# Age-related Dynamics of Spruce Forest Communities in Lithuania

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Research was conducted on the mostly widespread (6) types of spruce forests by using permanent and temporary sample plots. The goals are to clarify species composition of communities, changes of biodiversity and ecological conditions, to determine the most constant site type indicators and the regularities of natural regeneration.

The most changing component during the stand course of years is the ground cover vegetation. The most abundant species diversity and herbal projection cover is in cutovers, slightly lower is in mature stands. According to the structure of spruce communities five age stages of their development can be singled out: cutting area, crown closing, thicket, self-thinning and stabilization (sub-climax). Similarity between these stages is low (evaluating according the coefficient of Sørensen).

Ecological conditions are different at separate community stages. In cutovers not only light regime but also hydrological regime indicators are changing as well (in increasing tendency). Soil reaction increases slightly with increasing stand age.

There are very few vegetation indicators characteristic of a certain forest type that would be common at all stages of development. However, there is a number of determinants, which helps identify communities of different forest types. Species composition of undergrowth in the spruce forests varies greatly; nevertheless, 70 % of it comprises spruce, which occurs in mature stands more frequently.

**Key words:** spruce stands, age-related dynamics, forest ground cover, biodiversity, phytoindication, underwood, height growth of stands.

## Introduction

Stand structure and age (excluding site conditions) most crucially affect floristic composition and structure of forest phytocoenoses. With increasing age of stand the structure of the upper layer changes. Consequently, changes occur in the conditions for the formation of forest ground cover vegetation, undergrowth and underwood in the lower layers. Age-related changes in forest communities are distinct in stands of the species with dense crowns in particular. In Lithuania spruce stands are the most characteristic among them.

Studies conducted on the dynamics of age of forest communities are important from several points of view. Firstly, it is necessary to investigate the changes of indicators of site conditions in the course of stand age. It would enable us to create a dynamic system of diagnostic indices of reliable forest types. Secondly, regularities of biodiversity's changes with increasing age of stands should be determined to make possible best measures of its preservation to be chosen. Thirdly, clarification of the regularities of variation in natural forest communities provides the foundation (baseline) for determining the magnitude of anthropogenic changes. Fourthly, investigations of originating underwood permit us to define more precisely the regularities of stand development and processes of species' changes. Besides, the results of these investigations are the recording of phytocoenose composition of the investigated period. Therefore, in the future they may be valuable in clarifying climate-induced changes.

Long-term investigations comprising all stages of stand development starting with the forming up to maturity and decomposition can take hundreds of years. They have never been carried out in permanent research plots. Nevertheless, these processes have been investigated by other reliable enough methods, e.g. studying stands of different age growing under similar site conditions and making natural consecution of them. In Lithuania analysis of spruce-deciduous stands' formation, their regeneration after clear cutting, was performed using these methods (Kairiūkštis 1973, Kairiūkštis, Juodvalkis 1985). The issues of changes in the phytocoenotical structure of lower layers of these stands were analysed too (Вайтекус 1985, Вайтекус, Каразия 1986). However, the investigation of full dynamics of forest communities' structural variations depending on age and according to forest types is not accomplished yet. The question itself has not even been raised earlier, as in some studies (Regel 1945-1948) forest communities of different age stages were treated as if they were different associations of forest types. In Lithuania this question became actual only after the unified forest typological classification system has been created (Karazija 1988). Regularities revealed in similar research in different climate conditions and in forests of different communities' structure (Siren 1955, Leibundgut 1978, Георгиевский 1992, Jenssen, Hofmann 1996, Roder et al. 1996, Kuuluvainen et al, 1998, Vrska 1998 et al.) cannot be transferred to other places, they can be compared only.

The objectives of our research, the results of which are analysed in this article, were the following: a) to determine changes in species composition of Lithuania's spruce stands vegetation in the course of stands' age in order to find diagnostic indications for forest type identification; b) to find regularities in biodiversity changes; c) to evaluate variations of ecological conditions in the process of stands' development; d) to find changes of woody vegetation in order to know better the regularities of self-regeneration and stands' recreation and formation. At the same time it was an attempt to clarify certain methodical issues of forest communities' research and classification.

The paper deals with the analysis of the change in vegetation composition and structure of spruce stand communities in stands of different age as well as with the process of height growth of a tree. The analysis of the change in species composition of vegetation layer in stands is beyond the scope of the paper since investigations have been carried out in stands where spruce prevails in species composition independently of the fact how this composition has been formed.

## Material and methods

The investigations have been conducted on spruce stands, which have been forming on sites of mineral soils without distinct signs of bogging up. There are six types of such spruce stands in Lithuania (*Vaccinio-myrtillosa, Myrtillosa, Oxalidosa, Oxalido-myrtillosa, Hepatico-oxalidosa, Oxalido-nemorosa*). Data of permanent and temporary observation plots were used.

Permanent observation plots were set up in cutting areas (in areas of windfalls mostly), which were planted with spruce seedlings and young spruce stands were formed. Over a period of 15-30 years the plots were followed up regularly every two years, later every three-five years by mapping and carrying out inventory of all vegetation layers. The data on 25 plots have been used (205 descriptions).

Phytocoenosis structure of older spruce stands has been investigated in 152 temporary plots. Objects for investigation have been chosen in pure spruce stands or with insignificant admixture of other species. Stocking of the spruce stands is normal or close to it. In choosing the objects for investigation the priority was given to forests where at small distances stands of the same type but of different age had been found. Stand age of the plot investigated has been determined by 3-5 borings with the aid of an age borer, the height of 5-9 dominating trees has been measured with a heightmeter. Other inventory indices (tree diameter, sum of stands' cross-sections, volume) have been obtained measuring trees in temporary round plots, the area of which depended upon average stand diameter and varied from 100 $m^2$ in young stands to 800 $m^2$ in mature stands (Juknys et al. 1982). To make graphs of stands' growth process F. Korsun (Корсунь 1976) equation was applied to approximate original data. According to many authors (Schmidt 1967, Свалов 1978 et al.) this equation suits best for this purpose.

Undergrowth and underwood in every plot have been described in transects of 2 m wide or in the squares of 4 $m^2$ distributed systematically. Their total area was not less than 100 $m^2$ (Воробьев 1967, Мартынов 1992). Shrub quantity in separate types of undergrowth has been determined according to height groups. Abundance of different species has been determined as well according to the Braun-Blanquet scale. Underwood has been grouped according to tree species, age and vitality. Inventory of herb and moss cover has been carried out by the method of microsquares (1 $m^2$). In one plot of investigation they number 20. In these squares species composition and projection cover (Braun-Blanquet 1964, Сукачев, Зонн 1961, Воробьев 1967, Karazija 1978, 1988) of different species have been determined.

To ascertain the process of tree growth and quantity of underwood, along with the above data, the findings of special investigations of regeneration and data on the plots of statistical forest inventory have been applied.

In analysing changes in communities' composition the data on forest type were grouped according to age periods, the span of which increases with increasing stand age, as changes are the most rapid in the phase of stand formation (Karazija 1988).

The Sørensen (1948) coefficient was used to determine similarity of communities. Ecological conditions of communities' sites and their changes were evaluated making use of indices of plants' ecological values determined by H.Ellenberg (1950, 1991) and L.Ramenskij (Раменский 1953, 1956) phytoindication method and comparative ecological tables of plants. To compare biological diversity the Shannon index (Hunter 1990) was used.

## Results

*A change in quantitative and qualitative indices of forest ground cover vegetation*

Forest ground cover vegetation is the most changing structural element of forest communities excluding stand, which disappears completely after felling. In Table 1 some indices of forest ground cover vegetation of different stand age in forest communities are presented.

As shown in the Table, in the process of stand formation significant changes in indices of forest ground cover vegetation are observed in the communities of all forest types. In the first year after felling the number of ground cover vegetation species as well as projection cover diminishes because most of the plants, which have been growing under a stand, languish. However, in the second year plant species characteristic of cutting area, the total number of herb species and projection cover augment. Because of crown closure the number of herb species and projection cover decrease again. In stands aged from 20 to 50 years the number of herb species is least. In some communities projection herb cover approaches zero. Later due to self-thinning of a stand in lower layers vegetation becomes more abundant and ground cover vegetation typical of mature stands forms. These regularities are characteristic of spruce stands communities of all forest types. However, in spruce stands (Fig.1) on more fertile sites (*Hepatico-oxalidosa, Oxalido-nemorosa* forest types) change range is more significant in comparison to these on less fertile sites (*Myrtillosa, Myrtillo-oxalidosa* forest types).

