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# Seasonal changes in chlorophyll fluorescence to assess the stress tolerance of Siberian pines at treeline

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Due to climate change, the boundaries of the ranges of many plants are shifting both in latitudinal and altitudinal directions. In particular, the forest boundary shifts upward in the mountains. A transect with four sampling plots was laid on the slope of the Ergaki Ridge (Western Sayan), crossing the treeline (upper border) of the forest as it transits from the mountain taiga to the rocky-tundra belt. It has been revealed that Siberian pine (*Pinus sibirica* Du Tour) plants use various survival strategies when spreading above the treeline, which manifests itself in a change in the shape of the crown form from stem-like to krummholz, as well as seasonal changes in the pigment complex and parameters of chlorophyll fluorescence in needles. In all habitats of *P. sibirica*, an important parameter for predicting an increase in the needle weight, which, in turn, ensures the productivity of the entire plant, is the maximum rate of non-cyclic electron transfer in the summer. In spring and autumn (in the course of transition from winter dormancy to vegetation and back), the ratio of chlorophylls and carotenoids from forest to mountain-tundra communities decreases in the pigment complex of needles. Siberian pine specimens growing above the treeline and having mechanisms for dissipating excess light energy by light-induced non-photochemical fluorescence quenching have a clear advantage in gaining needle weight over other plants from the same sample plots. For trees from sample plots located in forest environment, a high proportion of non-photochemical fluorescence quenching is rather a disadvantage. The considered parameters of chlorophyll fluorescence can be used to identify *P. sibirica* individuals resistant to habitat conditions above the treeline and their subsequent use in breeding to increase the area of woodlands under climate change.

***Keywords:*** *Pinus sibirica*, treeline, fluorescence, chlorophyll, carotenoids.

**УДК 574.24**

# Сезонные изменения флуоресценции хлорофилла для оценки стрессоустойчивости сосны сибирской на верхнем пределе распространения

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Из-за изменения климата границы ареалов многих растений смещаются как в широтном, так и в высотном направлениях, в частности, граница лесов в горах смещается вверх. На склоне хребта Ергаки (Западный Саян) была заложена трансекта с четырьмя пробными площадями, пересекающая верхнюю границу леса при переходе от горно-таёжного к гольцово-тундровому поясу. Выявлено, что растения сосны сибирской (*Pinus sibirica* Du

Tour) используют различные стратегии выживания при распространении выше границы леса, что проявляется в изменении формы кроны со стволовой на стланниковую, а также в сезонных изменениях пигментного комплекса и параметров флуоресценции хлорофилла хвои. Во всех местообитаниях *P. sibirica* важным параметром для прогнозирования увеличения массы хвои, которое, в свою очередь, обеспечивает продуктивность всего растения, является максимальная скорость нециклического переноса электронов в летнее время. Весной и осенью (при переходе от состояния зимнего покоя к вегетации и обратно) в пигментном комплексе хвои уменьшается соотношение хлорофиллов и каротиноидов от лесных к горно-тундровым фитоценозам. Экземпляры сосны сибирской, растущие выше границы леса и имеющие механизмы рассеивания избыточной световой энергии путём светоиндуцированного нефотохимического тушения, имеют явное преимущество в наборе массы хвои перед другими растениями с тех же пробных площадей. Для деревьев с пробных площадей, расположенных в лесных фитоценозах, высокая доля нефотохимического тушения является скорее помехой. Рассмотренные параметры флуоресценции хлорофилла могут быть использованы для выявления особей *P. sibirica*, устойчивых к условиям обитания выше границы леса, и их последующего использования в селекции для увеличения площади лесных массивов в условиях изменения климата.

***Ключевые слова:*** *Pinus sibirica*, верхняя граница леса, флуоресценция, хлорофилл, каротиноиды.

Climate change exerts a substantial impact on forest ecosystems' functioning. The geographic ranges of many boreal forest conifers experience shifts, in both latitudinal and altitudinal directions [1–4]. Such a tendency – a higher temperature stimulates the altitudinal shift of forest distribution range – has been reported for a number of geographical areas, like Kola peninsula, polar Ural Mountains, Putorana plateau [5, 6], as well as in East Sayan [7], West Sayan [8], and Kuznetsk Alatau [9].

Whether the seedlings and saplings of a mountain forest dominant species are able to survive above the treeline is a crucial point shaping up the species composition of such forests. For Siberian pine/fir forests, a species playing the pioneering role is Siberian pine (*Pinus sibirica* Du Tour) [10]. A great advantage of Siberian pine is its symbiotic distributor species, nutcracker (*Nucifraga caryocatactes* L.), that collects the pine seeds and hides them in the litter and under the mosses cover. However, the survival of the pine seedlings above the treeline is minor. The seedlings to saplings and adult trees to saplings ratios are much lower above the treeline that under the canopies of closed forests [11]. Above the treeline, krummholz Siberian pine forms with multiple small stems have been mostly found because of the harsh environment with strong winds and shallow snow cover [12].

Nevertheless, a question is open of defining ecological and physiological traits that distinguish those tree specimens that cope to survive and develop under the harsh conditions of mountain environment. Under the altitudinal zonation, the mechanisms should be described that allow the seedlings and saplings of Siberian pine to adapt to multiple stress factors.

To find the most adapted individuals, the methods of plant phenomics are fairly suitable that are based on physiological and biochemical traits of a plant organism at the level of the phenotype [13, 14]. Some authors [15–19] believe that the methods based on chlorophyll fluorescence are a perspective for plant phenotyping.

