influenced birch forest called "Areshistavi" (N42.64256 E44.64430), which is situated near town Stepantsminda on Kuro Mountain and in Snogorge. In this site only dwarf birch trees are found, growing exclusively in the soil depressions. About 90% of the plane areas are covered by grasses and herbs with plant cover dominated by *Bromopsis variegata* M. Bieb., *Campanula biebersteiniana* Schult., *Carum causicum* (M. Bieb.) Boiss., *Heracleum roseum* Steven, *Nardus stricta* L., *Primula amoena* M. Bieb., *Rubus idaeus* L., and *Viola caucasica* Kolenati.

Field research

Description of the plants: For all studied species: 1. General description of population were done. Taking of coordinates by GPS; altitude; exposition; degree of slope; general description of a habitat; vegetation coverage, species composition of community; 2. Plot size of 1 square m (20 in total for one testing place) were randomly selected; 3. Number of *Primula* at given plot were defined and photographs were taken using "fish-eye" lens. The number of individuals was different for all selected plots. Plants fertility (the presence of fruits), number of full and empty fruits and ovule number per full fruit were determined.

Phenology: The phenological phases were determined for all the six *Primula* species: 1. The first phase of vegetative growth, before beginning of blooming; 2. Bud phase; 3. The pollination phase - flower is opened, flower is pollinated, or not yet pollinated; 4. Fading phase - which include the process of beginning of fading of crown petals start of reproduction, zygote and preliminary

core of endosperm formation; 5. Seed formation phase - petals of crown fade, fruit begins increasing in size, embryo- and endospermogenesis are carried out; 6. Seed ripening phase - fruit and embryo are growing; 7. Seed dispersal - fruit opens, and ripe seeds are dispersed; 8. The second phase of vegetative growth. After seed dispersal, leaves grow and reproductive meristem and flower primordium are formed. Duration of phenological phases was determined for each population. 20 individuals for each species were selected (40 individuals for *P. amoena*- in the meadow and in forest). Constant monitoring of their phenological rhythm was done. All the flowers of each plant were labelled and monitored to determine the time required for the transition from one stage to the next.

Definition of the sky exposition: The sky exposition is the percent of open part of the sky defined by 180° above the concrete place, from where sun rays fall on the surface of soil. Its analogous notion is canopy openness, which is more reasonable for the forest ecosystem, where the sky is closed for the soil surface mainly by plants. Though in this case topography of the slope also plays a great role in both forest and alpine zones, where height of vegetation is not so significant. That is why we use the term sky exposition, as the general index of habitat lighting, which affects its microclimate, and, in particular, defines its temperature and humidity.

Special lens (“fish-eye”) was used to define sky exposition, which took a photograph of environment by 180°. Photographing was conducted by digital photograph Nikon CoolPix 5000. Photographing for definition of the sky exposition took place only once in alpine zone, in the first week of July. But in the case of forest species we took photographs using “fish-eye” lens twice, first before leafing, the second time - when the forest was completely leafed. In the case of *P. woronowii* observations were carried out during 2 years in early spring and at the beginning of summer.

Statistical processing of data: The calculation of sky exposition was done using digital images imported into Gap Light Analyzer software. The data were used to calculate the fraction of the hemispherical image not obscured by objects (i.e. percent sky exposition). The groups of the sky exposition were separated according to percent indices, used further in regressive analysis to determine correlation with reproductive indices. The independent variable was sky exposure, the dependent variables were plant reproductive characteristics.

To calculate numerous numeral data statistical program SPSS v. 22.0 was used. Medium and standard deviation were defined for every numeral line using graphic program SigmaPlot. Statistic difference between average indices ($p \leq 0.05$) was determined by means of one-way analysis of variance, which was conducted by means of ANOVA.

Results

Sky exposition in habitats of species of *Primula*: While comparing averages of the sky exposition on the level of

species, summer forest of *P. woronowii* appeared to have the lowest index, and *P. algida* growing only in meadows in alpine zone had the highest, which grows only in meadows in alpine zone. Summer sky exposition of *P. macrocalyx* and *P. amoena* growing in young beech and subalpine birch forest is nearly equal (Fig. 1).

According to habitat type, we have picked up three groups: forest species in early spring, forest species in summer and alpine species. We have compared indices in these three groups. It appeared that the sky exposition index had a highest average rate in a distribution zone of alpine *Primula* species, while the forest species had the lowest (Fig. 2).

