Partitioning of nutrients and biomass in Scots pine canopy

Malle Mandre[a] and Hardi Tullus[b]

[a] Department of Ecophysiology, Forest Research Institute, Estonian Agricultural University, Viljandi mnt. 18B, 11216 Tallinn, Estonia; mma@rmk.ee
[b] Faculty of Forestry, Estonian Agricultural University, Kreutzwaldi 5, 51014 Tartu, Estonia

Abstract. Spatial partitioning of nutrients in the canopy of *Pinus sylvestris* L. was evaluated quantitatively and morphological differences between different canopy layers were studied in 45–55-year-old trees in a *Myrtillus* site type forest stand. A significant variation was revealed in the biomass and growth of pine needles and shoots, density of needles, and number of buds on shoots between different canopy layers. The mass and length of shoots depend significantly on the content of N, K, and Ca in spring, before budbreak. In autumn, when growth has stopped, the content of nutrients plays a less significant role.

Key words: *Pinus sylvestris* L., partitioning of nutrients, morphology.

INTRODUCTION

The growth and functioning of trees require balanced mineral nutrition not only for quantitative but also for qualitative biomass production. Roots are responsible for most of the absorption of mineral elements. Although leaf blades of plants can absorb nutrients, their absorption rate is low, being limited by the resistance of the cuticle. Most of the conifer foliage is characterized by well developed cuticle, which reduces the successful entry of nutrients into needle cells. Although nutrient uptake and translocation mechanisms in conifers have not been explored extensively, the limited evidence suggests that they are basically similar to those occurring in herbaceous plants (Schaedle, 1991). In any case, nutrients have a highly significant effect on the growth and reproduction as well as on morphological partitioning among various plant structures such as roots, stems, and leaves. The effects of nutrient partitioning in trees are of importance in the formation of canopy architecture as well as in their acclimation to environmental stresses (Rook, 1991).

The direction of translocation of nutrients is primarily regulated by the relative sink strength of an organ. Neither source–sink relationships nor the content of nutrients are static, and almost all plant organs can act as a sink at some stage of their development.

The content of nutrients in conifers is characterized by the temporal and spatial dynamics governed by the physiological state and the structural peculiarities of the plant as well as by various environmental factors (Mandre, 1995). It has been found to vary at different evolutionary stages and in different plant organs (Ericsson, 1978; Kramer & Kozlowski, 1979; Rieger et al., 1992; Hampp et al., 1994). The relationship between the temporal and the spatial allocation of nutrients and the development of the different plant organs affects significantly the growth pattern of individual trees (Einig & Hampp, 1990; Mandre et al., 1998).

There is a strong evidence indicating that the distribution patterns of foliage biomass along the canopy are mainly determined by light distribution (Pearcy & Sims, 1994), temperature (Waring, 1991), and availability of nutrients in trees (Field & Mooney, 1986; Vessey & Layzell, 1987). Undoubtedly, the anatomic properties of leaves are affected by their location in the canopy (Kappel & Flore, 1983). For aspen, a relationship was established between the variability of nutrients and biomass partitioning in the leaves of different canopy layers (Mandre et al., 1998).

Nutrient partitioning in plants can be influenced by a variety of factors and the question whether a particular organ is adequately supplied with assimilates, and can therefore fully realize its growth potential, may not have a simple answer. Despite intense research in this area, there is still little information about nutrient partitioning in conifer canopies and in the whole organism in natural forest conditions.

This study aimed at the establishment of the spatial partitioning of nutrients in the canopy of Scots pine growing in a *Myrtillus* site type forest stand. The dependence of biomass formation and morphological characteristics of the canopy as well as the accumulation of nutrients in needles on their location in the canopy will be reported in this paper. Our results are expected to contribute to the elaboration of both optimal volumes for pruning and recommendations for selection of trees for thinning.

MATERIALS AND METHODS

The investigations were performed on 45–55-year-old Scots pine (*Pinus sylvestris* L.) growing in a *Myrtillus* site type pine stand in Central Estonia (Alatskivi forest, longitude 27°07′ E, latitude 58°35′ N).