We hypothesized that chlorophyll fluorescence and pigment content in needles are likely tightly connected to the environmental stress induced by altitude, especially in trees growing above the treeline. The goal of this study was to test seasonal alterations of chlorophyll fluorescence and pigment composition as a tool for phenotyping of *Pinus sibirica* saplings and trees in terms of their stress-tolerance against the adverse environmental factors along an altitudinal gradient of West Sayan (Eastern Siberia).

## Materials and methods of research

An altitudinal transect has been set up in the vicinity of Oyskoe Lake within the Yergaki National Park (West Sayan mountains) located in Ermakovskiy Region of Krasnoyarsk Krai. The transect crossed the treeline where taiga belt changes over to rocky-tundra belt (Fig. 1).

The climate of the area was estimated with the help the meteorological station Olen'ya Rechka (WMO 29974, N 52º48', E 93º14'; 1404 m a.s.l.) in 5 km from the lake. The mean temperature in January is −17.7 ºC, in July is +13.2 ºC. Precipitation totals up to 1200 mm, with an average of 440 mm precipitation during the summer months.

An altitudinal transect has been set up in the vicinity of Oyskoe Lake within the Yergaki National Park (West Sayan mountains) in Ermakovskiy Region of Krasnoyarsk Krai. The transect consisted of four sample plots (SP):

SP1 (N 52º50'40.4" E 93º16'24.2", 1636 m a.s.l.) is an area occupied by *Pinus sibirica* krummholz form with the height up to 1 m and stems diameter of 3 to 5 cm.

SP2 (N 52º50'26.3" E 93º16'26.9") is a sparse pure forest of *Pinus sibirica* with canopy

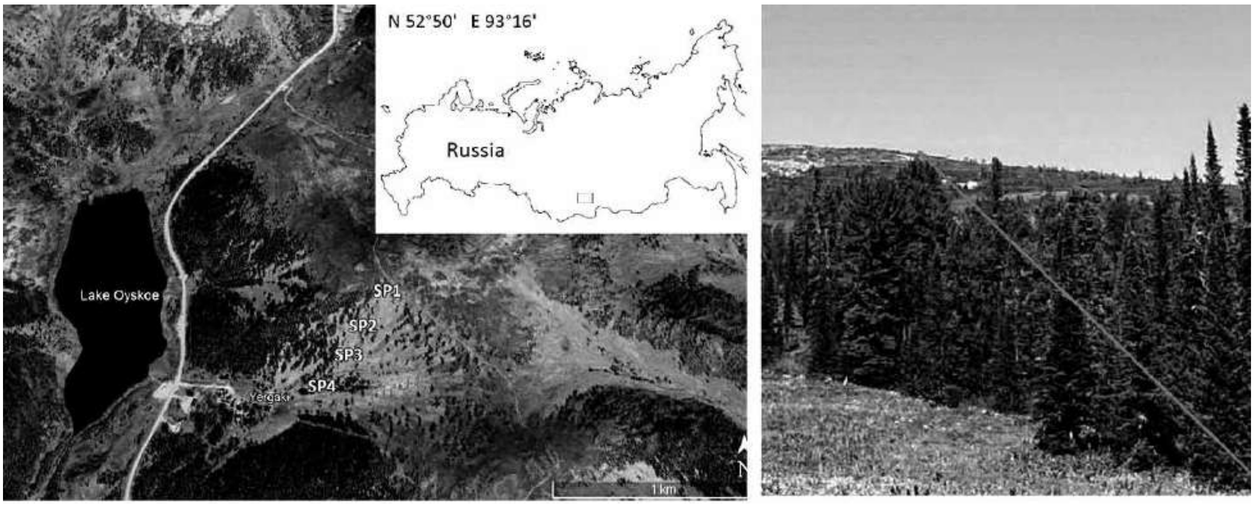

**Fig. 1.** The studied area on Russia's map (left). A photograph of the sample plot (red line on the right)

closure of about 0.1, tree height up to 5 m, and stem diameter of 8 to 12 cm.

SP3 (N 52º50'17.2" E 93º16'21.0", 1505 m a.s.l.) is a mixture short-grass forest of *Pinus sibirica* and *Abies sibirica* Ledeb. with a proportion of ca. 6P4A. The canopy closure is 0.4. *Pinus sibirica* trees are 15 m in height and 15 to 20 cm in diameter.

SP4 (N 52º50'14.6" E 93º15'28.4", 1455 m a.s.l.) is a mixture tall-grass forest of the pine and fir with *Abies sibirica* domination, the proportion being ca. 6A4P. The canopy closure is 0.7. The height of pine stems reaches up to 15 m and the diameter 15 to 20 cm.

On the southward slopes of the mountain chain in the study area, the upper limit of *P. sibirica* distribution has been estimated to be between 1500 and 1600 m a.s.l. [10]. The frontline where pine trees having a typical tree-like form with upright stems may be found goes between SP1 and SP2. The treeline is about between SP2 and SP3. The sample plots are located on the southward slope, with SP4 being at the bottom of the hill on a flatter area.

The sample trees were young specimens of Siberian pine of ca. 40 years old. On each sample plot, 20 trees were chosen and three second-order shoots were taken from middle crown part of each tree. Thus, the total number of sample shoots amounted 240 at each sampling season. The sampling seasons were spring (April 2023 and 2024), summer (July 2023 and 2024), and autumn (November 2023). In April and November, the transportation of the specimens was done in a car-based refrigerator Alpicool TW-35 with the negative temperature function. The temperature during the transportation was as the air temperature at the needles' sampling.

The measurements of the chlorophyll fluorescence were performed within 24 hours after samplings with the help of fluorimeters Junior PAM and IMAGING-PAM M-Series MAXI Version (Heinz Walz GmbH, Germany) under the photosynthesis curve record mode, three replicas per measurement.