The number of typical forest vegetation species and projection cover vary similarly. Only the range of change is less. Besides, the maximum of the total number of species and their projection cover are observed in cutovers during stand restoration whilst typical forest plants are most abundant in communities of mature stands (Table 1). The least number of typical forest vegetation species and the minimal projection cover in the communities of all forest types have been found at the stage of dense young stands. However, these two minima in terms of time frequently do not coincide: at first the number of species diminishes, later - projection cover.

Regularities of the changes in moss cover are slightly different. In the first year following felling the quantity of moss decreases in particular. In older cutovers the number of moss species augments and preserves with slight variations till the stage of mature stand communities, although the species themselves (species composition) change. Projection cover of moss and the change in it depend upon site conditions. In spruce stands of less fertile (poorer) sites the distinct maximum of moss projection cover is observed in mature stands. Density of moss cover in mature spruce stands and yet forming young stands on more fertile sites (*Hepatico-oxalidosa, Oxalido-nemorosa* forest types) is similar though species composition differs. Moss cover in communities (aged 20-45-years) of formed dense young stands on all sites is slightly thinner (Table 1).

In accordance with the variations in the indices of ground cover vegetation which include the number of plant species and extent of cover all investigated spruce stand communities in the age range may be

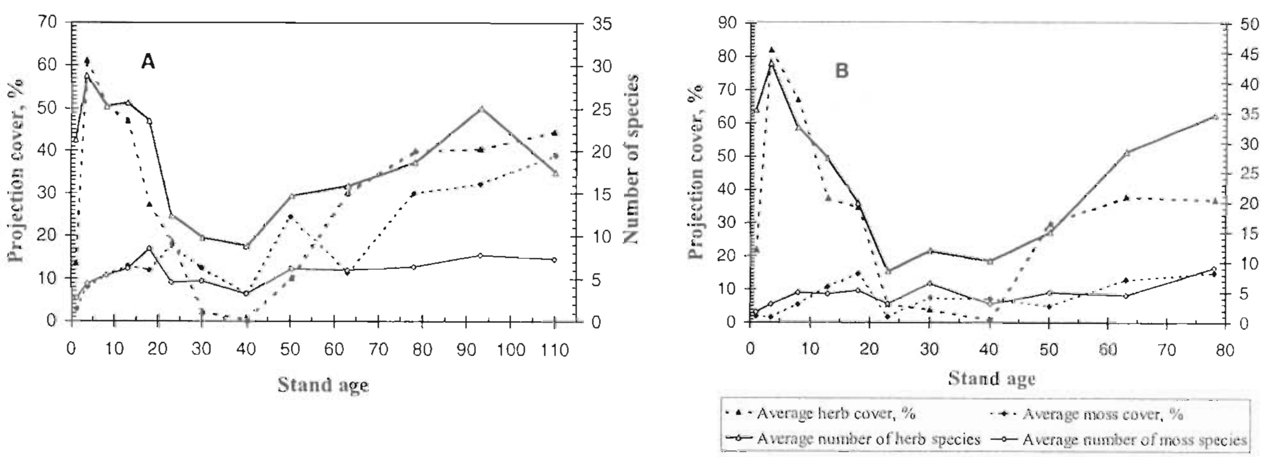


**Figure 1.** The number of grass and moss species and stand age-related change in projection cover in spruce stand communities of *Myrtllo-oxalidosa* (A) and *Oxalido-nemorosa* (B) types.

**Table 1.** Age-related changes in forest ground cover vegetation

| Indexes | Stand (cutover) age (years) | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 1 | 2-5 | 6-10 | 11-15 | 16-20 | 21-25 | 26-35 | 36-45 | 46-55 | 56-70 | 71-85 | 86-100 | >100 |
| *Vaccinio myrtillosa* type | | | | | | | | | | | | | |
| The number of deceriptions | 4 | 5 | - | - | - | - | 1 | - | - | 1 | 3 | 5 | 2 |
| Average number of herb-semishrub species | 12.0± 2.1 | 22.2± 3.1 | | | | | 7 | | | 11 | 17.5± 3.0 | 16.4± 4.1 | 13.0± 4.0 |
| of them forest plants* | 7.3± 0.9 | 11.5± 4.7 | | | | | 5 | | | 8 | 13.5± 2.7 | 13.8± 3.6 | 11.5± 2.5 |
| Average projection cover of herb-semishrub, % | 19.4± 3.9 | 64.8± 6.4 | | | | | 4.1 | | | 13.9 | 27.9± 7.6 | 36.6± 5.7 | 22.6± 4.7 |
| of them forest plants | 10.2± 3.0 | 5.0± 2.4 | | | | | 3.0 | | | 13.6 | 24.8± 5.9 | 36.0± 4.9 | 22.4± 5.0 |
| Average number of moss species | 1.7± 0.6 | 4.2± 1.0 | | | | | 2 | | | 3 | 4.5± 1.1 | 5.0± 0.9 | 9.0± 1.7 |
| Average projection cover of moss, % | 5.2± 1.3 | 3.8± 1.6 | | | | | 2.0 | | | 66.1 | 31.9± 4.5 | 50.9± 5.7 | 70.9± 6.7 |
| *Myrtillosa* type | | | | | | | | | | | | | |
| The number of deceriptions | 5 | 15 | 5 | 2 | 2 | 4 | 4 | 3 | 1 | - | 2 | 4 | 6 |
| Average number of herb-semishrub species | 12.3± 2.9 | 20.4± 2.2 | 13.2± 3.2 | 12.5± 3.5 | 6.0± 3.1 | 9.0± 1.2 | 10.7± 2.9 | 8.5± 1.5 | 10 | | 15.0± 4.0 | 12.3± 2.2 | 16.5± 3.7 |
| of them forest plants | 5.6± 1.7 | 8.8± 1.1 | 5.6± 1.6 | 7.5± 2.5 | 3.0± 1.0 | 4.3± 0.3 | 8.2± 2.7 | 7.5± 1.0 | 8 | | 12.5± 3.0 | 10.8± 1.4 | 13.3± 2.5 |
| Average projection cover of herb-semishrubs, % | 7.0± 2.1 | 63.0± 6.6 | 58.4± 7.1 | 33.5± 9.5 | 37.0± 9.9 | 29.0± 7.2 | 14.0± 5.8 | 1.6 ±0.9 | 5 | | 28.0± 13.0 | 46.5± 4.8 | 45.3± 4.5 |
| of them forest plants | 3.9± 1.3 | 14.8± 2.7 | 18.4± 5.5 | 18.0± 6.0 | 10.5± 4.5 | 12.7± 3.8 | 6.2± 2.9 | 1.0± 0.7 | 5 | | 27.0± 9.5 | 42.6± 3.4 | 40.2± 5.7 |
| Average number of moss species | 2.5± 0.7 | 5.0± 0.5 | 6.4± 0.2 | 6.0± 1.0 | 4.5± 0.5 | 4.7± 1.5 | 4.5± 1.0 | 4.5± 1.5 | 3 | | 8.5± 2.5 | 7.0± 1.1 | 8.0± 0.9 |
| Average projection cover of moss, % | 2.6± 1.2 | 10.2± 2.0 | 27.6± 5.7 | 15.0± 6.0 | 23.0± 9.0 | 24± 12.1 | 16.3± 6.6 | 13.5± 7.5 | 12 | | 33.5± 15.5 | 57.0± 6.7 | 52.8± 5.5 |

* Species growing only in the forest or having spread mostly in forest communities are assigned to forest plants

grouped into 5 stages of stand development, depending upon stands' age and their structure: cutover (stand restoration), crown closing (stand forming), thicket (pole stand), self-thinning and stabilization.

Although these stages are singled out according to the indices of forest ground cover vegetation they coincide with the phases of stand development and should be coordinated with corresponding economic measures. The stage of cutover (stand restoration) encompasses spruce stands aged up to 10 years, closing - 10-25 years, thicket - 25-45 years, self-thinning - 45-70 years, older forest communities should belong to the stage of stabilization. However, the limits of these stages cannot be very stringent as they depend upon site conditions and economic effect. As seen from Table 1, on more fertile sites these stages are shorter than on poorer ones.