Twelve trees with a similar canopy and habitus were selected for analysis. Trees for morphometric measurements were felled in October, when the annual growth of needles and shoots had stopped. The canopy of each tree was divided into ten equal horizontal layers (1st – the lowest, 10th – the highest). For each layer the total dry mass of needles (% of the total mass of the crown) was

determined. For morphometric measurements the apical shoot ($n = 12$) of the largest branch from each canopy layer ($n = 10$) of the sample tree was taken to reduce the variation of the results. The number of buds on shoots (No shoot^{-1}) was counted. The average length (mm, $n = 200–300$), dry mass (mg, $n = 100$), and specific mass of needles, expressed as the ratio of needle mass to length (mg mm^{-1}), were determined. The dry mass of different organs was measured after drying at 70 °C.

Needles were taken from ten canopy layers (L) to establish the vertical partitioning of nutrients. The needles were sampled before budbreak in late March and at the beginning of October when growth processes had already stopped. For nutrient analysis (N, P, K, Ca, Mg) only one-year-old needles were used, as they are the most important source of assimilates and nutrients for new developing organs (Ericsson, 1978). The analyses were carried out in three replications using 1–5 g of dried and homogenized plant material. To measure the main mineral elements, potassium, calcium, and magnesium were detected with an atomic absorption analyser AAA-1N, nitrogen was analysed using Kjeldahl's method, and phosphorus was analysed by the molybdenum blue method. All analyses were made at the Estonian Centre of Plant Material Control.

The regression trendlines and the R-squared values (R^2) at the significance level $p < 0.01$ for the investigated parameters were calculated using the MS Excel 5.0 package. One-way analysis of variance was tested by analysis of ANOVA according to Statgraphics 5.0.

RESULTS AND DISCUSSION
Morphological parameters

Tree canopies can be genetically controlled, while they in turn can exert a certain control over the growth rate of the tree. Relative biomass partitioning in the crown, stem, and root system of Scots pine varies predictably with tree age.

In young seedlings of Scots pine, a very large proportion of photosynthates is used for the production of the biomass of needles and roots, accounting for a half and one-fourth of the total biomass, respectively. As trees grow older, their canopies develop and the proportion of the total biomass attributed to the branches and the stem increases notably. At the same time, the partitioning of biomass to the needles and roots declines considerably. In middle-aged pines the bulk of biomass is contained in the stem, while the share of the needles and roots decreases further (Kozlowski et al., 1991). An analogous partitioning of biomass in 20-year-old pines was observed also by Linder & Troeng (1981). In older trees more than half of the biomass is accounted for by the stems (Kozlowski et al., 1991).

The distribution of the foliage appears to affect growth primarily by altering the quality of the foliage that can be maintained by a stand under a given site conditions. Our study revealed an uneven partitioning of phytomass and significant

morphological differences between the different layers of 45–55-year-old canopies (Fig. 1,Table 1). Analysis of the allocation of the needle mass in the canopy showed that in 45–55-year-old pines just over 35% of the total needle mass is contained in the 5th–6th layers. A similar allocation of the assimilating mass has been observed in canopies of *Picea glehnii*, as well as in the broad-leaved species *Betula platyphylla* (Kikuzawa & Umeki, 1996), *Populus tremula* L. (Mandre et al., 1998), and *Salix viminalis* (Ross & Ross, 1996). Thus it is evident that the assimilating mass and the photosynthetic productivity of trees are allocated predominantly in the middle layers of the canopy. For conifers, this conclusion is supported by studies of Woodman (1971), Ågren et al. (1980), and Troeng & Linder (1982).