The recorded data were treated through the WinControl software [20]. To assess the speed of breaking of winter dormancy, the pine shoots were set in the water and kept in this condition for 10 days under +24 ºC and daylight fluorescent lamps.

This part of analysis (abscisic acid detection and measurement) was performed in accordance with the methods described by Rudikovskii et al. [21]. The sample from every tree was combined from three shoots' samples.

The extraction of carotenoids and chlorophylls was performed in accordance with the methods described in [22–24], three replicas from every shoot.

Statistical analysis was done with the help of SigmaPlot 12.5 software. The indicators mean ± mean error (M ± m) are calculated. Normality of data was estimated through Shapiro-Wilk test. In case of successful normality test, to estimate the significance of differences among several variables ANOVA was applied. The difference between two variables was explored through Student's *t* test. In case the data distribution was different from normality, non-parametrical Mann-Whitney test was applied. For multiple comparisons, one-way ANOVA Tukey test was used. On the graphs, lowercase letters, plus (+) and asterisks (*) sings denote the significant differences at $p < 0.05$.

## Results and Discussion

For conifers occupying habitats above the treeline, the main risks are twofold. Firstly, it is high solar radiation in spring and early summer. Pioneer trees are exposed to high irradiances, which supports fast growth but also give rise to the danger of photoinhibition [25]. The radiation leads to photoinhibition of photosynthesis at the background of low though positive temperatures. The second risk is a short vegetation period. In autumn, when trees evoke the mechanisms to withstand the cold and are about to enter the winter dormancy, some negative consequences are possible due to abrupt frosts and fast freezing shallow soil. The studies undertaken in spring, summer, and autumn gave the opportunity to follow the seasonal variations of the photosynthetic apparatus functioning as well as the variation in the pigments in Siberian pine.

Figure 2 depicts changes of maximum rate of non-cyclical electron transport (ETR) as well as abscisic acid content at a dormancy breaking of the needles in April and transition from growth to winter dormancy in November.

According to the data obtained, the needles' ETR increase took place in two days (SP4), 5 days (SP3), 8 days (SP2) after their placement under laboratory conditions. The needles from SP1 have not broken the dormancy after 10 days in laboratory (Fig. 2). These data correspond well to the ABA content in needles. The