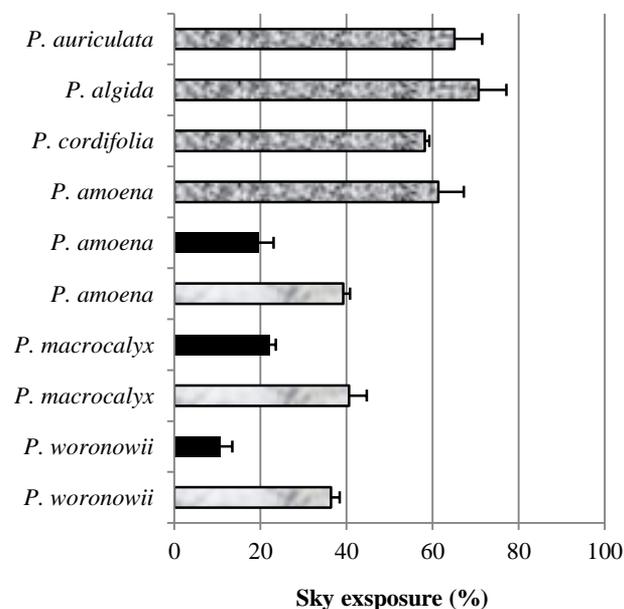


Fig.1. Mean and standard deviation of sky exposition of *Primula* species in different habitats. □ Spring forest; ■ Summer forest; ▒ Subalpine and Alpine meadows.

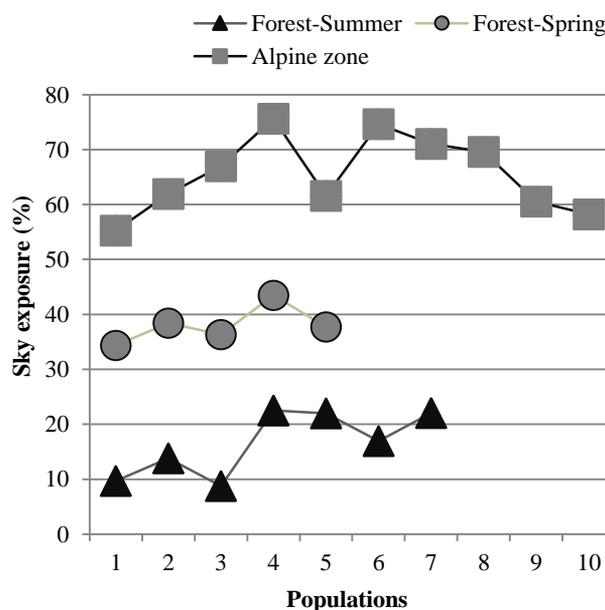


Fig. 2. Mean of sky exposition of *Primula* species in different habitats. Alpine zone; Spring forest; Summer forest (n=150).