*Change of biodiversity's ecological conditions and indicators.*

With increasing age of spruce stand the changes in forest ground cover vegetation result in the variation in the extent of biological diversity. It has been determined that variations in the Shannon index (Fig.2) depend not only upon stand age but also on site conditions too. The communities of fertile sites - *Hepatico-oxalidosa* and *Oxalido-nemorosa* possess higher indices of diversity while these on less fertile sites -

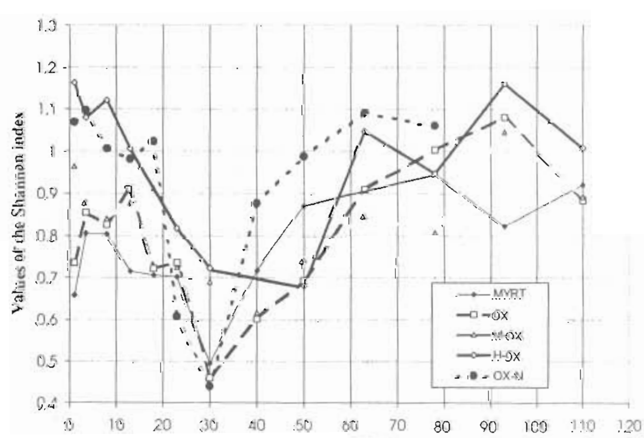


**Figure 2.** The variation in the Shannon index depending upon age of spruce stands of different forest types. Forest types indices: myrt - *Myrtillosa*, ox – *Oxalidosa*, m-ox – *Myrtyllo-oxalidosa*, h-ox – *Hepatico-oxalidosa*, ox-n – *Oxalido-nemorosa*.

Continuation of **Table 1**

| Indexes | Stand (cutover) age (years) | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 1 | 2-5 | 6-10 | 11-15 | 16-20 | 21-25 | 26-35 | 36-45 | 46-55 | 56-70 | 71-85 | 86-100 | >100 |
| *Oxalidosa* type | | | | | | | | | | | | | |
| The number of decериptions | 4 | 11 | 8 | 6 | 3 | 7 | 3 | 4 | 4 | 14 | 2 | 3 | 3 |
| Average number of herb-semishrub species | 18.0± 1.4 | 25.7± 2.1 | 23.3± 2.0 | 20.3± 2.5 | 16.3± 2.0 | 14.1± 3.3 | 8.7± 2.1 | 13.7± 4.3 | 17.0± 2.3 | 23.2± 1.7 | 19.0± 2.0 | 22.3± 3.9 | 25.7± 4.0 |
| of them forest plants | 12.5± 1.9 | 13.4± 0.9 | 12.9± 1.2 | 10.7± 1.5 | 11.3± 1.7 | 10.4± 2.9 | 7.0±2 .1 | 11.7± 3.8 | 15.0± 2.1 | 20.6± 1.6 | 19.0± 2.0 | 20.3± 3.9 | 23.7± 3.4 |
| Average projection cover of , % | 21.0± 8.6 | 81.4± 5.5 | 80.2± 8.6 | 64.2± 8.3 | 34.7± 9.7 | 13.9± 3.7 | 5.0± 2.3 | 4.2± 1.7 | 10.8± 4.7 | 41.6± 5.5 | 29.0± 7.0 | 52.3± 8.8 | 59.3± 6.2 |
| of them forest plants | 7.8± 2.5 | 18.2± 2.1 | 12.0± 3.4 | 9.7± 2.2 | 7.7± 1.4 | 5.9± 1.3 | 3.8± 3.1 | 3.5± 1.0 | 10.3± 4.4 | 39.0± 5.2 | 29.0± 7.0 | 50.3± 7.6 | 55.7± 6.9 |
| Average number of moss species | 2.0± 0.7 | 4.0± 0.8 | 4.9± 0.5 | 6.3± 1.1 | 6.7± 0.3 | 1.9± 1.0 | 5.3± 0.9 | 3.5± 0.5 | 4.3± 0.5 | 5.7± 0.8 | 4.5± 1.5 | 8.3± 0.3 | 5.3± 2.2 |
| Average projection cover of moss, % | 2.5± 1.5 | 5.2± 1.5 | 10.1± 2.7 | 9.5± 3.4 | 10.7± 7.4 | 7.1± 3.1 | 7.6± 4.6 | 7.0± 3.4 | 18.5± 5.5 | 17.4± 2.3 | 19.5± 9.5 | 24.3± 4.8 | 15.3± 5.7 |
| *Myrtillo-oxalidosa* type | | | | | | | | | | | | | |
| The number of decериptions | 7 | 15 | 8 | 5 | 2 | 5 | 9 | 12 | 6 | 9 | 5 | 4 | 4 |
| Average number of herb-semishrub species | 21.3± 1.7 | 28.8± 1.7 | 25.2± 2.0 | 25.6± 0.4 | 23.5± 2.5 | 12.4± 2.5 | 9.8± 1.0 | 8.8± 1.7 | 14.7± 2.3 | 15.9± 2.0 | 18.6± 4.5 | 25.0± 4.3 | 17.5± 4.8 |
| of them forest plants | 12.9± 1.6 | 14.2± 1.3 | 10.4± 1.6 | 14.2± 1.8 | 15.5± 2.5 | 7.4± 1.6 | 7.8± 0.6 | 8.0± 1.6 | 11.8± 1.7 | 13.1± 1.9 | 15.6± 3.9 | 19.3± 3.3 | 16.0± 4.2 |
| Average projection cover of herb-semishrub, % | 13.7± 5.5 | 61.2± 5.0 | 50.4± 8.6 | 47.0± 8.3 | 27.5± 3.5 | 18.6± 4.7 | 2.3± 0.9 | 0.4± 0.1 | 10.2± 3.5 | 30.1± 7.1 | 40.0± 5.7 | 40.5± 9.0 | 44.5± 3.9 |
| of them forest plants | 10.7± 4.9 | 13.3± 2.2 | 6.6± 2.3 | 12.6± 2.4 | 10.0± 2.0 | 9.2± 2.2 | 1.6± 0.7 | 0.3± 0.1 | 8.2± 2.7 | 28.0± 5.1 | 37.9± 6.2 | 37.5± 8.0 | 39.9± 4.3 |
| Average number of moss species | 2.7± 0.3 | 4.4± 0.5 | 5.4± 0.9 | 6.2± 1.0 | 8.5± 0.5 | 4.6± 1.3 | 4.7± 0.3 | 3.2± 0.4 | 6.2± 1.3 | 6.0± 0.7 | 6.4± 1.3 | 7.8± 1.8 | 7.3± 0.7 |
| Average projection cover of moss, % | 2.9± 0.8 | 8.1± 2.5 | 10.7± 4.1 | 13.0± 4.8 | 12.0± 2.0 | 17.8± 6.3 | 12.6± 0.5 | 6.6± 2.5 | 24.5± 7.6 | 11.4± 4.2 | 30.0± 7.7 | 32.3± 12.2 | 39.0± 12.1 |

Continuation of **Table 1**

| Indexes | Stand (cutover) age (years) | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 1 | 2-5 | 6-10 | 11-15 | 16-20 | 21-25 | 26-35 | 36-45 | 46-55 | 56-70 | 71-85 | 86-100 | >100 |
| *Hepatico-oxalidosa* type | | | | | | | | | | | | | |
| The number of decериptions | 7 | 2 | 3 | 1 | - | 1 | 1 | - | 2 | 4 | 2 | 7 | 1 |
| Average number of herb-semishrub species | 32.9± 2.3 | 31.5± 7.5 | 40.7± 7.2 | 16 | | 7 | 8 | | 25.0± 2.0 | 24.8± 4.0 | 23.5± 1.5 | 32.7± 0.9 | 35 |
| of them forest plants | 25.9± 1.5 | 24.5± 5.5 | 21.7± 3.2 | 9 | | 6 | 8 | | 23.0± 2.0 | 22.2± 3.5 | 23.0± 1.0 | 30.9± 1.0 | 34 |
| Average projection cover of grass-semibushes, % | 28.4± 5.3 | 90.5± 8.5 | 82.3± 8.7 | 32 | | 4 | 2 | | 23.5± 0.5 | 65.5± 5.9 | 65.0± 1.0 | 55.0± 6.6 | 49 |
| of them forest plants | 23.5± 2.2 | 21.0± 3.0 | 14.7± 0.7 | 9 | | 4 | 2 | | 22.0± 0.5 | 64.0± 5.4 | 64.8± 1.0 | 53.6± 6.3 | 48.7 |
| Average number of moss species | 0.6± 0.6 | 0.5± 0.5 | 3.3± 1.4 | 4 | | 3 | 6 | | 7.5± 1.5 | 7.0± 1.5 | 5.0± 1.0 | 4.3± 1.1 | 6 |
| Average projection cover of moss, % | 1.0± 1.0 | 0.5± 0. 5 | 3.5± 1.4 | 10 | | 7 | 3 | | 6.0± 2.0 | 10.5± 4.1 | 8.5± 3.5 | 4.7± 1.6 | 4.3 |
| *Oxalido-nemorosa* type | | | | | | | | | | | | | |
| The number of decериptions | 6 | 10 | 4 | 4 | 3 | 4 | 2 | 8 | 3 | 5 | 4 | | |
| Average number of herb-semishrub species | 35.5± 2.5 | 43.4± 3.0 | 32.5± 3.7 | 27.3± 4.4 | 20.0± 2.1 | 8.5± 3.7 | 12.0± 7.0 | 10.2± 3.1 | 15.0± 2.7 | 28.4± 4.0 | 34.5± 6.0 | | |
| of them forest plants | 22.5± 2.9 | 21.7± 1.7 | 19.5± 1.5 | 17.3± 2.9 | 14.7± 2.3 | 7.3± 3.3 | 10.5± 4.8 | 9.6± 2.9 | 14.0± 2.1 | 26.2± 3.5 | 29.3± 3.7 | | |
| Average projection cover of herb-semishrub, % | 21.8± 3.8 | 81.9± 5.6 | 67.0± 5.4 | 37.3± 7.9 | 34.7± 6.8 | 5.5± 3.8 | 4.0±2 .1 | 0.9± 0.5 | 29.7± 12.4 | 37.8± 7.4 | 36.8± 5.3 | | |
| of them forest plants | 12.5± 2.6 | 19.4± 1.4 | 20.3± 3.9 | 19.2± 4.2 | 15.7± 0.7 | 4.7± 3.5 | 3.0±2 .0 | 0.8± 0.5 | 29.3± 9.9 | 36.4± 7.0 | 34.5± 4.8 | | |
| Average number of moss species | 1.7± 0.7 | 3.1± 1.0 | 5.0± 0.9 | 4.8± 0.5 | 5.3± 0.3 | 3.2± 0.7 | 6.5± 2.5 | 3.0± 0.4 | 5.0± 2.5 | 4.6± 1.0 | 9.2± 3.3 | | |
| Average projection cover of moss, % | 2.0± 1.1 | 1.6± 0.5 | 5.5± 1.3 | 10.8± 2.7 | 14.7± 0.4 | 1.8± 1.4 | 7.5± 5.5 | 7.0± 2.6 | 5.0± 2.5 | 13.0± 7.3 | 14.9± 7.4 | | |