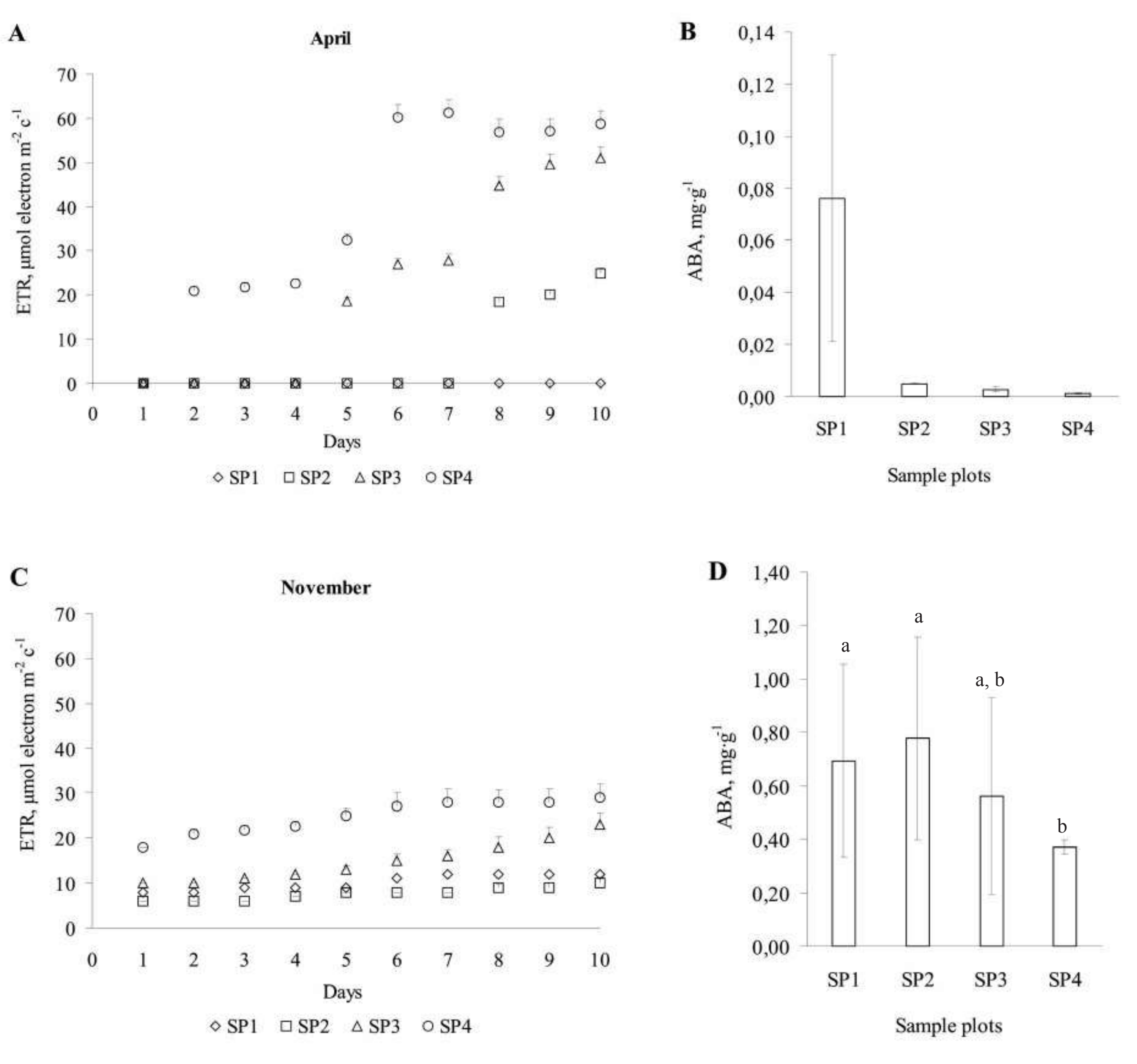

**Fig. 2.** The depth of the needles' winter dormancy as estimated through non-cyclical electron transport (ETR) dynamics at the breaking of winter dormancy in the laboratory (A, C) and abscisic acid (ABA) content (B, D) among the sample plots (SP). The marks *a* and *b* indicate significant differences in the parameter between the test areas at $p < 0.05$

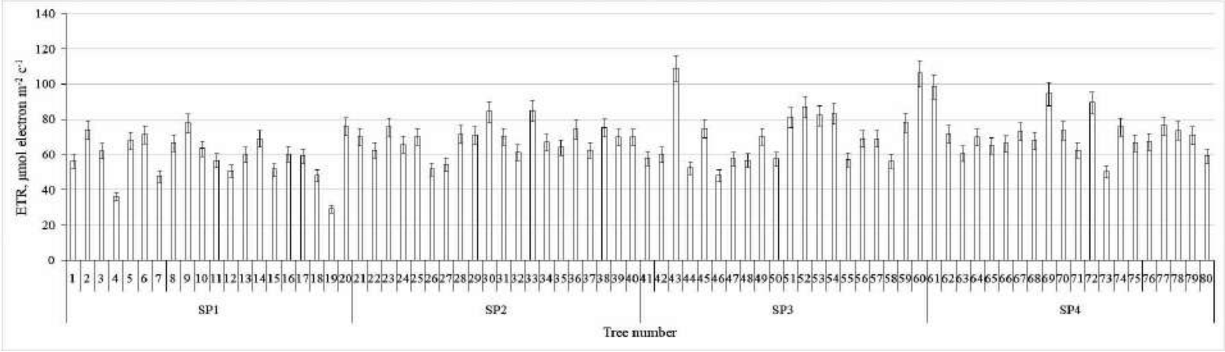

**Fig. 3.** The maximum rate of non-cyclical electron transport (ETR) in needles of Siberian pine [19]

maximal ABA content was observed on SP1 and was significantly lower on other sample plots achieving the minimum on SP4. Supposedly, the distribution of ABA among sample plot reflects a lower environmental stress exerted on trees.

In November, ETR values were above zero on the day of sampling. They grew in the laboratory much slower than in spring. It is explained by the accumulation of ABA during the transition to winter dormancy. The highest electron transport rate was found in needles on SP4 for which the ABA content is low.

In July, an express estimation of the maximal rate of non-cyclical electron transport (ETR) was done for the 80 sample trees in situ with the help of PAM fluorimeter Junior-PAM (Fig. 3).

A one-way ANOVA showed a significant difference in ETR ($p < 0.05$) between SP1 and any other sample plot (Fig. 3). No significant difference in ETR between SP2, SP3, and SP4 has been found. For all the studied trees from forest communities (SP3 and SP4) as one sample, the correlation coefficient between the maximum speed of electronic transport, ETR, and the absolutely dry mass of needles has the value 0.85. Lower correlation coefficients were received on the upper sample plots SP1 and SP2 (0.58 and 0.57, correspondingly). This may be due to a shorter growing season, when it is necessary to increase biomass in a short time, and the needles photosynthesize more actively. The high variability of the parameter in Siberian pine within every sample plot may be an evidence of trees' different adaptability to the local conditions and different success of them in the biomass growth [16]. After ETR estimation in each of the 80 sample trees within the sample plots, four specimens of pines were selected that showed contrasting minimal and maximal ETR values (Fig. 3). The samples from the selected trees have been taken for a deeper analysis in the laboratory. The fluorescent properties of the needles (Fig. 4) and photosynthetic pigments composition (Fig. 5) were studied.