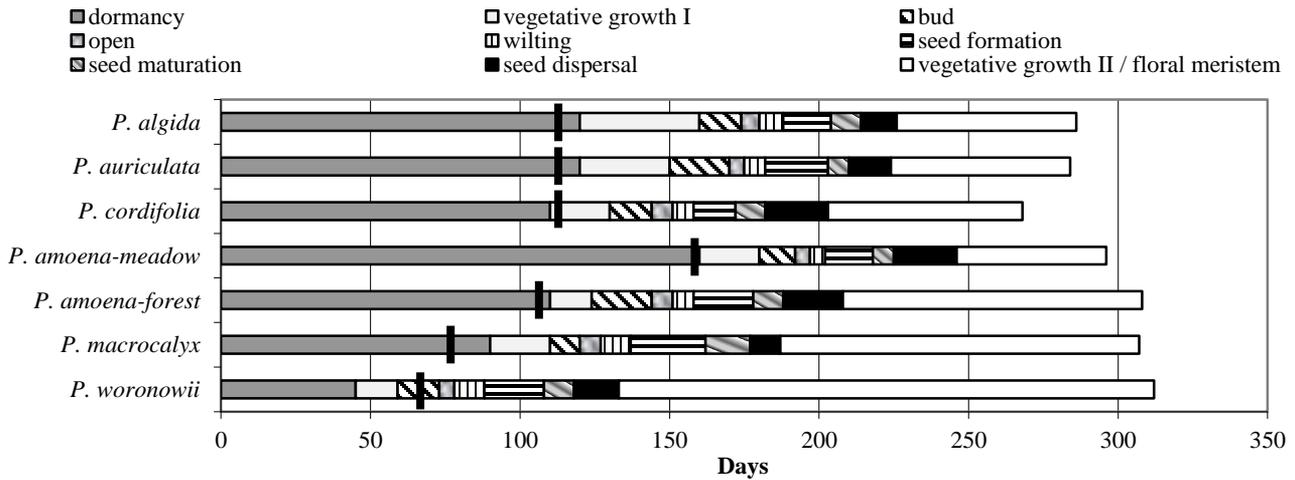


Fig. 3. Phenological studies of *Primula* species. The black line indicates the time of snow melting for selected habitat. Days count begins on January 1 and continue for a full 365 days a year.

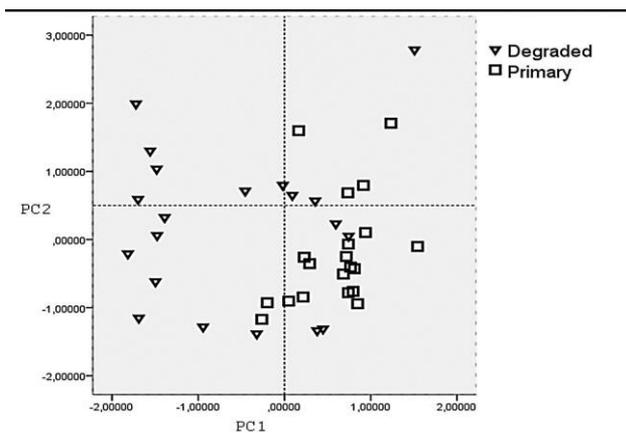


Fig. 4. Scatter plot of discriminant function analysis (DFA) of the 40 plots of studied sites based on 4 principal components of 10. Plant height, without fruits, Number of ovule, Number of full fruits. data resulting from PCA (n=40).

Phenological rhythm: Study of average duration of phenological stages for every species showed that *P. woronowii*, species of oak-hornbeam forest, started vegetation phase and flowering earliest. It started flowering as soon as snow melted and finished before forest leaves completely.

The next is *P. macrocalyx*, which is also forest species. However, in contrast to *P. woronowii* it started flowering a little later after melting of snow and continued even after beech forest was completely leafy. Among alpine species *P. amoena* and *P. algida*'s populations, spreading in alpine zone on the highest altitude above sea level, started flowering very late. By that time young individuals of *P. amoena* in subalpine birch forest already finished their reproductive process. The same can be said for *P. algida*, individuals which finished flowering on subalpine meadow early, but were still in flowering in shady places, such as at the edge of forest, while individuals bloomed on the open place and also got ripe fruits. That is the course of phenological phases in alpine zone, controlled by height above sea level, as well as microtopography and thus most important (Fig. 3).

Degraded and Primary habitats: One-way analysis of variance (ANOVA) determined significant differences between two habitat types - primary and degraded birch forests, with regard to plant height, leaf length, number of ovules and number of fertile seeds in fruits ($p < 0.05$) (Table 1).

Principal Component Analysis showed high loads of characters on PC1 and PC2. All of these analysed characters showed very small loads on PC3 (Table 2).

The DFA scatter plot showed distribution of the degraded and Primary habitats against the first two canonical discriminant functions axes. Degraded is located in the left part of the plot and Primary right part of the plot (Fig. 4).

Plant seed production: Our results have shown that forest degradation did not significantly affect the vitality of primrose. In case of *P. amoena* the higher population density was observed in forests with higher anthropogenic disturbance compared to primary forest. On the contrary, seed fertility of primroses was comparatively low in the degraded forest (Table 1).

Regarding the fertility of this plant, in the forest "Lifu", where anthropogenic influence were not observed, all individuals of primrose in all randomly chosen sites bore fruit and no fruitless primrose was observed. The same random selection was done in degraded forest (Areshistavi), where all individuals in 9 plots from 20 did not bear fruits (Fig. 5).