The length and mass of an individual needle and the ratio of needle mass to length for Scots pine were assumed to increase from the lowest living branch towards the top of the canopy. Such a dynamics of the needle parameters is considered normal for Scots pine (Flower-Ellis & Persson, 1980). However, the total mass of needles attains maximum values in the middle canopy layers (5th–6th layers). Needle density (No cm^{-1}), which may reflect light conditions for growing needles in the canopy (Thompson, 1985), decreases towards the top of the tree. Lower needle density can enhance penetration of light into the canopy (Margolis et al., 1995). Needle mass per unit shoot increases toward the top of the tree. Differences in this parameter reflect differences in both photosynthetic capacity and adaptation to various water and temperature regimes between different canopy layers (Margolis et al., 1995). The trees studied by us displayed a relatively stable needle mass to length ratio for the 6th–8th layers. Also, the number of
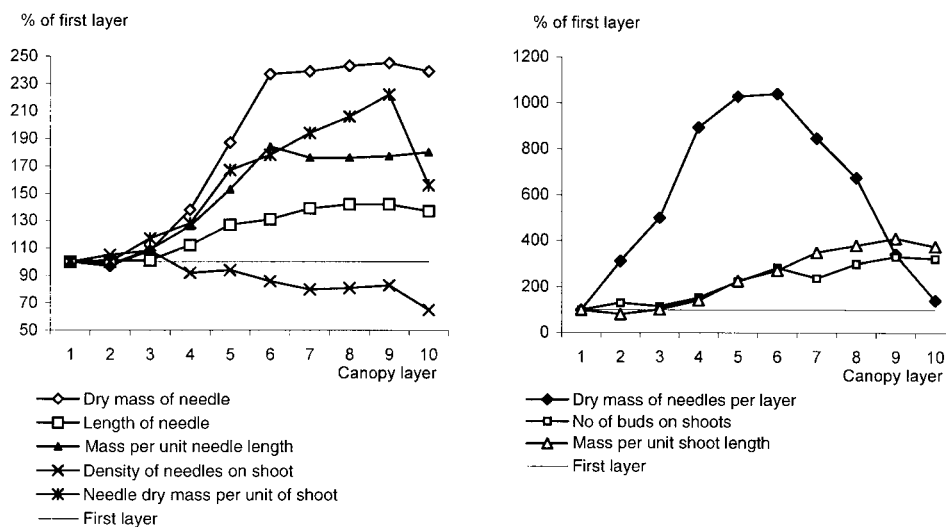

Fig. 1. Vertical variation of morphological parameters for different canopy fractions (% of the parameters of the first layer).

166

Table 1. Variation of needle parameters in different canopy layers of Scots pine ($\pm$SD)

Canopy layer	Dry mass of needles per layer, % of total in canopy	Dry mass of needle, mg	Length of needle, mm	Mass per unit needle length, mg mm^{-1}	Density of needles on shoot, No cm^{-1}*	Needle dry mass per unit of shoot, g cm^{-1}	No of buds on shoots, No shoot^{-1}	Dry mass of shoots per unit length, g cm^{-1}
1st	1.7±0.06	9.2±0.05	44.9±3.61	0.200±0.02	10.0±2.22	0.18±0.01	1.3±0.02	33.9±2.1
2nd	5.3±0.14	8.9±0.11	45.6±3.20	0.195±0.02	10.5±1.21	0.18±0.02	1.7±0.14	27.6±0.9
3rd	8.5±0.16	9.9±0.25	45.5±3.90	0.217±0.04	10.8±1.04	0.21±0.01	1.5±0.28	34.6±1.2
4th	15.2±0.15	12.7±0.15	50.3±2.42	0.252±0.01	9.2±1.11	0.23±0.005	2.0±0.07	47.7±3.1
5th	17.5±1.21	17.4±0.61	56.9±1.78	0.306±0.01	9.4±0.81	0.30±0.004	2.9±0.07	76.5±3.6
6th	17.7±1.14	21.5±0.86	58.6±1.96	0.367±0.02	8.6±0.66	0.32±0.01	1.9±0.09	92.3±4.9
7th	14.4±0.78	22.0±0.25	62.6±5.41	0.351±0.03	8.0±0.56	0.35±0.003	3.1±0.08	118.2±5.6
8th	11.5±0.96	22.4±0.94	63.9±5.08	0.351±0.12	8.1±0.42	0.37±0.002	3.9±0.12	128.6±5.1
9th	5.8±0.71	22.5±1.16	63.7±2.80	0.353±0.07	8.3±0.53	0.40±0.001	4.3±0.17	139.0±7.2
10th	2.4±0.114	22.0±1.28	61.3±2.86	0.359±0.03	6.5±0.21	0.28±0.001	4.2±0.21	127.0±6.9

* Number of needle pairs on shoot

167

Table 2. Differences between the morphological parameters of pine in different canopy layers and the dependence of the values of the parameters on the location of the layer in the canopy

Parameter	One-way analysis of variance		Regression analysis	
	F-ratio	Significance	R^2	Significance
Length of needles	7.002	0.0000	0.871	<0.011
Dry mass of needles	8.314	0.0000	0.872	<0.050
Mass per unit needle length	16.209	0.0000	0.894	<0.005
Density of needles on shoot	2.486	0.0159	0.803	<0.042
Number of buds on shoot	10.507	0.0000	0.860	<0.038
Mass per unit shoot length	10.421	0.0000	0.922	<0.034

buds was considerably larger in the upper layers. Dispersion analysis revealed significant differences in the investigated parameters between different canopy layers and regression analysis indicated the dependence of their values on the location of the corresponding layers in the canopy (Table 2).