In April, the mean values of maximum photochemical quantum yield of photosystem

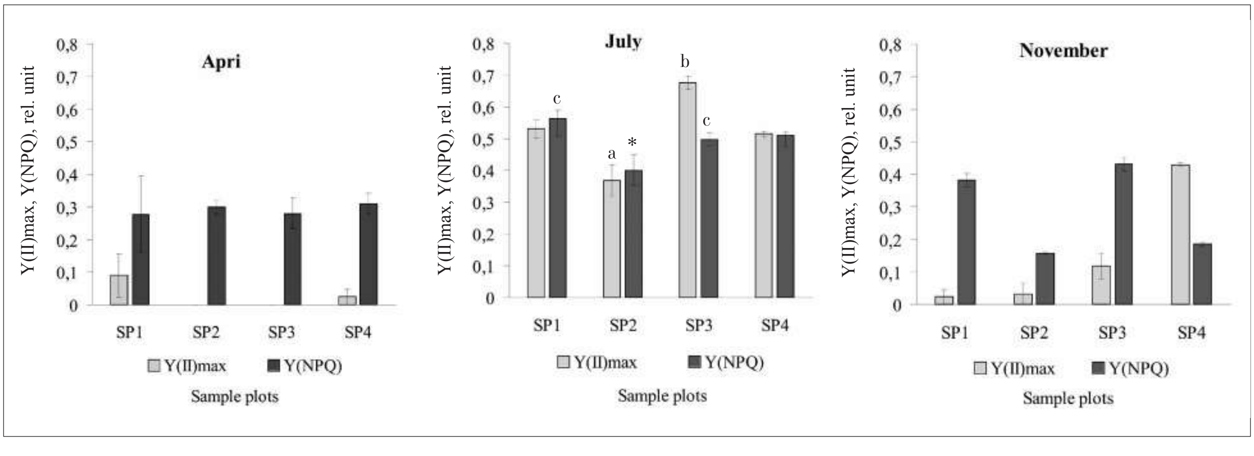

**Fig. 4.** Seasonal changes of maximum photochemical quantum yield of photosystem II, $Y(II)_{max}$, and quantum yield of light-induced non-photochemical fluorescence quenching, Y(NPQ), in *Pinus sibirica* needles. The marks *a*, *b* and *c* indicate significant differences between sample plots in the $Y(II)_{max}$, * – in Y(NPQ) ($p < 0.05$)

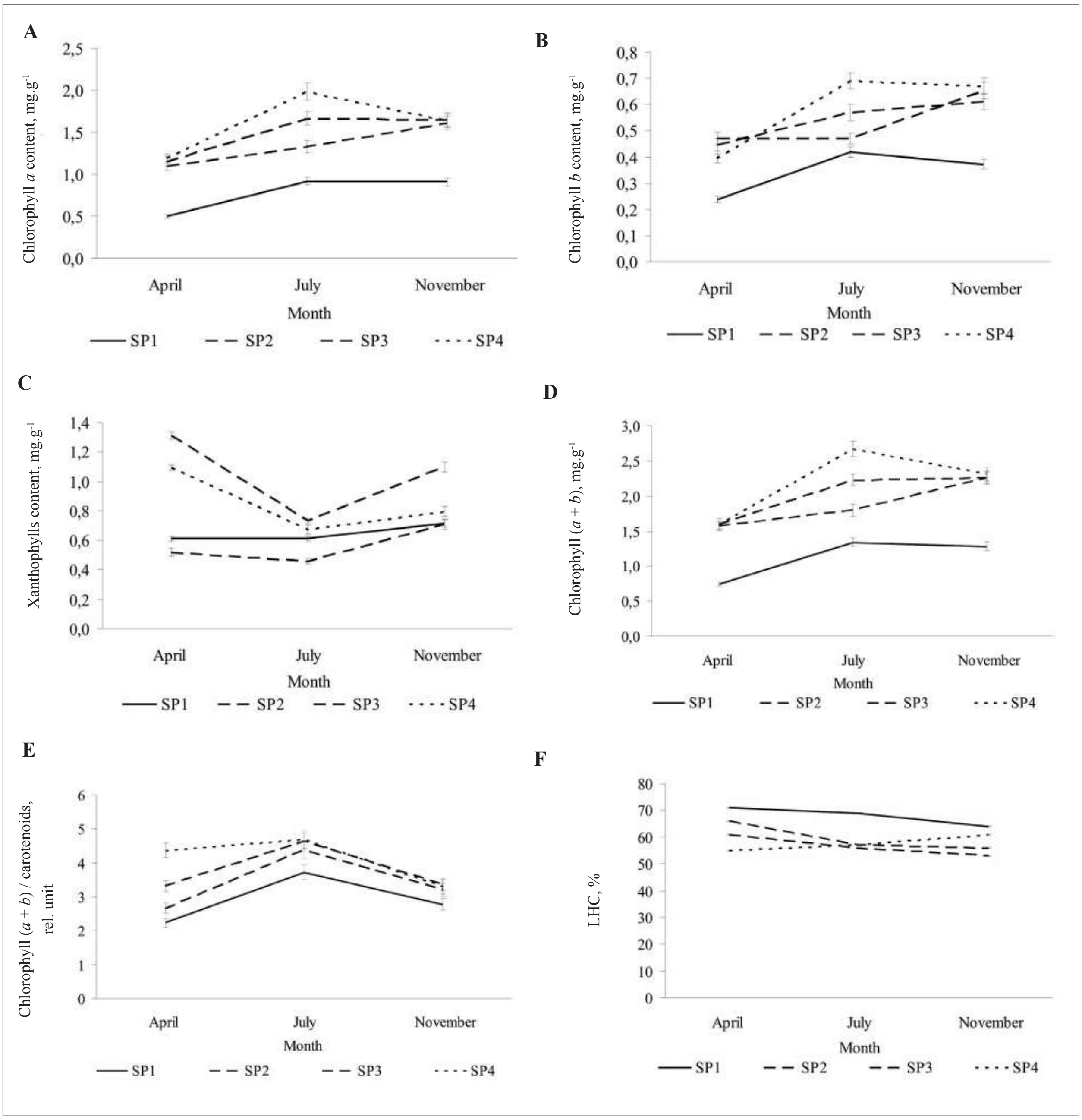

**Fig. 5.** Seasonal variations of chlorophyll *a* (A), chlorophyll *b* (B), xanthophylls (C), chlorophyll *a*+*b* (D), chlorophyll to carotenoids ratio (E), light-harvesting complexes – LHC (F) in Siberian pine needles, recalculated to dry mass

II ($Y(II)_{max}$) for SP1 are higher than for other sample plots, the variability being quite significant. An explanation may be that the shoots are partly covered by snow. The quantum yield of light-induced non-photochemical fluorescence quenching (Y(NPQ)) values on all the sample plots amounts a half of the summer maximal values. In spring, no significant differences for this parameter were found among the sample plots.