Interesting result was obtained, when we defined thickness of individuals with and without flowers on the plots with different sky exposition, in summer, in completely leafy forest. In the most closed research place (Udziro) some regularity was found - when the sky exposition was less than 5 %, in those places no young individual of *P. woronowii* developed flowers. It should be noted, that flowerless individuals were observed in cases of different sky expositions, but we could not find blooming individuals on the plots with the less than 5 % index. Such closed places are located under underwood elements, nut, cornel and other bushes. In spite of this *P. woronowii* individuals grow in such places but do not bloom (Fig. 6).

Table 1. Mean \pm SD data in parenthesis of *Primula* cover percentage, *Primula* individuals, *Primula* with fruit, *Primula* without fruit, Plant height, Number of fruits with seeds, Number of empty fruits, Leaf length, Leaf number, Ovule number. One-way analysis of variance (ANOVA) was conducted for all values.

F and significance values ($P < 0.05$) are presented (N = 40).

Character	Degraded	Primary	Mean Square	F	Significance
Primulacov	11,55 \pm 7,60	7,75 \pm 5,46	144.400	3.292	0.078
Primulaind	5,60 \pm 3,64	3,90 \pm 2,15	28.900	3.224	0.081
Withfruit	1,50 \pm 1,50	2,20 \pm 1,32	4.900	1.936	0.172
Withoutfr	3,85 \pm 4,13	1,70 \pm 1,62	46.225	4.687	0.037
Plantheihg	15,00 \pm 13,29	28,75 \pm 4,20	1890.625	19.450	0.000
NumberFullfruit	2,75 \pm 3,09	6,30 \pm 1,72	126.025	20.126	0.000
NumberEmptyfruit	1,15 \pm 1,63	,95 \pm 1,23	.400	.191	0.664
Leaflength	21,80 \pm 2,35	25,55 \pm 2,70	140.625	21.887	0.000
Leafnumb	5,30 \pm 1,92	4,90 \pm 1,71	1.600	.483	0.491
Ovule	11,06 \pm 10,90	18,75 \pm 3,33	590.592	9.088	0.005

Table 2. The results of principal component analysis.

Characters	Component		
	PC1	PC2	PC3
Plantheihg	,933	,173	-,063
Withoutfr	-,898	,182	-,165
Ovule	,895	,183	-,164
NumberFullfruit	,841	,013	-,395
Lieflength	,509	,159	-,387
Primulacov	-,378	,891	-,021
Withfruit	,563	,741	,001
Primulaind	-,642	,716	-,180
NumberEmptyfruit	,342	,303	,777
Liefnumb	,297	,073	,662

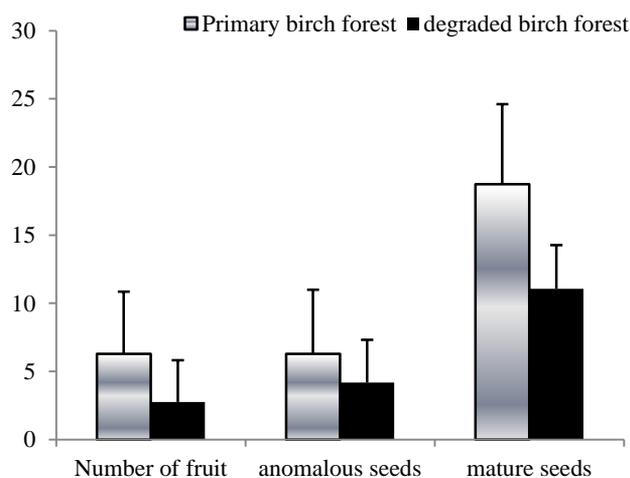


Fig. 5. Number of fruits, anomalous seeds and mature seeds (Mean and standard deviation) in primary and degraded birch forest (n=40).

Discussion

Phenology of primrose species spreading in different habitats was studied. It was found that the individuals of primrose (*P. woronowii*) growing in the closed oak-hornbeam forest at the altitude of 400-1000 m began flowering at the earliest. Certainly, phenological rhythm is

mainly dependent on the height of habitat above the sea level and temperature (Larcher, 2003; Körner, 2012). But considerable difference which is striking in the case of this species, that it starts flowering in the forest as soon as snow starts melting, simultaneously across the entire range of its distribution, at 400-1000 m, while *P. macrocalyx* spreading nearly on the same altitude (700-1700 m), grows in beech forest, blooms much later after melting of snow, after leafing in the forest, other alpine species, begin flowering in May and end it at the end of July according to the height above the sea level, but, due to melting period of the snow, they have got bigger interval, than *P. woronowii*.