lower ones. With increasing age of stands the change in the Shannon index is explicitly seen - the lowest diversity index is for spruce stands communities aged 30-40 years. However, the range of change in the Shannon index is not as wide as that (Fig.1) of the variation in the number of species. Moreover, some tendencies of index variation are difficult to explain. For instance, diversity index of cutovers of the first year of some forest types is higher than that of older cutovers, although the number of species in the communities of these cutovers is less everywhere. Besides, no significant species diversity of vegetation in cutovers' communities is revealed.

With increasing age of spruce stands phytocoenosis structure of the communities' changes. The dominating species of the communities change in particular. The plants that are mostly widespread (the average projection cover comprises 3 %) at least at one stage of stand development are presented in Table 2. Such plants are most numerous in communities on sites (*Oxalidosa*, *Myrtillo-oxalidosa* types) of average fertility. On poorer sites (*Myrtillosa* type) the quantity of dominating species diminishes due to a general decrease in biological diversity whilst on more fertile sites (*Oxalido-nemorosa* type) it diminishes because an increase in species diversity results in a decrease in the abundance of different plant species. Thus, the abundance of all more or less dominating species considerably changes. These species, which dominate in ground cover vegetation of mature stands noticeably, decrease in cutovers and vice versa. *Luzula pilosa* L. being a typical forest species is an exception. In cutting areas it does not vanish but even spreads slightly and reduces at the stage of thicket of young stand as all other species. Other species respond to cutting differently. Some of them completely vanish (*Mycelis muralis* (L.) Dum., *Hylocomium splendens* (Hedw.) B.S.G et al), some species consid-

**Table 2.** The change of mostly widespread species of ground cover vegetation at different stages of spruce stand development

| Plant species | The average projection cover $\bar{x}$ and stability* at different stages of community development | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | Cutting area | | crown closing | | thicket | | self-thinning | | stabilization | |
| 1 | 2 | | 3 | | 4 | | 5 | | 6 | |
| | | | | | *Myrtillosa* tipe | | | | | |
| *Molinia coerulea* (L.) Moendr. | 4.4 / | V | 8.6/ | V | 1.6/ | I | | | 1.2/ | II |
| *Pteridium aquilinum* (L.) Kuhn. | 18.7/ | IV | 13.9/ | IV | 1.1/ | II | | | 2.9/ | III |
| *Rubus idaeus* L. | 8.1/ | V | 0.4/ | III | 0.1/ | III | | | 0.1/ | VI |
| *Vaccinium myrtillus* L. | 10.9/ | V | 6.3/ | V | 1.2/ | V | | | 25.7/ | V |
| *Vaccinium vitis idaea* L. | 2.6 / | V | 4.7/ | V | 0.2/ | III | | | 4.2/ | V |
| *Dicranum spec.* | 2.3 / | V | 1.4/ | IV | 0.9/ | III | | | 7.9/ | V |
| *Hylocomium splendens* (Hedw.) B.S.G. | + / | II | 0.6/ | III | 1.1/ | IV | | | 8.5/ | V |
| *Pleurozium schreberi* (Brid.) Mitt. | 2.2/ | V | 5.7/ | V | 4.3/ | V | | | 23.1/ | V |
| *Polytrichum spec.* | 5.9 / | IV | 2.5/ | IV | 0.3/ | III | | | 1.4/ | IV |
| *Sphagnum spec.* | 3.2 / | III | 7.3/ | III | 0.5/ | III | | | 1.4/ | III |
| | | | | | *Oxalidosa* type | | | | | |
| *Agrostis tenuis* Gribth. | 5.9 / | IV | 2.4/ | III | - | | + / | I | + / | II |
| *Calamagrostis arundinacea* (L.) Rith., C. epigeios (L.) Rith. | 13.2/ | IV | 9.2/ | V | 0.2/ | III | 0.6/ | III | 0.8/ | III |
| *Deschampsia caespitosa* (L.) Beam. | 4.9/ | IV | 4.7/ | III | + / | II | + / | II | 0.2/ | II |
| *Luzula pilosa* (L.) Willd. | 6.2 / | V | 1.6/ | V | + / | IV | 0.5/ | V | 1.1/ | V |
| *Oxalis acetosella* L. | 0.7 / | V | 0.7/ | IV | 0.3/ | IV | 14.8/ | V | 19.6/ | V |
| *Pteridium aquilinum* (L.) Kuhn. | 12.7/ | III | 10.7/ | III | 0.3/ | I | 0.4/ | II | 0.6/ | II |
| *Rubus idaeus* L. | 21.5/ | V | 6.3/ | V | + / | I | 2.4/ | IV | 3.0/ | IV |
| *Vaccinium myrtillus* L. | 1.6 / | V | 1.9/ | V | 0.4/ | V | 2.8/ | V | 7.3/ | V |
| *Hylocomium splendens* (Hedw.) B.S.G. | + / | I | 0.1/ | I | 0.6/ | III | 4.2/ | IV | 4.6/ | IV |
| Pleurozium schreberi | 3.2/ | V | 3.6/ | IV | 3.4/ | V | 5.9/ | V | 6.9/ | V |
| | | | | | *Myrtillo-oxalidosa* type | | | | | |
| *Calamagrostis arundinacea* (L.) Rith., C. *epigeios* (L.) Rith. | 6.9/ | IV | 7.3/ | IV | + / | II | 0.4/ | II | 0.7/ | III |
| *Carex spec.* | 5.1/ | V | 0.8/ | III | - | | + / | I | + / | II |
| *Deschampsia caespitosa* (L.) Bean. | 9.6/ | V | 7.7/ | IV | + / | II | 0.3/ | II | 0.2/ | II |
| *Juncus effusus* L. | 6.3/ | IV | 0.1/ | III | + / | I | + / | I | + / | I |
| *Luzula pilosa* (L.) Wild. | 3.1/ | V | 0.6/ | IV | + / | III | 0.8/ | V | 0.7/ | V |
| *Oxalis acetosella* L. | 0.1/ | III | 0.1/ | II | 0.1/ | II | 6.4/ | V | 10.3/ | V |
| *Rubus idaeus* L. | 8.9/ | V | 1.2/ | IV | + / | I | 0.4/ | III | 0.2/ | III |

