Journal of Elementology ISSN 1644-2296

Węgiel A., Bielinis E., Polowy K. 2019.
The stock and content of micronutrients in aboveground biomass of Scots pine stands of different densities.
J. Elem., 24(2): 615-628. DOI: 10.5601/jelem.2018.23.1.1621

RECEIVED: 6 February 2018
ACCEPTED: 30 October 2018

ORIGINAL PAPER

THE STOCK AND CONTENT OF MICRONUTRIENTS IN ABOVEGROUND BIOMASS OF SCOTS PINE STANDS OF DIFFERENT DENSITIES*

Andrzej Węgiel[1], Ernest Bielinis[2], Krzysztof Polowy[3]

[1] Department of Forest Management
Poznań University of Life Sciences, Poland
[2] Department of Forestry and Forest Ecology
University of Warmia and Mazury in Olsztyn, Poland
[3] Department of Forest Technology
Poznań University of Life Sciences, Poland

Abstract

For any plant, the micronutrient content in its tissues is of extreme importance, as both deficiency and excess can be harmful. Most of the nutrient balance studies focus on macronutrients, while micronutrients are usually neglected. The aim of the study was to estimate the impact of a stand density (number of trees per area) on stocks of four micronutrients: copper (Cu), iron (Fe), manganese (Mn) and zinc (Zn) in the aboveground biomass of mature Scots pine (*Pinus sylvestris* L.) stands of various densities. The nutrient content in dry mass and the stock of nutrients per hectare were assessed. Five sample plots, 0.5 ha each, were established in 82-year-old Scots pine stands of different densities (476-836 trees per ha). The dry mass of all trees on the experimental plots was estimated using allometric equations. The mass of aboveground biomass was calculated as the sum of the following compartments of trees: 1) stems (wood and bark), 2) dead branches, 3) thick branches, 4) thin branches and 5) needles. The content of the elements was determined in separate samples from tree compartments taken for chemical analysis. The content of Cu, Fe and Mn was the highest in needles, while Zn was the richest in the stem bark. The content of the investigated micronutrients decreased in the following order: Mn>Zn>Fe>Cu. Relative concentartions of the four micronutrients in the distinguished tree compartments were similar. No influence of a stand density on the micronutrient stock was found.

Keywords: *Pinus sylvestris*, copper, iron, manganese, zinc.

Andrzej Węgiel, PhD, Faculty of Forestry, Department of Forest Management, Poznań University of Life Sciences, Wojska Polskiego 28, 60-637 Poznań, Poland, e-mail: wegiel@up.poznan.pl.
* This work was supported by the European Regional Development Fund and Polish Ministry of Science and Higher Education (INT-09-0039).

INTRODUCTION

Nutrients are essential for the growth and development of trees. A shortage of available nutrients can significantly impact forest productivity (Mandre et al. 2010, Modrzewska et al. 2016, Paré, Thiffault 2016). Macronutrients are present in plants in high contents. Nevertheless, micronutrients, that achieve much lower contents, also play an important role. Such elements as copper (Cu), iron (Fe), manganese (Mn) and zinc (Zn) are vital for vegetation, but both their deficiency and excess can be harmful. The content of these elements in trees is believed to depend on climate, soil type, level of groundwater, the biological activity of the soil, species and age of tree, and the tree compartment (Roitto et al. 2005, Kosiorek et al. 2016).

Copper is an important micronutrient for plants because it takes part in defensive mechanisms and in biochemical reactions as a cofactor of enzymes and an electron carrier. Cu is involved in the metabolism of nitrogen compounds and sugars, regulates DNA and RNA production processes, and plays a role in cell wall lignification (Yruela 2009, Nagajyoti et al. 2010). Although Cu is essential, even a slight excess over the optimal level makes it extremely toxic for plants (Burkhead et al. 2009, Küpper, Andresen 2016). The Scots pine is highly sensitive to copper excess, which can cause significant inhibition in the tree's growth and development (Ivanov et al. 2016). An excessive amount of Cu can also affect plant pigment production, photosynthesis and respiration (Maksymiec 1997, Możdżeń et al. 2017).

Iron, like copper, plays a role in metabolic processes such as DNA synthesis, respiration, and photosynthesis. Its role as a catalyst in the synthesis of some proteins and chlorophyll is especially important (Krutul et al. 2017). Iron is not readily accessible to plants and is also potentially toxic (Jeong, Guerinot 2009, Küpper, Andresen 2016). To acquire iron from soil, but at the same time, to avoid iron excess in the cells, uptake and homeostasis must be strictly controlled by plants (Hell, Stephan 2003). Fe is a crucial micronutrient for plants, and its deficiency induces various morphological and biochemical changes (Briat et al. 1995).