Majority species of *Primula* are distributed in alpine zone (Whale, 1984), though some species grow in the forest habitat. Out of 22 species of primrose present in Georgia, 8 grow in forest, 8 - on alpine meadows and 6 occur both in subalpine forest and alpine zones. According to our data, alpine and forest habitats differ strongly by the indices of sky exposition. The sky exposition of alpine zone exceeds 6-8 times compared to the forest covered by leaves in summer. This indicates that lighting of microhabitat is higher in spring than in summer, which probably could be reason for the selection of this period for flowering by forest species of primrose.

The question arises, why primrose chooses for flowering seasonal period before leafing in forest? It is known that in forest species blooming in early spring, flower primordium forms, as a rule, in previous year, in late summer or autumn (Akhalkatsi & Gvaladze, 1992). It allows the species to begin flowering in spring as soon as snow melts, as the flower parts are already formed and only increase in size takes place. According to our data, alpine forest species begin flowering after melting of snow, later than forest species. But even in such a case primordium is already formed in previous year, but its development takes place more slowly in spring. In our opinion, early opening of flower in forest species and especially in *P. woronowii*, having lower sky exposition, is conditioned by accelerating of phenological phases of flowering that could explain the adaptation of this species to the forest habitat, where the sky exposition decreases 4-5 times and lighting and microclimate changes after leafing.

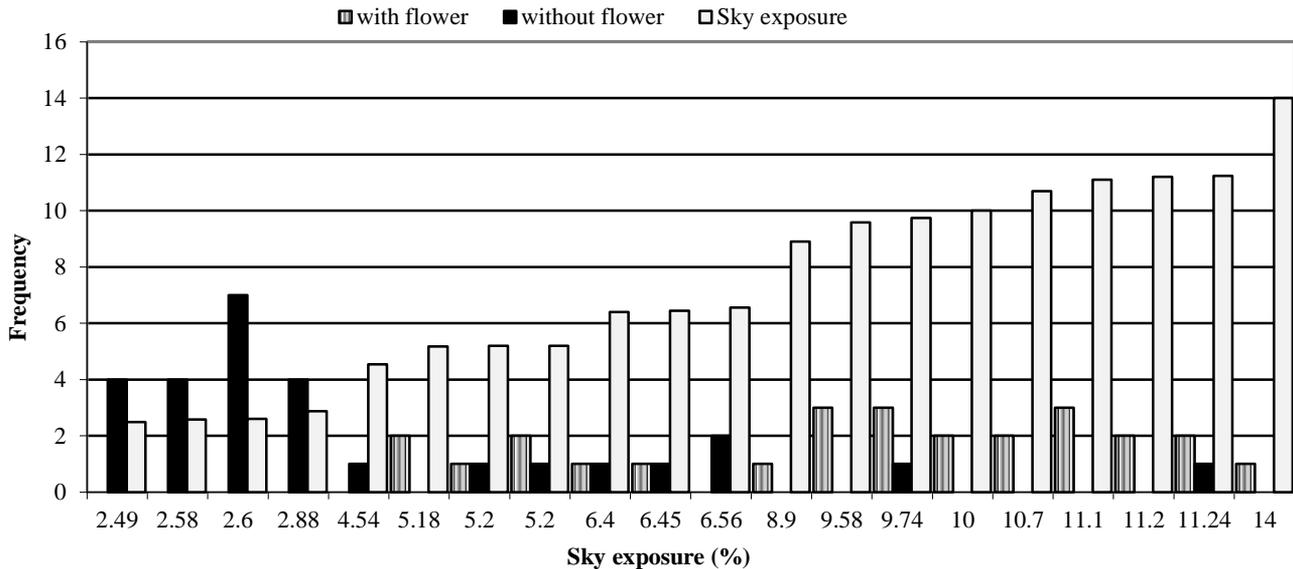


Fig. 6. Relations of sky exposure with frequency of individuals with flowers and without flowers in *P.woronowii* study area (n=20).

Our results indicate, that peculiarities of seed production of the species of primrose flowering in spring, reproduction of which takes place before the leafing in forest, express important correlation with microclimate factors conditioned by the sky exposition, such as intensity of lighting, temperature and humidity. It is expected that early or late beginning of vegetative season in forest species depend on climate change and finally affect successful reproduction of these species causing certain shifting of phases of flowering phenology. This process will affect quantitative and qualitative seed production, which finally defines plant reproduction and survival of species.