Continuation of **Table 2**

| 1 | 2 | 3 | 4 | 5 | 6 |
|---|---|---|---|---|---|
| *Vaccinium myrtillus* L. | 1.9/ V | 2.3/ IV | 0.3/ IV | 7.1/ V | 15.1/ V |
| *Hylocomium splendens* (Hedw.) B.S.G. | +/ I | +/ I | 0.8/ IV | 2.5/ V | 7.0/ V |
| *Pleurozium schreberi* (Brid.) Mitt. | 1.0/ III | 3.9/ IV | 5.6/ V | 5.7/ V | 14.0/ V |
| *Polytrichum spec.* | 5.2/ IV | 4.7/ III | 0.9/ III | 0.4/ III | 0.3/ III |
| *Sphagnum spec.* | 0.2/ III | 3.1/ IV | 0.8/ III | 0.7/ III | 1.9/ III |
| *Oxalido-nemorosa* type | | | | | |
| *Athyrium filix femina* (L.)Roth | 1.9/ IV | 1.0/ II | +/ II | 0.6/ III | 3.0/ V |
| *Calamagrostis arundinacea* (L.) Roth. | 5.7/ IV | 3.6/ III | +/ I | +/ I | 0.9/ III |
| *Deschampsia caespitosa* (L.) Bean. | 13.8/ V | 6.3/ V | +/ I | 0.1/ I | 0.3/ IV |
| *Juncus effusus* L. | 9.0/ V | +/ I | - | - | +/ I |
| *Oxalis acetosella* L. | 0.8/ V | 0.4/ V | 0.7/ IV | 9.0/ V | 13.7/ V |
| *Rubus idaeus* L. | 11.2/ V | 2.3/ V | +/ II | 1.3/ IV | 0.7/ IV |

* Stability class according to J.Braun-Blanguet

erably thin out (*Oxalis acetosella* L.), the distribution of other changes is less significant (*Majanthemum bifolium* (L.) Schmidt, *Trientalis europea* L., *Veronica officinalis* L., *Vaccinium myrtillus* L., *Pleurozium schreberi* (Brid.) Mitt. et all.).

Presented data indicate differences among dominating species, which have considerable influence on regeneration process in cutting areas on sites of different forest types. This was described earlier (Юрялёнис 1975; Karazija 1988; Karazija, Jurelionis 1976, 1977).

Along with the dominating species (Table 2), there are changes in prevalence of other species making up less projection cover in general phytocoenosis structure of forest communities. Their physionomic similarity diminishes. Similarity of spruce stands of different age of *Oxalidosa* type has been assessed by the Sørensen (1948) coefficient. For the calculation only projection cover of different plant species has been applied and the following indices of similarity of average community of mature forest have been obtained:

with average community on cutover sites - 0.23,

with the community at the stage of crown closing - 0.30,

with the community at thicket stage - 0.14,

with the community at the stage of self-thinning - 0.71,

with the communities of mature stands of other forest types similar by site conditions - 0.45-0.55.

Thus, the index of phytocoenotical similarity among mature stand communities and forming up communities of the same forest type is lower, as compared to mature forest communities of other types. Similarity index has been determined only according to different plants without dividing them into ecological groups. Significant changes in phytocoenosis structure imply possible changes in ecological conditions (not only light).

In Table 3 and Figure 3 indices of assessment of ecological conditions (light, soil humidity, soil reaction

**Table 3.** The indices of assessment of ecological conditions of forest communities at different stages, according to the Ellenberg indicator values of ecological needs of plants

| Index | Forest type index* | Stages of age | | | | |
|---|---|---|---|---|---|---|
| | | cutting area | crown closing | thicket | self-thinning | stabilization |
| Light | M | 6.30 | 5.91 | 5.64 | 4.30 | 5.60 |
| | Ox | 6.09 | 5.88 | 4.83 | 4.16 | 4.36 |
| | m-ox | 5.87 | 6.26 | 5.63 | 4.69 | 4.94 |
| | h-ox | 5.95 | 5.69 | 4.37 | 2.90 | 3.33 |
| | ox-n | 6.19 | 5.82 | 3.35 | 3.93 | 4.50 |
| Humidity | M | 5.41 | 5.01 | 4.76 | 5.03 | 4.96 |
| | Ox | 5.41 | 5.11 | 5.13 | 4.75 | 4.83 |
| | m-x | 6.32 | 5.61 | 5.53 | 4.82 | 5.26 |
| | h-ox | 6.03 | 5.47 | 5.38 | 5.00 | 5.05 |
| | Ox-n | 6.6. | 6.39 | 5.16 | 5.26 | 4.91 |
| Soil reaction | M | 2.52 | 2.84 | 2.95 | 3.49 | 2.77 |
| | Ox | 3.63 | 3.34 | 3.85 | 4.24 | 4.21 |
| | m-x | 3.01 | 2.79 | 3.18 | 3.78 | 3.57 |
| | h-ox | 4.22 | 3.97 | 3.74 | 4.51 | 5.30 |
| | ox-n | 4.02 | 4.31 | 4.52 | 5.22 | 4.89 |
| Nitrogenity | M | 3.17 | 2.34 | 2.64 | 4.24 | 2.96 |
| | Ox | 4.55 | 4.08 | 4.39 | 4.99 | 4.74 |
| | m-x | 3.56 | 3.43 | 4.42 | 4.27 | 4.02 |
| | h-ox | 4.65 | 4.76 | 4.37 | 5.51 | 5.33 |
| | ox-n | 5.49 | 4.68 | 5.84 | 5.81 | 4.84 |

* m – *Myrtillosa*, ox – *Oxalidosa*, m-ox – *Myrtillo-oxalidosa*, h-ox – *Hepatico-oxalidosa*, ox-n – *Oxalido-nemorosa*.

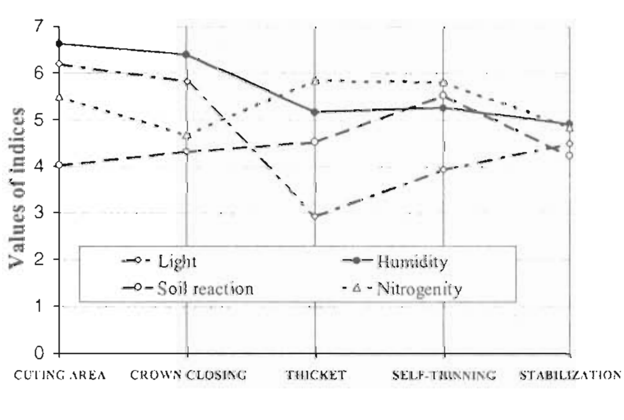


**Figure 3.** The Ellenberg's ecological indices at different age stages of spruce stands of *Oxalido-nemorosa* type

an trophism (provision with nitrogen)) of forest communities at different stages of their development are presented. They have been calculated applying indicator values of Ellenberg for plants' ecological needs. As seen from these data, the index of community's need for light changes most considerably. Its values for the communities of cutovers are highest and these for the communities at the stages of thicket and self-thinning are lowest. Humidity changes significantly too. Its index decreases gradually from the communities of cutovers to mature forest communities. This reflects signs of bogging up which appear in cutover and disappear when stand matures. With increasing age of stand the index of soil reaction slightly augments, i.e. acidity diminishes. A variation in the indices of nutrients quantity is less distinct, their dynamics in different types of forest slightly differs, but the maximal value is at the stage of self-thinning. However, the values of some indices in the communities of different types are doubtful, e.g. humidity index in the communities on humid sites (*Myrtillosa* type) is lower than that in the communities of drier sites (*Oxalidosa* type). Therefore, for comparison the indices of humidity and trophism have been calculated according to L. Ramenskij's ecological tables (Table 4) of plants. These indices show that the most significant drying is noted in the communities at the stage of thicket and self- thinning. At stabilization stage humidity slightly increases (excluding spruce stands on drier sites of *Oxalidosa* and *Hepatico-oxalidosa* types). The variation in trophism was not found to be distinct. With increasing age of stands the index of trophism slightly increases, however, on humid sites such an increase occurs up to the stage of self-thinning.

Data of phytoindicational analysis have demonstrated that due to the changes in stand age, species composition of the community and in phytocoenosis structure the indices of ecological conditions change too. Some indefiniteness of the trends of changes may be explained by the fact that tables of plants' ecological indices were used to assess them. The tables have been created using data of indicator values of plants of West and East Europe. It implies the necessity of creating more accurate local ecological tables. However, the assessment made according to the tables available enables us to state that with increasing age of stands the changes occuring in forest ecosystems are reversible and different stages of age belong to the same forest type. Therefore, of importance is classification of indicatory plant species that are typical of the communities at all stages of stand development.

