

Introduction

In a context of global climate change one of the most urgent problems is a stability of water and hydrological cycles in forest ecosystems. However, the possible response of certain species, their communities and ecosystems in different regions to a projected climate change still remains incompletely researched.

To understand the stability of communities and their constituent species to climatic variations, it is necessary to obtain quantitative estimates of plant key indicators, which can be regarded as the reference for these growth conditions.

Ecophysiological investigations in the Forest Institute of the Karelian Research Center of Russian Academy of Science on the territory of Republic of Karelia in forests of Eastern European taiga were conducted during more than 40 years (Fig. 1). On the base of field research works conducted during many years, scopes of natural variability of woody plants' main physiological characteristics were revealed in a wide range of environmental conditions of large region in the north-western taiga zone. Quantitative values of parameters of a CO₂ exchange, water regime, and mineral nutrition of trees (parameters crucial for a stability of woody plants), were determined for these environmental conditions.

Scotch pine (*Pinus sylvestris* L.) is one of the dominant species of East-European taiga zone in Russia. This paper presents results of our research work and literature studies of Scotch pine's (*Pinus sylvestris* L.) key physiological parameters' response to different soil conditions.



Figure 1. Area of research: Republic Karelia, East-European taiga zone of Russia

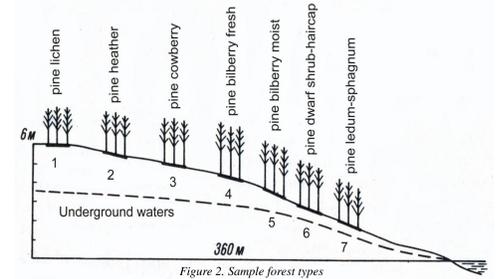


Figure 2. Sample forest types

Material and methods

A long-term investigation was carried out in a field laboratory "Gabozero" located in 50 kilometers to the north from Petrozavodsk. 50-60-years old pine trees of middle-aged forest stands were researched in 7 types of forests (fig 2): 1 - pine lichen, 2 - p. heather, 3 - p. cowberry, 4 - p. bilberry, fresh, 5 - p. bilberry, moist, 6 - p. dwarf shrub-haircap moist, 7 - p. ledum-sphagnum forests.

Sample areas were located at a short distance from each other, on the slope of a straight line, the length of 360 m from a top to a lake.

Water potentials were measured using the Scholander pressure bomb, rate of sap flow - the heat pulse method, and photosynthesis was measured by the Infralit-4 gas analyzer.

Phytomass and a content of mineral elements

(data from Kazimirov et al., 1997)

A productivity and mineral nutrition of forest stands were investigated for all seven forest types listed above. Middle-aged pine stands clearly differed in their productivity (Fig. 3) (Kazimirov et al., 1977).

According to the data obtained by N.I. Kazimirov et al (1977), the increase of an ecosystem productivity associated with an improved soil nutrition, caused the increase of phytomass of both the whole forest stands (Fig. 4), and certain parts of trees (needles, branches, roots, stems).

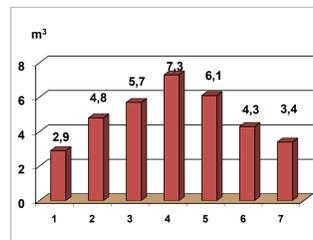


Figure 3. The dependence of current increment on the forest type

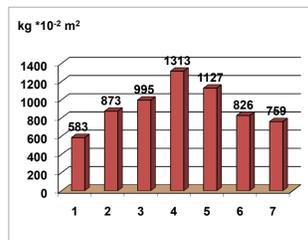


Figure 4. Forest stand phytomass in different types of forests

The change of soil conditions results also in the changes of phytomass fractions ratio. With the increase of stand productivity the share of needles, branches and roots mass naturally decreases and the share of a total mass of trunk phytomass naturally increases (Fig. 5)

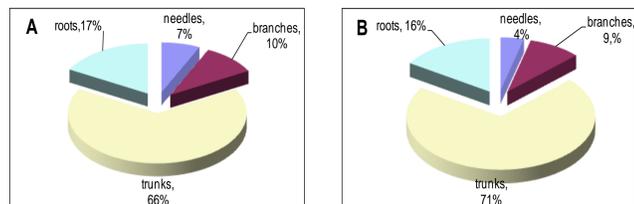


Figure 5. The change in organs mass ratio in two forest stands (lichen pine forest (A) and pine bilberry fresh (B)) differing by their productivity.

A content analysis of mineral elements in plant organs (needles, bark, roots and trunks) showed their dependence on the forest type (Fig. 6). Stable value of mineral elements content (4.51*0.06 kg t⁻¹, coefficient of variation 3.5%) was obtained calculating on a whole plant (a unit of stand phytomass) (Sazonova, Pridacha, 2005) (Fig. 7).