According to obtained data it is supposed that forest cutting decreasing the sky exposition in the habitat has negative effect on fertility of *Primula*. In spite of high diversity of *Primula* species in degraded habitats flowering of *Primula* was diminishing.

Our results showed that reproduction of *P. woronowii* depended on canopy openness. Seed production of this species in degraded forest decreased compared to the primary forest. Similar results were found in other studies as well as, when cutting of forest and, correspondingly, change of the sky exposition negatively affected fertility of orchids (Akhalkatsi *et al.*, 2014). Fertility of *P. woronowii* gives rather a high index of positive linear correlation with the sky exposition. In our opinion, the limit index of sky exposition (5%) in the distribution area, *P. woronowii* do not develop flowers. This is an important factor. It should be noted that forest is so dense? only during the summer period, when the flowering and the seed production is already completed. But most importantly, in this period formation of reproductive meristem and development of the flower primordium, take place for the next year. It is expected that the plant reacts to low lighting and microclimate conditions and does not produce flowers, as in spring, though the sky is bigger before foliation, but, supposedly not enough for successful reproduction. Induction of this, probably, happens in dense environment because of limited photosynthesis and deficiency of stock substances

(Larcher, 2003, Körner, 2012). Demography of *P. vulgaris* depends on changes of lighting conditions. This species is mainly a forest species and the reduction and loss of forest habitat has negative impact on its reproductivity (Valverde & Silvertown, 1998; Valdés & García, 2013).

The objective of this study was to compare the indicator species (*P. amoena*) density and fertility to habitat conditions in the primary and degraded Birch forest affected by human impacts. Principal component analysis showed that the most important factors differentiating *P. amoena* populations in degraded and primary habitats were: Ovule number, Plant height, *Primula* plants without fruit and with fruits.

An indicator species (based on frequency) for this type of habitat, *P. amoena* was chosen for reproductive studies in birch forest (Togonidze & Akhalkatsi, 2015). Though it is known that degradation of birch forest negatively affects the species diversity of plants and the number of species composing understory decreases (Honnay & Jacquemyn, 2007; Togonidze & Akhalkatsi, 2015), it does not refer to *P. amoena*. It was observed that the plant species composition were tightly related to structure, functional diversity, and activity of the microbial communities in the soil in above-ground forest ecosystems (Kizildag *et al.*, 2015). The number of its individuals was very high in birch forest, where anthropogenic activities were observed. However, the reproductive success of this species (number of fruit and mature seed), really decreased in the degraded forest.

From our results, it could be concluded that habitat degradation had a strong effect on reproduction of *Primula* species. Habitat fragmentation decreases the genetic diversity of plant populations (Aguilar *et al.*, 2008). At community level it could affect growing of existing vegetation until that end of blooming of primrose and thus hinder access of pollinators that would significantly reduce intensity of pollination. This process affected quantitative and qualitative seed production, which finally defined plant reproduction and survival of species.