**Table 4.** The indexes of assessment of ecological conditions of forest communities at different stages according to ecological tables of plants by Ramenskij

| Forest type | Stages of community age | | | | |
|---|---|---|---|---|---|
| | Cutting area | Crown closing | Thicket | Self-thinning | Stabilization |
| | | | Humidity | | |
| *Myrtillosa* | 74.4 | 72.7 | 72.2 | 72.8 | 75.0 |
| *Oxalidosa* | 71.3 | 71.6 | 71.9 | 71.2 | 70.9 |
| *Myrtillo-oxalidosa* | 74.5 | 74.3 | 73.6 | 74.3 | 74.6 |
| *Hepatico-oxalidosa* | 73.6 | 73.6 | 74.0 | 72.7 | 72.9 |
| *Oxalido-nemorosa* | 75.0 | 75.7 | 74.2 | 73.9 | 74.2 |
| | | | Fertility | | |
| *Myrtillosa* | 6.4 | 6.2 | 6.2 | 6.5 | 6.2 |
| *Oxalidosa* | 6.8 | 6.8 | 7.3 | 7.3 | 7.4 |
| *Myrtillo-oxalidosa* | 7.2 | 7.2 | 7.6 | 7.5 | 7.3 |
| *Hepatico-oxalidosa* | 7.7 | 7.3 | 7.9 | 7.8 | 7.9 |
| *Oxalido-nemorosa* | 7.9 | 8.1 | 8.3 | 8.3 | 8.1 |

It is expedient to group indicatory plants into typical indicators characteristic of one (concrete) forest type, possessing stenotope features and into determinants (Раменский 1938) indicating the boundaries of ecological areal of different forest types. In the communities of spruce stands very few typical indicators are observed at all stages of stand development. Species of ecological groups *Galeobdolon-Hepatica* and *Dryopteris-Anemone* (Karazija, 1988) may be partially assigned to them. Species of the first group indicate the communities of *Hepatico-Oxalidosa* type; in the communities of cutovers and young stands *Galeobdolon luteum* Huds. and *Stellaria holostea* L. are more stable among species of this group.Species of the second group are typical of the communities of *Oxalido-nemorosa* type. As mentioned above, in the communities of this type dominating and constant species are few, however, the species that do not grow on poorer sites any more are numerous. Therefore, appearance of any species (*Anemone nemorosa* L., *Dryopteris carthusiana* (Vill.) H.P. Fuchs., *Ajuga reptans* L., *Angelica sylvestris* L., *Crepis paludosa* (L.) Moench., *Festuca gigantea* (L.) Vill., *Milium efusum* L., *Poa nemoralis* L., *Ranunculus auricomus* L., *Sanicula europea* L.) of above group as well as broadleaved species such as *Aegopodium podagraria* L. in cutovers and in vegetation composition of young stands allow us to distinguish these communities from ones of forest types on less fertile sites. To identify and distinguish forest communities of *Oxalidosa* and *Myrtillo-oxalidosa* types from more fertile sites determinant *Vaccinium myrtillus* L. was found to be comparatively reliable. Although it considerably reduces after felling, single elements constantly remain in vegetation composition of cutovers and young stands. *Pteridium aquilinum* Kuhn. is typical of the communities of *Oxalidosa* type. *Molinia coeruela* (L.) Moench is the most significant indicator of the communities of cutovers and young stands of *Myrtillosa* type. They differ from the communities of *Myrtillo-oxalidosa* type by the fact that

*Oxalis acetosella* L. is not detected here. Communities of more humid sites' types are distinguished from the drier ones by above mentioned indicators of bogging up appearing in cutovers.

Thus, even significantly different communities of cutovers and young stands possess indicators allowing us to identify the forest types they have originated from. However, at the stage of thicket lower layers of vegetation sometimes completely vanish. Then other indicators are searched, which permit site conditions to be identified and forest development predicted.

*Dynamics of undergrowth and underwood*

With increasing age of stands changes occur in undergrowth and partially in species composition as well as in herb and moss cover. However, the process of a change is different. Firstly, the change in species composition is merely associated with a decrease in the number of species in young stands and in stands at thicket (pole stand) stage but not with appearance of new species. In rare cases on more humid sites *Salix* species being not typical of mature stands may appear following felling and in young stands. During felling stand's undergrowth is also cut. Therefore, young stand readily suppresses the suckers of shrubs and formation of undergrowth starts only under the cover of a young stand. Only in a part of forest communities at thicket stage there are species characteristic of undergrowth, whereas at the stage of self-thinning undergrowth appears everywhere and cover augments significantly, though the number of species changes slightly. As shown in Table 5, this tendency is very much alike in communities of all forest types. However, the number of species, species composition and rate of an increase in undergrowth abundance (projection cover) differ (in stands on more fertile sites undergrowth is denser and consists of a larger number of species). Although no essential changes occur in species composition in the course of age of stands, however, shrub species dominating in undergrowth change. *Coryllus avellana* L. as a typical species of undergrowth in spruce stands of more fertile sites prevails in the communities of mature stands only.

A similar tendency (excluding cutovers where soft deciduous trees start growing) of underwood turning up is observed in spruce stands. In formed young spruce stands (thicket stage) the layer of tree crowns eliminates the vegetation of lower layers, including underwood. When the layer of trees becomes thinner, i.e. at the stage of self-thinning, then herb cover appears, underwood starts growing.

Along with spruce underwood, young trees of other species grow in spruce stands. On all sites young oaks happen to be found, but their vitality is low. Therefore, in spruce stands they are of no economic or biological significance. This holds for young birches and asps (grown from suckers). In spruce stands on sites of average fertility young spruces comprise 70 % of the trees in underwood. Only on more fertile sites (*Hepatico-oxalidosa* and *Oxalido-*

**Table 5.** The indices of age related changes in undergrowth

| Forest community stage | Stands with under-growth, % | Average projection cover of under-growth, % | The number of under-growth species | | Dominating species* |
|---|---|---|---|---|---|
| | | | Total | Average number in a plot | |
| *Vaccinio-myrtillosa* type | | | | | |
| Stabilization | 100 | 4±1.8 | 4 | 1.9±0.2 | S.a. |
| *Myrtillosa* type | | | | | |
| Thicket (pole stand) | 43 | 2±1 | 3 | 1.7±0.3 | Sal. |
| Stabilization | 100 | 2±1 | 4 | 1.8±0.2 | Fr.a.,S.a. |
| *Oxalidosa* type | | | | | |
| Thicket | 43 | 1±1 | 6 | 2.9±0.6 | S.a. |
| Self-thinning | 100 | 5±1 | 9 | 3.3±0.5 | S.a., C.a. |
| Stabilization | 100 | 10±2 | 8 | 4.5±0.3 | C.a. |
| *Myrtillo-oxalidosa* type | | | | | |
| Thicket | 39 | <1 | 4 | 1.8±0.3 | Fr.a., S.a. |
| Self-thinning | 100 | 6±1 | 4 | 2.6±0.5 | S.a, Fr.a., C.a. |
| Stabilization | 100 | 9±2 | 9 | 3.1±0.4 | S.a., C.a. |
| *Hepatico-oxalidosa* type | | | | | |
| Self-thinning | 100 | 8±2 | 10 | 4.2±0.5 | C.a., S.a. |
| Stabilization | 100 | 12±2 | 9 | 4.7±0.4 | C.a. |
| *Oxalido-nemorosa* type | | | | | |
| Thicket | 45 | 1±1 | 9 | 4.8±0.6 | C.a., S.a. |
| Self-thinning | 100 | 9±3 | 9 | 3.7±0.3 | C.a. |
| Stabilization | 100 | 11±1 | 8 | 5.0±0.4 | C.a. |

* S.a. – *Sorbus aucuparia* L., Fr.a. – *Frangula alnus* Mill., C.a. – *Corylus avellana* L., Sal. – *Salix spec.*

*nemorosa* forest types) where hornbeam, lime, ash admixture and other deciduous trees appear, a relative quantity of spruce underwood is less. But spruce is the most vital species here too and is of greatest economic and phytocoenotic significance among trees of underwood. Therefore, the greatest attentionn is to be focused on the analysis of the change in its quantity. In Table 6 and Figure 4 the data of the change in spruce underwood quantity depending upon stand age (starting with stands aged 50 years) are presented. They show that at the stage of self-thinning of spruce stands the quantity of underwood is still not significant. In stands aged up to 60 years it is completely absent sometimes. At stabilization stage only - at the age of stand maturity when crown density of stands decreases spruce underwood becomes more abundant. No significant differences of regeneration regularities among forest types are observed; only in stands of *Hepatico-oxalidosa* type spruce underwood was found to be scanty. Figures in the Table indicate the number undergrowth trees independently of their age or vitality. Because of considerable shadow of spruce a part of suppressed young trees grows under the stand for a long time. Therefore, the quantity of perspective underwood is by far less. However, presented data indicate the regularities of the changes in natural regeneration, which reflect the processes of natural stand development. They also show the feasibility to apply natural regeneration of spruce for stand restoration in managing forest.