Nutrients

The strength and direction of nutrient transport and partitioning in different plant organs have been demonstrated to be regulated by source–sink relationships. It was shown earlier that foliar photosynthetic properties vary vertically in canopies for both broad-leaved and coniferous trees (Woodman, 1971; Kozlowski et al., 1991; Mandre et al., 1998). This allows us to assume also the existence of variability in nutrient partitioning in different pine canopy parts.

Indeed, our study showed a high variability of the accumulation of nutrients in the needles of Scots pine in different layers of the canopy. In March, before budbreak, and in October, after growth processes had stopped, variability was observed in the dynamics of N, P, Mg, K, and Ca and the total concentration of mineral elements (Fig. 2). At the beginning of budbreak, average amounts of N, P, and K are possibly transported to the newly developing organs, which act as a strong sink, and their concentration is somewhat lower than in autumn. Regression analysis indicated that at this time the partitioning of P between different canopy layers of Scots pine is relatively weakly correlated with the height of the layer (Table 3). However, a strong correlation was observed between the concentration of N, K, Ca, and Mg in the needles and the height of the canopy layer. In October, when the growth of trees has stopped and daily temperatures have fallen, the content of Ca, Mg, and P did not depend on the height of the canopy layer.

When studying the dependence of the morphological parameters of needles upon their nutrient content we observed several differences between the data collected in spring and those collected in autumn (Table 4).
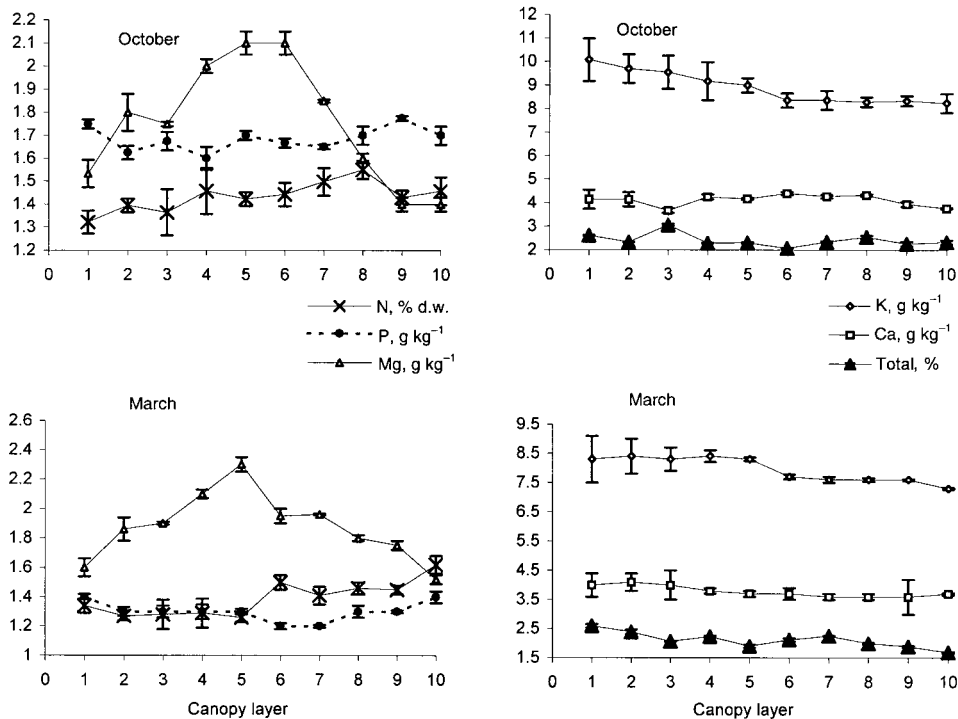
Fig. 2. Vertical distribution of nutrients in one-year-old needles of Scots pine from different layers.

Table 3. Relationship between the content of mineral nutrients in Scots pine needles and the height of canopy layers. Regression analysis and determination coefficient (R^2) were calculated for the significance level $p < 0.01$

Element	March	October
N	0.709	0.515
P	0.012	0.084
K	0.830	0.898
Ca	0.743	0.008
Mg	0.511	0.016

Regression analysis revealed a significant dependence of needle length, dry mass, and the mass per unit needle length on N, K, and Ca concentrations in different layers in spring and a slightly weaker dependence in autumn.