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References

- Aguilar, R., M. Quesada, L. Ashworth, Y. Herrerias and J. Lobo. 2008. Genetic consequences of habitat fragmentation in plant populations: susceptible signals in plant traits and methodological approaches. *Mol. Ecol.*; 17: 5177-5188.
- Akhalkatsi, M., G. Arabuli, R. Lorenz. 2014. Orchids as indicator species of forest disturbances on limestone quarry in Georgia (South Caucasus). *J. Eur. Orch.* 2014. 46: 123-160.
- Akhalkatsi, M. and G. Gvaladze. 1992. Seasonal changes in the ultrastructure of the embryo sac. *Galanthus nivalis* L. (Amaryllidaceae). *Bot. J.*; 77: 66-73.
- Akhalkatsi, M. and J. Wagner. 1997. Comparative embryology of three Gentianaceae species from the Central Caucasus and the European Alps. *Plant Syst. Evol.*, 204: 39-48.
- Akhalkatsi, M. and J. Wagner. 1996. Reproductive phenology and seed development of *Gentianella caucasea* in different habitats in the Central Caucasus. *Flora*, 191: 161-168.
- Gigauri, Kh., M. Akhalkatsi, O. Abdaladze and G. Nakhutsrishvili. 2016. Alpine plant distribution and thematic vegetation indicator on Gloria summit in the Central Greater Caucasus. *Pak. J. Bot.*, 48(5): 1893-1902.
- Goddard, M., A. Dougill and T. Benton. 2010. Scaling up from gardens: biodiversity conservation in urban environments. *Trends Ecol Evol.*, 25: 90-98.
- Gordo, O. and J.J. Sanz. 2010. Impact of climate change on plant phenology in Mediterranean ecosystems. *Glob Change Biol.*, 6: 1082-1106.
- Honnay, O. and H. Jacquemyn. 2007. Susceptibility of common and rare plant species to the genetic consequences of habitat fragmentation. *Conserv. Biol.*, 21: 823-831.
- Khanduri, V., C. Sharma and S. Singh. 2008. The effects of climate change on plant phenology. *Environmentalist.*, 28: 143-147.
- Kizildag, N., H. Aka Sagliker and C. Darici. 2015. Influence of two different parent materials and plants on soil carbon and nitrogen mineralization in a Mediterranean climate. *Ekoloji.*, 24: 64-72.
- Körner, Ch. 2008. Winter crop growth at low temperature may hold the answer for alpine treeline formation. *Plant Ecol Divers.*, 1: 3-11.
- Körner, Ch. Alpine treelines. 2012. Springer, Basel, ISBN. 978-3-0348-0395-3.
- Larcher, W. 2003. Physiological plant ecology. ecophysiology and stress physiology of functional groups. Springer, ISBN. 978-3-540-43516-7.
- Li, W., J. Yang, H. LI and C. Zhang. 2020. Effect of environmental factors on species diversity among the plant communities in the mount Lao Nature Reserve, Shandong Province of China. *Pak. J. Bot.*, 52(4): 1189-1195.
- Molau, U. 1993. Relationship between flowering phenology and life history strategies in tundra plants. *Arctic Alpine Res.*, 25: 391-402.
- Nakhutsrishvili, G., O. Abdaladze and A. Kikodze. 2005. Khevi, Kazbegi Region. Institute of Botany, Tbilisi.
- Nakhutsrishvili, G., M. Akhalkatsi and O. Abdaladze. 2006. Biotope type of the treeline of the Central Greater Caucasus. In: *Nature Conservation (Concepts and Practice)*. (Eds.): D. Gafta and J. Akeroyd, Spinger Berline, Heidelberg, pp. 211-225.
- Nakhutsrishvili, G. 2013. The vegetation of Georgia. (South Caucasus). Berlin, heidelberg, germany: springer-Verlag.
- Newman, B.J, P. Ladd, M. Brundrett and K.W. Dixon. 2013. Effects of habitat fragmentation on plant reproductive success and population viability at the landscape and habitat scale. *Biol. Conser.*, 159: 16-23.
- Shakarishvili, N. and L. Osishvili. 2013. Sexual phenotype of *Capparis herbacea* (Capparaceae). *Turk. J. Bot.*, 37: 682-689.
- Tabari, M., P. Fayaz, K. Espahbodi, J. Staelens and L. Nachtergale. 2005. Responses of oriental beech (*Fagus orientalis*Lipsky) seedlings to canopy gap size. *Forestry*, 78: 443-450.
- Théry, M. 2001. Forest light and its influence on habitat selection. *Plant Ecol.*, 153: 251-261.
- Togonidze, N. and M. Akhalkatsi. 2015. Variability of plant species diversity during the natural restoration of the subalpine birch forest in the central great caucasus. *Turk. J. Bot.*, 39: 58-471.
- Valdés, A. and D. García. 2013. Recruitment limitations in *Primula vulgaris* in a fragmented landscape. *Basic Appl Ecol.*, 14: 565-573.
- Valverde, T. and J. Silvertown. 1998. Variation in the demography of a woodland understory herb (*Primula vulgaris*) along the forest regeneration Cycle: Projection matrix analysis. *J. Ecol.*, 86: 545-562.
- Whale, D.M. 1984. Habitat requirements in *Primula* species. *New Phytol.*, 97: 665-679.
- Whale, D.M. 1983. The response of *Primula species* to soil waterlogging and soil drought. *Oecologia*, 58: 272-277.
- Wolkovich, E., B. Cook, J. Allen, T. Crimmins, J. Betancourt and S. Travers. 2012. Warming experiments under predict plant phenological responses to climate change. *Nature*, 485: 494-497.

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