*Stand growth*

Every forest type is a characteristic of certain stand productivity and the process of growth. They are of great significance for defining economic peculiarities of the forest type. In case the productivity differs noticeably and particularly the process of stand growth these peculiarities could be applied as diagnostic for typological identification of forest communities. It holds for the process of height growth of stands especially which is influenced least by random factors and which serves as a dynamic index that can be used for indication purposes at any stage of stand age.

The results of height analysis presented in Figure 5 show that there are no differences in the process of height growth in different forest types. Differences of the average height of stands of all age classes among different forest types are approximately proportional to the difference at maturity age (young stands are an exception). Potential differences in the productivity and growth of stands of close forest types according to site conditions are less than the dispersion of growth indices within a type. It indicates that productivity and growth of stands are conditioned not only by edaphic conditions of site but by natural and anthropogenic factors (stand origin, way and quality of regeneration, history of stand development, nurturing, etc.) as well. Consequently, a possibility for application of the indices of productivity and growth of stands for typological diagnosis of forest communities is limited.

**Table 6.** The average quantity of spruce underwood in spruce stands of different age classes, units ha⁻¹

| Forest type | Age classes (every 10 years long) of stands | | | | | |
|---|---|---|---|---|---|---|
| | VI | VII | VIII | IX | X | XI ir > |
| *Vaccinio-yrtillosa* | 750±468 | 1517±222 | 3012±481 | 6507±1034 | 5810±1889 | 5620±1218 |
| *Myrtillosa* | 430±128 | 1175±690 | 3883±1166 | 7162±1205 | 5850±2812 | 6367±2588 |
| *Oxalidosa* | 546±127 | 2605±556 | 2650±207 | 6556±1458 | 4650±842 | 5033±2368 |
| *Myrtillo-oxalidosa* | 986±183 | 1560±209 | 4512±855 | 6247±1039 | 5150±781 | 5367±947 |
| *Hepatico-xalidosa* | 720±336 | 1367±410 | 1980±534 | 2450±786 | 3276±766 | 2817±1029 |
| *Oxalido-nemorosa* | 220±23 | 2450±737 | 2908±657 | 5890±788 | Absent | |

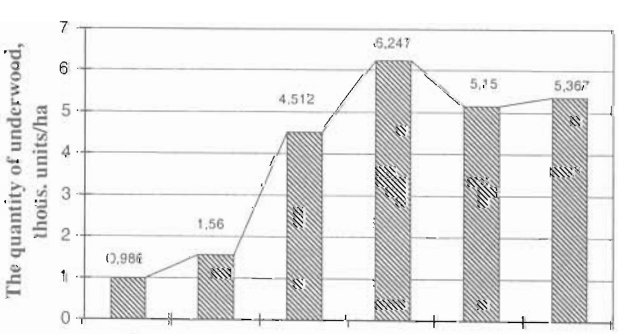


**Figure 4.** A change in the quantity of spruce underwood depending upon age of spruce stands of *Myrtillo-oxalidosa* type

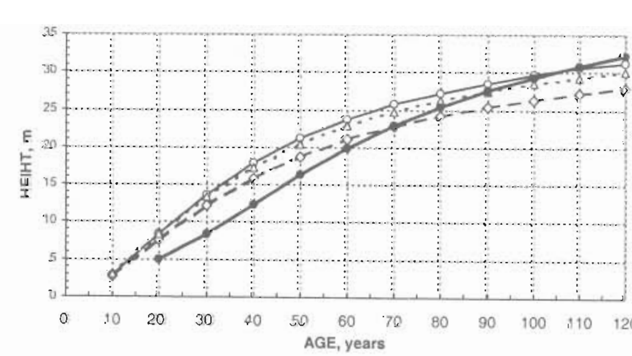


**Figure 5.** A comparison of curves of height growth of spruce stands (1 - site quality class I after Tiurin; 2 - *Oxalidosa* type; 3 – *Myrtillosa* type; 4 – *Vaccinio-myrtillosa type* )

When comparing the process of growth of spruce stands of different forest types with the data of the Tiurin tables (Jankauskas, 1951) of spruce stands' growth process that were used earlier, productivity class of stands was found to go down with increasing age. The growth of the 50-year-old spruce stands of *Myrtillo-oxalidosa* type corresponds to class Ia, while at the age of 100 years it is between class II and III. In comparison with the tables of the growth of spruce stands of Lithuania made by J.Butėnas (1968) such a significant transfer is not observed already, though a tendency remains yet.

## Discussion

Different data on the changes of biodiversity in the process of stands' growth are presented in the literature. E.P.Odum (1975) describes a change in the diversity of forest communities in the process of aging in Pidmont region (USA). He points out that a decrease in species' diversity is feasible only in an overmature stand (aged over 200 years). In beech stands of *Melico-Fagetum* type in Germany M.Jensenn and G.Hofmann (1996) find the most significant plant species diversity at disintegration stage (Desintegrationsstadium) of stands when instability is most significant, a new generation of stand forms and the influence of external factors is most considerable. In pine stands of Byelorussia no significant trends in biodiversity changes related to stand age have been determined (Ярошевич 1970, Романова 1996). According to A.Georgievskii (Георгиевский 1992) data of investigations in spruce stands' gaps formed after windfalls, herb vegetation projection cover increased, species being not characteristic of dense stands spread, though the general quantity of species change negligibly, even decrease in certain types of forest. A. W. Sokolowski (1990) points out a distinct increase in species diversity in cutting areas in Poland (Bielovеza National Park).

Such a variety of data cannot be explained by differences in climate conditions and stand species composition alone. Methods of investigations may have an influence too. First of all the question of including cutting areas into the forest formation process arises. Communities of cutting areas are closer to meadow communities rather than to forest according to phytocoenosis structure. However, quite a lot of forest vegetation species is found there and numerous research works in cutovers confirm this (Schretzenmayer 1950, Мелехов 1959, 1967, Чертовской 1963, Lõhmus 1970 et al.). Therefore, their biodiversity is greatest. In the process of natural forest development this is not so pronounced as the vegetation in gaps formed after windfalls where all the timber is left differs from the vegetation in areas of clean cutting (Fischer et al. 1990).

The second point of importance is a division of forest formation process to stages and their limits' determination criteria. In accordance with **the theory of succession-climax** (Clements, 1916) which has been dominating for a long time, when overmature stand disintegrates mosaic-like areas independently of each other should form, i.e. stand of different age. The whole mesoecosystem of forest should transit to the stable state with relatively constant species combination and maximum diversity of species and structure. According to this theory there should be no stages of development. Single cases of stands' disintegration should be treated as exceptional. Since the data on mature stands' disintegration caused by storms, fires, pests as well as due to biological forest peculiarities accumulate, conception of **cyclic forest development** was posed (Daubenmire 1968, Remmert 1985 et al.). It narrowed considerably the range of application of the climax theory. In accordance with this conception the development of forest is cyclic and stages can be singled out in this process. Different authors distinguish different quantity of them. H.Leibundgut (1978) has singled out seven, while other authors note other numbers of stages (phases). M.Jensenn and G.Hofmann (1996) present a model of cyclic development of beech stands of *Melico-Fagetum* type. The model has been constructed according to the data of long-term investigations by different authors. In accordance with this model forest ecosystem neither strive to stable state nor is it steered merely by random external factors. It passes a cycle consisting of five stages. The stage of disintegration and formation of a new generation has the greatest resemblance (is the closest) to the stage of cutover singled out by us. Species diversity is the greatest in both of them. Low variation of species diversity in gaps formed by windfalls of taiga spruce stands (Георгиевский 1992) may be explained by small dimensions of these gaps and taiga conditions characteristic of few sinantropic species.

Stages of stands' development distinguished by many authors include disintegration of stands too. Under Lithuania's conditions such a stage cannot be singled out in spruce stands according to the available data, as stands do not reach it in managed forests. The question may be raised whether natural formation of stands will run according to the model of cyclic development. The answer based on experiments cannot be given yet. However, it is very likely that natural development of Lithuania's spruce stands is cyclic. The data of spruce biology and peculiarities of its growth and regeneration (Karazija 1998) in Lithuania support this assumption, as well as analysis of the regularities of spruce stands' development in other regions (Георгиевский 1992; Дыренков и др. 1970, Leibundgut 1978 et al.) and influence of Lithuanian climate conditions on spruce stands (Labanauskas 1974, Krogertas 1972). The fact that most of the investigated plots (data of which were used in this article) were singled out in cutovers or multiple windfalls confirms this. However, age stages of naturally formed spruce stands may be not so distinct, their limits may be shifted in this or that direction. Regularities of undergrowth changes and regeneration ascertained by our research in Lithuanian forests differ from the data presented by other authors (Fischer et al. 1990, Sokolowski 1991, Jensenn, Hofmann, 1996, Saniga, Vesely 1998).