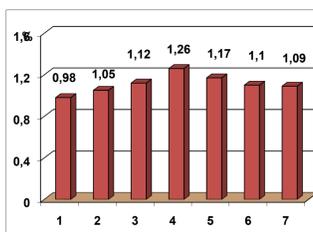


Figure 6. The dependence of needles nitrogen content on the forest type

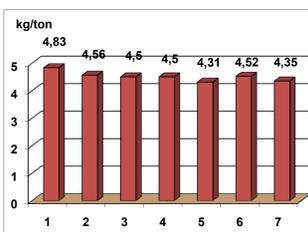


Figure 7. Mineral elements content in a unit of stand phytomass

Differences in the calculation on an organ and on a whole plant are indicative of the existence of a homeostasis maintenance mechanism on an organism level through a redistribution of mineral elements between organs.

A comparison of the data on a content of mineral elements in plant organs and on their structural characteristics showed that a deterioration of soil conditions results in the increasing share of organs, rich in mineral elements (needles, roots) and decreasing share of the poorer ones (trunks). Such changes lead to the fact that a content of mineral elements in a unit of forest stand mass is a constant, not depending on soil conditions. Hence, a formation of relatively high stocks of needles and roots, (i.e. organs with assimilating and absorbing functions) in worse growing conditions is an adaptive mechanism aimed at a support of a mineral elements content level, necessary for normal vital functions.

Water

Investigations of water regime characteristics: water potentials ($\Psi_{sh, max}$ preceding dawn and day $\Psi_{sh, min}$) of needled shoots (Sazonova, 1987; Sazonova, 2006) and sap flow rates (U) (Kaibiyainen et al., 1981; Kaibiyainen, 2003) in three forest types (pine cowberry, p. bilberry fresh and p. dwarf shrub-haircap forests) were held. The comparison of $\Psi_{sh, max}$ and $\Psi_{sh, min}$ of pine needled shoots in different forest types revealed no significant difference ($p > 0.05$) within their variability limits (-0.3 to 1.5 MPa) and between the means for the period of vegetation values (-0.44 ± 0.07 ... -0.43 ± 0.05 MPa and -1.01 ± 0.14 ... -0.97 ± 0.07 MPa). These values appeared to be constant in all years of the research (no significant difference, $p > 0.05$).

The resemblance in values of water moving forces defined the likeness of sap flow rates (\bar{U}). Mean for the vegetation (May to September) daily average \bar{U} appeared to be almost the same for pine cowberry, p. bilberry and p. dwarf shrub-haircap forests. (Fig. 8).

It is known that almost all the moisture absorbed during the year is spent on transpiration. Therefore, the value of \bar{U} can be considered as an average annual value of both intake and consumption of moisture. The amount of moisture, which each stand absorbs and evaporates during a year was calculated by the formula (1-1):

$$G = 24 \cdot \bar{u} \cdot S \cdot N \quad (1-1)$$

where \bar{u} is the mean for a year daily average rate of sap flow, moving through a trunk xylem (g cm⁻² hour⁻¹), N – the number of days, S – the area of stand's "active" (with a moving sap flow) xylem (m²).

$$S = s \cdot n \quad (1-2)$$

where s is the area of average tree's "active" xylem (m²), n – the number of trees in a stand.

Pine cowberry, pine bilberry fresh and pine dwarf shrub-haircap forests turned out to absorb and evaporate different amounts of moisture during the year (Fig. 9). Differences in G values are primarily related to the difference in the area of active xylem and the mass (surface) of transpiring needles in different forest types.

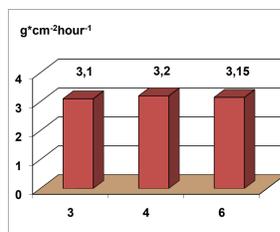


Figure 8. Mean for a vegetation period daily average sap flow rates in pine cowberry (3), pine bilberry fresh (4) and pine dwarf shrub-haircap (6) forests.

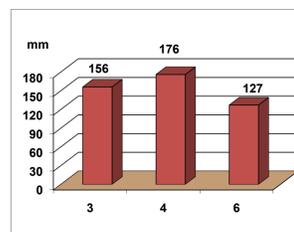


Figure 9. The consumption of moisture by stands of pine cowberry (3), pine bilberry fresh (4) and pine dwarf shrub-haircap (6) forests.

Other important characteristics of water regime (and eventually water cycles) are:

A) coefficient of xylem's conducting ability, i.e. the amount of water, that moves through a unit of an "active" xylem of a forest stand during a year (G/S).