In July, the $Y(II)_{max}$ value was recorded in needles from SP3. It is the sample plot where Siberian pine dominates in the stand. On SP4 where the *Abies sibirica* trees are dominanted, the $Y(II)_{max}$ value in Siberian pine is lower. On the uppermost SP1, the potential photochemical activity of photosystem II was high but due to low chlorophyll and high light-harvesting complexes (LHC) complex (Fig. 7). ETR was lower compared to other sample plots. The Y(NPQ) values exceeding the $Y(II)_{max}$ values are recorded in needles on SP1 and SP2 where a dissipated as heat excess energy is required.

In November, the $Y(II)_{max}$ values go down up the slope. The Y(NPQ) values decrease relative the summer levels but the ratios of the values among the sample plots are preserved.

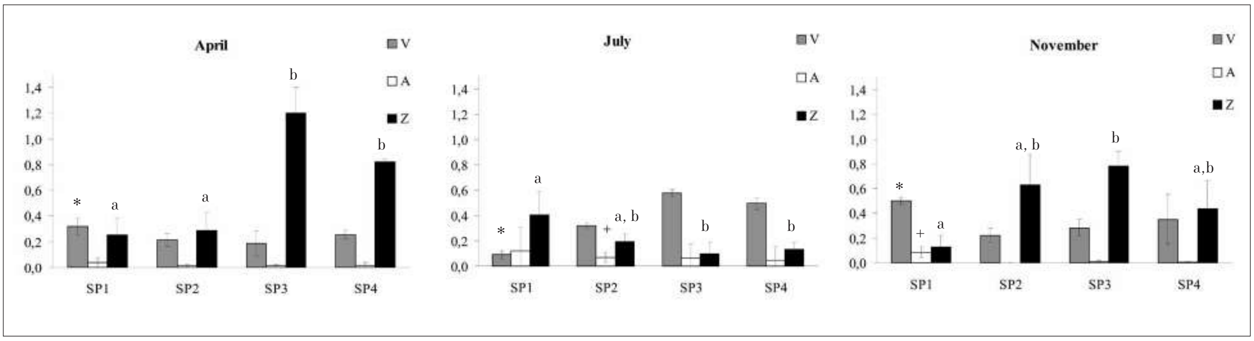

**Fig. 6.** Seasonal variations of carotenoid proportions in xanthophyll cycle in *Pinus sibirica* needles: V – violaxanthin, A – antheraxanthin, Z – all three stereoisomers of zeaxanthin. The marks *a*, *b* and *c* indicate significant differences between sample plots in the zeaxanthin content, * – in the violaxanthin content, + – in the anthraxanthin content ($p < 0.05$)

Figure 5 depicts the seasonal variations of photosynthetic pigment content in Siberian pine needles from different altitudes.

The minimal chlorophyll content in Siberian pine needles is recorded in spring (April), while the maximal in summer (July) (Fig. 5 A, B, D). However, the content levels differ on among the sample plots. Regarding chlorophyll *a* (Fig. 5A), the statistically significant differences ($p < 0.05$) are found for SP1 relatively all other sample plots. In July, all the sample plots differ significantly. In November, SP3 and SP4 do not differ significantly.

Regarding chlorophyll *b* content (Fig. 5B) in winter/spring on SP1, it differs significantly ($p < 0.05$) from all other sample plots. In summer, SP1 does not differ from SP2. In autumn, SP2 does not differ from SP3. It should be mentioned that the highest chlorophyll *b* content is found in forested sample plots (SP3, SP4) while minimal in plots above the treeline, SP2 and especially SP1. This relationship is recorded for SP1 round the year and for other sample plots in summer, at the time of active vegetation.

On the SP2 to SP4, the quantitative differences of chlorophyll content are likely due to differences in illumination conditions. For SP1 Siberian pine growing above the treeline as krummholz, the lowered chlorophyll content may be an adaptation trait. Likely, this is a common feature of conifer saplings under excessive light conditions. The similar data were obtained for *Pinus sylvestris* and *Picea obovata* saplings on clear-cut sites [26]. The dynamics of the total chlorophyll $a + b$ had generally the same trend that of chlorophyll *a* alone.

The xanthophylls content of (Fig. 5C) was higher in spring, decreases in summer and increases again in autumn.

In plant acclimation to light stress under low temperatures, the xanthophyll cycle plays an important role that takes part in the non-photochemical fluorescence quenching. Under frost acclimation, the non-photochemical fluorescence quenching mediated by zeaxanthin transforms from a short-term dynamic reaction into a long-term stable quenching during all the winter season [27].

The minimal values of chlorophyll/carotenoids ratio were characteristic right of SP1 (Fig. 5E). At the absence of photosynthetic activity, there is no need in heat energy dissipation, which is also seen in a low proportion of zeaxanthin to violaxanthin (Fig. 6). Needles of trees from SP3 and SP4 are in dormancy in April but potentially ready to exit from the state under elevated temperature. That is why the proportion of zeaxanthin in xanthophyll complex is significantly higher.

In November, the $Y(II)_{max}$ high levels were only in needles of trees on the lowermost sample plot SP4 (Fig. 4). The above indicates the preseved photosynthetic activity and a minimal role of non-photochemical quenching. The trees from SP2 and SP3 are in a transition from active functioning to the winter dormancy. Their needles contain zeaxanthin several times more than violaxanthin. In summer, the levels of xanthophyll are lowering. An elevated zeaxanthin relative to violaxanthin can be found only in needles from SP1 where the sunlight dissipation and non-photochemical quenching of fluorescence is required.