Differences in development of natural and managed forests, different composition of stands may be an explanation for that. At the stage of stand disintegration and after felling the quantity of sciophites in the structure of forest communities decreases, light-loving species being not characteristic of crown-closed stands start regenerating. This is characteristic of all forests. Therefore, evaluation of community's need for light according to the indicator value determined by Ellenberg always increases. However, composition of communities of this forest development stage differs from the point of view of species strategy depending on forest features (peculiarities). In areas of clear cutting, in regions of intensive forestry non-forest species - apophits and sinantrops (Schretzenmayer 1950, Sokolowski 1991 et al.) start spreading. This is going on in cutting areas in Lithuanian forests. This phenomenon is not characteristic of areas without clear cutting (Fischer et al. 1990), especially in taiga forests (Георгиевский 1992).

The data of our research have revealed a significant increase in humidity in cutting areas. Appearance of hygrophyts in communities' structure reflects this, as well as phytoindicative evaluation of communities according to Ellenberg and Ramenskii. This phenomenon reveals itself in all northern forests (Мелехов 1967, Чертовской 1963, Lõhmus 1970). It is not expressed clearly in regions situated more southward (Poland, Germany). Another phenomenon is stressed there - prevalence of eutrophic species in cutting areas (Sokolowski 1991, Roder et al. 1996). This does not show up under Lithuanian conditions. Evidently, this is due to differences conditioned by climate.

It has been noticed some four decades ago that growth process of Lithuanian stands differs from the data of the tables created in Russia and used at that time. The explanation for this phenomenon is the peculiarities of Lithuanian stands' growth. Therefore, local tables of growth process have been created. There has been one more hypothesis concerning growth differences. The idea was that they were conditioned by a large quantity of young stands of cultural origin, as research data of pre-war period did not exhibit such differences (Lietuvos TSR miškai, 1962). To verify this hypothesis an attempt has been made to separate stands of cultural origin and derive curves of the growth of natural spruce stands and of cultural origin. However, from the available data we could not draw a conclusion about different growth processes of cultural and natural spruce stands. At present the phenomenon when the process of stands' growth does not correspond to the norms of tables reveals itself in many European countries (Polok 1968, Jensenn Hofmann 1996, Rigling, Schweingruber 1997 et al.) and Russia (Сеннов 1996). A hypothesis has been put forward that the growth of stands had accelerated over the last decades in Europe. As far as the same is observed in Russia too, it becomes dubious whether accelerated growth of young stands in Lithuania can be explained by the peculiarities of local conditions.

## Conclusions

1. In the course of stands' aging ground cover vegetation is the most changing element of spruce stands' community structure (excluding the stand which disappears completely after felling). Cutting areas in which typical forest and cutover species grow are characteristic of the most significant projection cover and species diversity of herb cover. In the communities of mature forest slightly less projection cover and species diversity are found, but the quantity of species typical of forest is most significant. The most considerable thinning of herb cover is observed in young stands. Similar dynamics is typical of moss cover, only the range of changes is by far less. Additionally, projection cover of moss is rather different in spruce stands of different forest types - in mature spruce stands on poorer sites the quantity of moss is largest.

2. In accordance with the changes in forest vegetation indices depending upon stand age the investigated spruce stand communities may be divided into 5 stages of stand development - cutover (stand restoration), crown closing (stand forming), thicket (pole stand), self-thinning and stabilization (sub-climax). These stages should be coordinated with the corresponding economic measures.

3. Biodiversity's (estimated by the Shannon index) dependence on sites' conditions and stands' age has been verified. Spruce stand communities of more fertile sites distinguish themselves by greater biodiver-

sity. In the course of stands' age the Shannon index changes just as the number of species does: it is lowest in the communities at thicket stage, highest - in the communities of cutovers and mature forest. However, the range of the Shannon index variations is not as wide as the range of changes in the number of species and projection cover.

4. Not only the number of species of ground cover vegetation and projection cover change with increasing stand age, but composition of dominating species as well. Changes are most evident in cutovers, where aggressive species start prevailing, which influence forest regeneration process. Many of them are the species of wide ecological amplitude, but composition of dominating species in cutovers' communities of different forest types is slightly different.

5. Making use of phytoindication methods (applying indices of ecological needs of plants, determined by Ellenberg and ecological tables of plants) created by Ramenskij, it has been determined that ecological conditions of forest communities change in the course of stand age. Index of the plants' need for light changes most considerably. Highest values of it are in cutovers, and then follow communities of mature forest. Humidity index is highest in cutovers, indicating signs of bogging up. With increasing age of stands humidity decreases, while the extent of soil reaction slightly augments. However, ecological conditions of communities at all stages do not differ considerably and changes are reversible.

6. Assessment of similarity of communities at different stages of forest development has been made according to the Sørensen coefficient by using projection cover of different plant species only. It has demonstrated that similarity among the communities of the same forest type at different stages of development is less than among the communities of different forest types at the same stage. It means that even the best similarity indices applied in geobotany do not express ecological similarity in case they are used formally. To improve ecological sense of indices the species must be united in ecological groups and additional ecological signs must be introduced while transforming indices' calculating formulae.

7. Great changeability in the communities' structure attaches importance to the indicators. It has been ascertained that in spruce stands there are very few vegetable indicators typical of a concrete forest type, which remain at all stages of stand development. However, determinants are numerous. They enable the communities of different forest types to be identified distinguishing them from ecologically close types. The best determinant for distinguishing spruce stands of the poorest sites from mesotrophic sites in Lithuanian condition is *Oxalis acetosella* L., mesotrophic from eutrophic - *Vaccinium myrtillus* L.; to distinguish eutrophic spruce stands on drier sites (*Hepatico-oxalidosa*) from more humid sites (*Oxalido-nemorosa*) such plant species of ecological groups as *Galeobdolon-Hepatica* and *Dryopteris-Anemone* may serve.

8. Undergrowth in spruce stands is usually more abundant at the stage of self-thinning and becomes more abundant when stand age increases. Species composition of it changes slightly while abundance of certain species changes more considerably. Since many of shrub species are plants of wide ecological area, indicator value of undergrowth in determining types of spruce stands is not great.

9. Young spruces occupy more than 70 % of underwood in spruce stands. They start growing at the stage of self-thinning and particularly increase in mature stands. In addition, trees of other species are found in underwood too. Their composition depends on sites' conditions.

10. The differences of character of height growth of spruce stands have not been determined in different forest types; the average intensity of the growth is different only. However, significant dispersion conditioned by natural and anthropogenic factors have been observed within a forest type. For this reason indicator value of this index is low. It has been determined that the real process of stand growth differs from the indices of tables - in young age stands grow really faster. It may be explained by the hypothesis put forward in the literature that in recent decades the growth in Europe has been accelerating.

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# ВОЗРАСТНАЯ ДИНАМИКА ЛЕСНЫХ СООБЩЕСТВ ЕЛЬНИКОВ ЛИТВЫ

**С. Каразия**

*Резюме*

Исследования проведены в ельниках различного возраста наиболее распространенных (6) типов леса на постоянных и временных пробных площадях. Цель – выяснить изменение видового состава, биоразнообразия и экологических условий, определить наиболее стабильные индикаторы местопроизрастаний и закономерности лесовосстановления.

Наиболее изменяющимся в связи с возрастом древостоя компонентом лесных сообществ является живой напочвенный покров. Наибольшим разнообразием видов растений и наибольшим проективным покрытием травостоя отличаются сообщества вырубок, несколько меньше эти показатели в спелых древостоях. По показателям структуры можно выделить 5 стадий возрастного развития ельников: вырубка, формирование молодняка, густой жердняк, изреживание, стабилизация (субклимакс). Сходство сообществ этих стадий (по коэффициенту Сёренсена) весма низкое.

Различаются экологические условия в различных стадиях. На вырубках увеличивается только количество света и влаги. Реакция почвы незначительно увеличивается с возрастом древостоя.

Растительные индикаторы, свойственные конкретному типу леса и стабильные во всех стадиях, почти отсутствуют. Однако имеются довольно много детерминантов, позволяющих идентифицировать сообщества различных типов леса.

Состав подроста ельников разнообразный и зависит от типа леса, но доминирует (70 %) еловый подрост, который более обильно появляется в спелых древостоях.

**Ключевые слова:** ельники, возрастная динамика, живой напочвенный покров, видовое разнообразие, фитоиндикация, подрост, рост древостоя.