Formation of buds in late summer and their number on the shoots, which determine foliage density and assimilation area, displayed a significant correlation with the content of Ca and K in the needles in spring and especially in autumn (Table 4). However, the relationships between the nutrients and the number of buds formed on the shoot are not yet fully understood.

Table 4. Relationship of the average values of the morphological parameters of needles and the formation of buds on shoots with the content of non-structural carbohydrates and nutrients in needles. Regression and determination coefficient (R^2) value were calculated for the significance level $p < 0.01$

Nutrient	Length of needles		Dry mass of needles		Mass per unit needle length		Number of buds on shoots	
	March	October	March	October	March	October	March	October
N	0.475	0.630	0.578	0.556	0.571	0.545	0.007	0.441
P	0.115	0.005	0.122	0.085	0.149	0.057	0.007	0.171
K	0.728	0.927	0.786	0.956	0.754	0.455	0.592	0.658
Ca	0.913	0.043	0.895	0.018	0.948	0.022	0.591	0.645
Mg	0.474	0.051	0.008	0.210	0.008	0.028	0.054	0.009

Summing up our findings it should be stressed that the growth of pine needles and shoots and the formation of the biomass and density of needles as well as the number of buds on shoots vary significantly among different layers of the canopy. The development of morphological differences is significantly correlated with the partitioning of nutrients. The formation of the architecture of pine canopy and its growth depend on the number of buds on shoots, which in turn depends on the accumulation of nutrients in the needles.

ACKNOWLEDGEMENTS

REFERENCES

Ågren, G. J., Axelsson, B., Flower-Ellis, J. G. K., Linder, S., Persson, H., Staaf, H. & Troeng, E. 1980. Annual carbon budget for a young Scots pine. In *Structure and Function of Northern Coniferous Forests – An Ecosystem Study* (Persson, T., ed.). *Ecol. Bull.* (Stockholm), 32, 307–313.

Einig, W. & Hampp, R. 1990. Carbon partitioning in Norway spruce: amounts of fructose 2,6-bisphosphate and intermediates of starch/sucrose synthesis in relation to needle age and degree of needle loss. *Trees*, **4**, 9–15.

Ericsson, A. 1978. Seasonal changes in translocation of ^{14}C from different age-classes of needles on 20-year-old Scots pine trees (*Pinus sylvestris*). *Physiol. Plant.*, **43**, 351–358.

Field, C. B. & Mooney, H. A. 1986. The photosynthesis–nitrogen relationship in wild plants. In *On the Economy of Plant Form and Function* (Givnish, T. J., ed.), pp. 25–55. Cambridge University Press.

Flower-Ellis, J. G. K. & Persson, H. 1980. Investigation of structural properties and dynamics of Scots pine stands. In *Structure and Function of Northern Coniferous Forests – An Ecosystem Study* (Persson, T., ed.). *Ecol. Bull.* (Stockholm), 32, 125–138.

Hampp, R., Egger, B., Effenberger, S. & Einig, W. 1994. Carbon allocation in developing spruce needles. Enzymes and intermediates of sucrose metabolism. *Physiol. Plant.*, **90**, 299–306.

Kappel, F. & Flore, J. A. 1983. Effect of shade on photosynthesis, specific leaf weight, chlorophyll content of leaves, and morphology of young peach trees. *J. Am. Soc. Hort. Sci.*, **108**, 541–544.

Kikuzawa, K. & Umeki, K. 1996. Effect of canopy structure on degree of asymmetry of competition in two forest stands in Northern Japan. *Ann. Bot.*, **77**, 565–571.

Kozlowski, T. T., Kramer, P. J. & Pallardy, S. G. 1991. *The Physiological Ecology of Woody Plants.* Academic Press, San Diego.

Kramer, P. J. & Kozlowski, T. T. 1979. *Physiology of Woody Plants.* Academic Press, New York.

Linder, S. & Troeng, E. 1981. The seasonal course of respiration and photosynthesis in strobili of Scots pine. *For. Sci.*, **27**, 267–276.

Mandre, M. 1995. Changes in the nutrient composition of trees. In *Dust Pollution and Forest Ecosystems. A Study of Conifers in an Alkalized Environment.* (Mandre, M., ed.), pp. 44–65. *Publ. Inst. Ecol.*, **3**. Tallinn.

Mandre, M., Tullus, H. & Tamm, Ü. 1998. The partitioning of carbohydrates and biomass of leaves in *Populus tremula* L. canopy. *Trees*, **12**, 160–166.