Ruban [28] reported that the mechanism of the light-dependent non-photochemical depression is effective only under closed reaction centers in photosystem II, that is, under high illumination. In the literature [29, 30], there are evidences that the stress vulnerability increases under high illumination. The cause is that stress being the source of various metabolic disorders impacts the energetic exchange and firstly the photosynthesis. In this case, a plant corrects of input and the use of light energy as a simplest way to adapt and correct the metabolism [28]. So, the mechanism of non-photochemical depression is included as a component in the system of non-specific plant reaction under stress.

## Conclusions

The evaluations of the results should be done in the terms of a comparison of the adaptations of Siberian pine from the habitats above and at the treeline with the typical forest habitats. At higher altitudes, the length of seasonal growth obviously decreases. In spring, a standard situation is that the needles are in the necessary dormancy while the solar radiation reaches high levels. The light dependent mechanisms protecting the photosynthetic apparatus are not yet active. Thus, Siberian pine plants use various survival strategies above and below the treeline. It is manifested in seasonal changes of pigment complexes and parameters of chlorophyll fluorescence of needles. High ETR values are typical for trees with the highest biomass of needle for all sample plots. Regarding the maximum quantum yield of photosystem II, $Y(II)_{max}$, and quantum yield of light-induced non-photochemical fluorescence quenching, Y(NPQ), Siberian pine trees growing above the forest boundary and having mechanisms for dissipating excess light energy have a clear advantage in gaining needle mass over other plants from the same sample plot. For trees from other sample plots, a high proportion of non-photochemical quenching is rather a hindrance. Another parameter that has high correlation coefficients with needle mass for all sample plots is the chlorophyll content. The concentration of carotenoids, even in summer, is especially important for plants on the upper sample plot (SP1), which is in good agreement with the need of processes of non-photochemical quenching.

Thus, the considered parameters of chlorophyll fluorescence and the pigment composition of needles can be used to identify *Pinus sibirica* specimens that are resistant to habitat conditions above the forest boundary, their subsequent use in breeding to increase the area of forested areas under climate change conditions has a practical perspective.

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## References

1. Lyu L., Suvanto S., Nöjd P., Henttonen H.M., Mäkinen H., Zhang Q.B. Tree growth and its climate signal along latitudinal and altitudinal gradients: comparison of tree rings between Finland and the Tibetan Plateau // Biogeosciences. 2017. V. 14. P. 3083–3095. doi: 10.5194/bg-14-3083-2017

2. Klinge M., Dulamsuren C., Erasmi S., Karger D.N., Hauck M. Climate effects on vegetation vitality at the treeline of boreal forests of Mongolia // Biogeosciences. 2018. V. 15. P. 1319–1333. doi: 10.5194/bg-15-1319-2018

3. Kruse S., Gerdes A., Kath N.J., Epp L.S., Stoof-Leichsenring K.R., Pestryakova L.A., Herzschuh U. Dispersal distances and migration rates at the arctic treeline in Siberia – a genetic and simulation-based study // Biogeosciences. 2019. V. 16. No. 6. P. 1211–1224. doi: 10.5194/bg-16-1211-2019

4. Kharuk V.I., Im S.T., Petrov I.A. Alpine ecotone in the Siberian Mountains: vegetation response to warming // J. Mt. Sci. 2021. V. 18. P. 3099–3108. doi: 10.1007/s11629-021-6876-2

5. Grigoriev A.A., Shalaumova Yu.V., Vyukhin S.O., Balakin D.S., Kukarskikh V.V., Vyukhina A.A., Camarero J.J., Moiseev P.A. Upward treeline shifts in two regions of Subarctic Russia are governed by summer thermal and winter snow conditions // Forests. 2022. V. 13. Article No. 174. doi: 10.3390/f13020174

6. Moiseev P.A., Hagedor F., Balakin D.S., Bubnov M.O., Devi N.M., Kukarskih V.V., Mazepa V.S., Viyukhin S.O., Viyukhina A.A., Grigoriev A.A. Stand biomass at treeline ecotone in Russian Subarctic Mountains is primarily related to species composition but its dynamics driven by improvement of climatic conditions // Forests. 2022 V. 13. Article No. 254. doi: 10.3390/f13020254

7. Petrov I.A., Shushpanov A.S., Golyukov A.S., Dvinskaya M.L., Kharuk V.I. Dynamics of tree and shrub vegetation in the Eastern Sayan Mountain Tundra // Russ. J. Ecol. 2021. V. 52. P. 399–405. doi: 10.1134/S1067413621050118

8. Kharuk V.I., Im S.T., Dvinskaya M.L. Forest-tundra ecotone response to climate change in the Western Sayan Mountains, Siberia // Scand. J. For. Res. 2010. V. 25. No. 3. P. 224–233. doi: 10.1080/02827581003766959

9. Petrov I.A., Kharuk V.I., Dvinskaya M.L., Im S.T. Reaction of coniferous trees in the Kuznetsk Alatau alpine forest-tundra ecotone to climate change // Contemp. Probl. Ecol. 2015. V. 8. P. 423–430. doi: 10.1134/S1995425515040137

10. Pakharkova N., Borisova I., Sharafutdinov R., Gavrikov V. Photosynthetic pigments in Siberian pine and fir under climate warming and shift of the timberline // Forests. 2020. V. 11. Article No. 63. doi: 10.3390/f11010063

11. Tantsyrev N.V., Shobairi S.O.R., Usoltsev V.A., Sun L., Zhang H., Li C., He J., Hemmati Roudbari S., Asghari Beirami B., Ayombekov Q. Geographical pecu-

liarities of *Pinus sibirica* Du Tour natural regeneration as related to its seed crops // Curr. World Environ. 2024. V. 19 No. 1. P. 109–123. doi: 10.12944/CWE.19.1.4