B) coefficient of needles' transpiration activity, i.e. the amount of water, that a unit of stand needles' mass evaporates during a year (G/m).

The calculation of these coefficients revealed no response to growth conditions. Thus, the coefficients also appeared to be constants (Fig. 10 and Fig. 11)

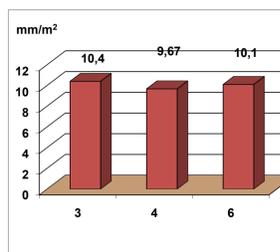


Figure 10. Coefficients of needles' transpiration activity in pine cowberry (3), pine bilberry fresh (4) and pine dwarf shrub-haircap (6) forest types

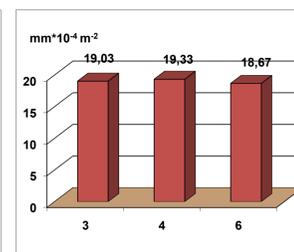


Figure 11. Coefficients of xylem's conducting ability in pine cowberry (3), pine bilberry fresh (4) and pine dwarf shrub-haircap (6) forest types

It was shown that there is a strict compliance and a close correlation between different elements of structure in the system of pine water transport. In particular, we have shown (Kaibiyainen et al., 1986), that the relationship between the area of stem's active xylem (S_{st}) and a mass of needles (m_{nd}) is described by a linear equation:

$$m_{nd} = 51.66 S_{st} \quad (R^2 = 0.98)$$

Constant coefficients of conduction and transpiration capacity of active xylem and needles can be considered as the evidence of a balanced water conducting system in a functional sense. Pine's adaptation to changing conditions of a soil hydrological regime is due to changes in the mass of needles and the area of the conducting xylem, i.e., according to L.K. Kaybiyaynen (2003), has the character of structural adaptations.

Photosynthesis

The research of photosynthesis (P) in three different (by their productivity) forest types (pine heather, pine bilberry fresh and pine dwarf shrub-haircap moist forests) during summer months (June-July) of several vegetation periods was made (Bolondinskiy, 1994). The comparison of photosynthesis' seasonal variations in pine trees of different forest types identified several features associated with the growth conditions. However, the comparison of average for the research period mean daily P values revealed no significant differences ($p > 0.05$) (Fig. 12).

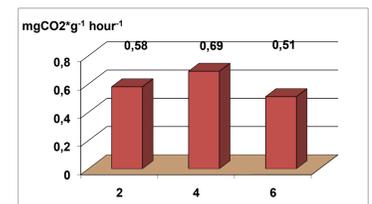


Figure 12. Pine trees photosynthesis in pine heather (2), pine bilberry fresh (4) and pine dwarf shrub-haircap (6) forest types (no significant difference, $p > 0.05$)

The closeness of compared values is primarily due to the fact that the main environmental factor determining a rate of photosynthesis for a long term is a solar radiation. A linear connection ($R^2 = 0.980 - 0.998$) between a photosynthesis' efficiency and a total solar radiation during the most time of researched vegetation periods was revealed (Bolondinskiy, Kaibiyainen, 2003). A disturbance of the rule was observed in spring, that can be explained through the depressive effect of low temperatures. Its preservation during the rest of a growing season indicates a weak influence of other environmental factors on a rate of photosynthesis.

Conclusion

Thus, an adaptation of pine stands to different conditions of growth takes place primarily through changes in both a total phytomass of a stand, and its individual components (needles, branches, roots, tree trunks). These changes are intended primarily to maintain a certain level of carbon, water and mineral status of pine trees. Results of our study revealed constant parameters of CO₂ exchange, water and mineral metabolism to be supported by a plant organism at a certain level. Thus, the adaptation strategy of coniferous plants to changing environmental conditions aimed at maintaining a homeostasis by changing a mass of plant organs.

This adaptation strategy is supported by a number of structural features inherent in a plant as a vital form. First of all, it is a large mass of plants, a large area of assimilating mixed-age surface, a prolonged duration of a life cycle, a large amount of non-living (lignified) tissues in a conduction system. All of these creates a large pool of structural components and the ratio between them can vary without disturbing the integrity of a plant organism.

The results obtained in our work can be used in models of SVAT class (Soil-Vegetation-Atmosphere-Transfer) (Oltchev et al., 2008) to predict a possible response of vegetation, as the main component of ecosystems, to a global climate change and pollution of environment.

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Acknowledgements:

This study was carried out within the frameworks of the Northern Eurasian Earth Science Partnership Initiative (NEESPI) and supported by grants of the Russian Foundation for Basic Research (RFBR 08-04-01254-a, 09-04-00299-a, 10-04-10122-s).