Margolis, H., Oren, R., Whitehead, D. & Kaufmann, M. R. 1995. Leaf area dynamics of conifer forests. In *Ecophysiology of Coniferous Forests* (Smith, W. K. & Hinkley, T. M., eds.), pp. 181–225. Academic Press, San Diego.

Pearcy, R. W. & Sims, D. A. 1994. Photosynthetic acclimation to changing light environment: scaling from the leaf to the whole plant. In *Exploitation of Environmental Heterogeneity by Plants* (Caldwell, M. M. & Pearcy, R. W., eds.), pp. 145–174. Academic Press, San Diego.

Rieger, A., Guttenberger, M. & Hampp, R. 1992. Soluble carbohydrates in mucorrhized and non-mycorrhized fine roots of spruce seedlings. *Z. Naturforsch.*, **47c**, 201–204.

Rook, D. A. 1991. Seedling development and physiology in relation to mineral nutrition. In *Mineral Nutrition of Conifer Seedlings* (van den Driessche, R., ed.), pp. 85–111. CRC Press, Boca Raton, Florida.

Ross, J. & Ross, V. 1996. Phytometrical characteristics of the willow plantation at Tõravere. In *Short Rotation Willow Coppice for Renewable Energy and Improved Environment* (Perttu, K. & Koppel, A., eds.), pp. 133–145. SLU/Repro, Uppsala.

Schaedle, M. 1991. Nutrient uptake. In *Mineral Nutrition of Conifer Seedlings* (van den Driessche, R., ed.), pp. 25–59. CRC Press, Boca Raton, Florida.

Thompson, B. E. 1985. Seedling morphological evaluation – what you can tell by looking. In *Evaluating Seedling Quality: Principles, Procedures, and Predictive Abilities of Major Tests* (Duryea, M. L., ed.), pp. 59–71. Oregon State University, Corvallis.

Troeng, E. & Linder, S. 1982. Gas exchange in a 20-year-old stand of Scots pine. I. Net photosynthesis of current and one-year-old shoots within and between seasons. *Physiol. Plant.*, **54**, 7–14.

Vessey, J. K. & Layzell, D. B. 1987. Regulation of assimilate partitioning in soy-bean: initial effects following change in nitrate supply. *Plant Physiol.*, **83**, 341–348.

Waring, R. H. 1991. Responses of evergreen trees to multiple stresses. In *Response of Plants to Multiple Stresses* (Mooney, H. A., Winner, W. E. & Pell, E. J., eds.), pp. 371–390. Academic Press, San Diego.

Woodman, J. N. 1971. Variation of net photosynthesis within the crown of a large forest-grown conifer. *Photosynthetica*, **5**, 50–54.

Biomassi ja toitainete jaotumus hariliku männi (*Pinus sylvestris*) võras

Malle Mandre ja Hardi Tullus

On uuritud toitainete jaotumust ja okaste ning võrsete morfoloogiliste näitajate erinevusi hariliku männi (*Pinus sylvestris*) võra erinevates kihtides. Analüüsideks valiti mustika kasvukoha tüüpi puistus Alatskivil 12 haabituselt ja võra kujult sarnast 45–55-aastast puud. Proovipuud langetati kahel aastaajal: märtsis, enne pungade puhkemist ja oktoobris, kui okkad ning võrsed on saavutanud täis-pikkuse ja nende kasv on lõppenud. Võra jaotati 10 kihiks, igast kihist määrati okaste mass (% üldmassist), okka mass (mg), okka pikkus (mm), võrsete okas-tatus (tk cm^{-1}), okka mass võrse pikkusühiku kohta (g cm^{-1}), pungade arv võrsetel (tk võrse kohta) ja teised morfoloogilised näitajad. Määrati okaste makro-elementide N, P, K, Mg ja Ca sisalduse varieeruvus võra erinevates kihtides. Selgus, et võra keskosas (5. ja 6. kihis) on okaste üldmass võras suurim, kuigi üksiku okka mass, pikkus ja paksus ning pungade arv võrsel on suurim võra ülemistes kihtides. Kevadel, kui organism vajab uute organite moodustamiseks enam toitaineid, sõltuvad okaste pikkus ja mass oluliselt N, K ja Ca sisaldusest. Sügisel, kui okaste kasv on lõppenud, on seos toiteelementide sisalduse ja okaste massi ning pikkuse vahel ebaoluline.