12. Velisevich S.N., Bender O.G., Goroshkevich S.N The influence of scion donor tree age on the growth and morphogenesis of Siberian stone pine grafts // New Forests. 2020. V. 52. P. 473–491. doi: 10.1007/s11056-020-09805-2

13. Furbank R.T., Tester M. Phenomics – technologies to relieve the phenotyping bottleneck // Trends Plant Sci. 2011. V. 16. No. 12. P. 635–644. doi: 10.1016/j.tplants.2011.09.005

14. Demidchik V.V., Shashko A.Y., Bandarenka U.Y., Smolikova G.N., Przhevalskaya D.A., Charnysh M.A., Pozhvanov G.A., Barkosvkyi A.V., Smolich I.I., Sokolik A.I., Yu M., Medvedev S.S. Plant phenomics: fundamental bases, software and hardware platforms, and machine learning // Russ. J. Plant Physiol. 2020. V. 67. No. 3. P. 397–412. doi: 10.1134/S1021443720030061

15. Rolfe S.A., Scholes J.D. Chlorophyll fluorescence imaging of plant-pathogen interactions // Protoplasma. 2010. V. 247. P. 163–175. doi: 10.1007/s00709-010-0203-z

16. Dutta S., Cruz J.A., Jiao Y., Chen J., Kramer D.M., Osteryoung K.W. Non-invasive, whole-plant imaging of chloroplast movement and chlorophyll fluorescence reveals photosynthetic phenotypes independent of chloroplast photorelocation defects in chloroplast division mutants // Plant J. 2015. V. 84. No. 2. P. 428–442. doi: 10.1111/tpj.13009

17. Kalaji H.M., Jajoo A., Oukarroum A., Brestic M., Zivcak M., Samborska I.A., Cetner M.D., Łukasik I., Goltsev V., Ladle R.J. Chlorophyll *a* fluorescence as a tool to monitor physiological status of plants under abiotic stress conditions // Acta Physiol. Plant. 2016. V. 38. Article No. 102. doi: 10.1007/s11738-016-2113-y

18. Smolikova G., Kreslavski V., Shiroglazova O., Bilova T., Sharova E., Frolov A., Medvedev S. Photochemical activity changes accompanying the embryogenesis of pea (*Pisum sativum*) with yellow and green cotyledons // Funct. Plant Biol. 2018. V. 45. No. 2. P. 228–235. doi: 10.1071/FP16379

19. Pakharkova N.V., Gaevsky N.A., Gette I.G. Parameters of *Pinus sibirica* photosynthetic apparatus for phenotyping trees in the high-altitude zone of the Western Sayan // J. Sib. Fed. Univ. Biol. 2024. V. 17. No. 2. P. 119–133 (in Russian).

20. WALZ – High Quality Instrumentation for Plant Sciences [Internet resource] http://www.walz.com (Accessed: 15.11.2024).

21. Rudikovskii A.V., Stolbicova A.V., Rudikovskaya E.G., Dudareva L.V. Role of phytohormones in the formation of dwarf and tall Siberian crabapple (*Malus baccata* L. Borkh.) // Zemdirbyste. 2019. V. 106. No. 2. P. 167–172. doi: 10.13080/z-a.2019.106.022

22. Lichtenthaler H.K. Chlorophylls and carotenoids: Pigments of photosynthetic biomembranes // Methods in Enzymology / Eds. S.P. Colowick, N.O. Kaplan. San Diego: Academic Press, 1987. P. 350–382. doi: 10.1016/0076-6879(87)48036-1

23. Küpper H., Seibert S., Parameswaran A. Fast, sensitive, and inexpensive alternative to analytical pigment HPLC: quantification of chlorophylls and carotenoids in crude extracts by fitting with Gauss peak spectra // Anal. Chem. 2007. V. 79. No. 20. P. 7611–7627. doi: 10.1021/ac070236m

24. Rudikovskaya E.G., Dudareva L.V., Shishparenok A.A., Osipova S.V., Stavitskaya Z.O., Rudikovskii A.V. Peculiarities of accumulation of photoprotective compounds by fruit of Siberian crabapple, *Malus domestica* Borkh. and their hybrids growing in conditions of Eastern Siberia // Sci. Hortic. 2019. V. 253. P. 303–308. doi: 10.1016/j.scienta.2019.04.034

25. Robakowski P. Susceptibility to low-temperature photoinhibition in three conifers differing in successional status // Tree Physiol. 2005. V. 25. No. 9. P. 1151–1160. doi: 10.1093/treephys/25.9.1151

26. Tuzhilkina V.V. Photosynthetic activity of coniferous undergrowth in connection with industrial logging // Theoretical and Applied Ecology. 2024. No. 2. P. 22–28 (in Russian). doi: 10.25750/1995-4301-2024-2-022-028

27. Öquist G., Huner N.P.A. Photosynthesis of overwintering evergreen plants // Annu. Rev. Plant Biol. 2003. V. 54. P. 329–355. doi: 10.1146/annurev.arplant.54.072402.115741

28. Ruban A.V. Evolution under the sun: optimizing light harvesting in photosynthesis // J. Exp. Bot. 2015. V. 66. No. 1. P. 7–23. doi: 10.1093/jxb/eru400

29. Pospíšil P. Mechanisms of non-photochemical chlorophyll fluorescence quenching in higher plants // Photosynthetica. 1997. V. 34. P. 343–355. doi: 10.1023/A:1006803832366

30. Maslova T.G., Markovskaya E.F., Slemnev N.N. Functions of carotenoids in leaves of higher plants (review) // Biol. Bull. Rev. 2021. V. 11. No. 5. P. 476–487. doi: 10.1134/S2079086421050078