Manganese participates in the structure of photosynthetic proteins and enzymes. Mn takes part in the photosynthesis during the water splitting process and is mainly located in needles (Dučić, Polle 2005, Gielen et al. 2016). Therefore, its excess seems to be particularly damaging to the photosynthetic apparatus of plants (Mukhopadhyay, Sharma 1991, Millaleo et al. 2010).

Zinc is a necessary element for all plants. It influences the activity of many enzymes, and takes part in the regulation of carbohydrate metabolism and protein synthesis. It is one of the structural components of ribosomes and cell walls (Broadley et al. 2007, Ivanova et al. 2010, Krutul et al. 2017) and plays a key role in the efficient course of photosynthesis (Diatta et al.

2016). The excess of Zn in plants impedes photosynthesis, thus strongly affecting plant growth (Küpper, Andresen 2016).

Nutrient stocks in forest ecosystems constantly fluctuate in time. A number of studies have been conducted to measure these changes (Joki-Heiskala et al. 2003, Akselsson et al. 2007, Paré, Thiffault 2016). Nutrient budget is the balance between nutrient inputs and outputs of an ecosystem over a specified time period (Ranger, Turpault 1999). The budget studies use some empirical and assumed input and output levels of nutrients, as the variables for calculations (Egnell, Valinger 2003). Harvest is a main factor causing nutrient losses in managed forests and forest plantations. Nutrients removed in harvesting operations can be compensated by inputs from atmospheric deposition and from mineral weathering (Merino et al. 2005, Palviainen, Finér 2012). Preserving a natural balance of both macro- and micronutrients is fundamental to sustainable forestry (Paré, Thiffault 2016).

One of the main goals of forest management is to enhance the growth of a tree stand and to improve its quality on a sustainable basis. A stand density (defined as a number of trees per area unit) is one of few things that can be controlled efficiently, mostly by thinning (Zeide 2004). Proper thinning involves removing some trees in order to increase the growth of the remaining ones (Tahvonen et al. 2013).

The relationship between a stand density and the accumulation of nutrients in biomass varies depending on the considered period. In the long term, the number of trees decreases but the overall biomass increases together with the nutrient stock (Augusto et al. 2000, Palviainen, Finér 2012). In the short term, the situation could be opposite. Directly after thinning, the number of trees drops considerably, and the overall biomass and nutrient stocks are smaller than before it (Jacobson et al. 2000, Blanco et al. 2006). However, a few years after thinning, following a period of stimulated growth, the stand's biomass could be the same as before. It is not yet clear if stocks of macronutrient follow the same pattern.

For Scots pine (*Pinus sylvestris* L.) stands of a similar age, we predict that there will be a correlation between the stand density and the amount of stored micronutrients. Less dense stands should have less micronutrients accumulated. This can be caused by harvesting and removing trees with biomass which contains micronutrients (Barron-Gafford et al. 2003, Noh et al. 2013). Furthermore, in stands of lower density there are biggest trees, which could have a lower content of nutrients (Skonieczna et al. 2014).

The aim of the study was to estimate the impact of a stand density on four micronutrient stocks (Cu, Fe, Mn and Zn) in the aboveground biomass of mature Scots pine stands of various densities (476-836 trees per ha), but with similar biomass. All sampled stands where 5-10 years after thinning and showed no correlation between the stand density and biomass. For these stands, the content of nutrients in biomass and stocks per hectare were assessed.

MATERIAL AND METHODS

This study was carried out in 5 sample stands of Scots pine (*Pinus sylvestris* L.), located in Drawno Forest District, northwestern Poland (E 15°50′-16°0′, N 53°10′-53°13′). This area is characterized by nutrient-poor habitats on Podzols. In such habitats, the Scots pine is the dominant tree species, and it forms homogeneous stands with a small admixture of birch. The sample plots, 0.5 ha each (Table 1), were selected so that a stand density

Table 1

Main characteristics of five 82-year-old Scots pine sample stands

Sample stand	Density, tree ha^{-1}	Mean DBH ±SD (cm)	Mean height ±SD (m)	Basal area (m^2 ha^{-1})	Volume (m^3 ha^{-1})	Aboveground biomass (Mg ha^{-1})
SP1	476	28.2±4.5	22.9±1.7	30.5	319	154
SP2	590	25.7±4.7	20.8±1.4	31.5	302	145
SP3	672	23.6±4.3	19.6±1.5	30.3	275	133
SP4	756	23.9±5.3	20.1±2.0	35.6	337	162
SP5	824	21.8±4.0	19.3±1.7	31.7	286	142

would be the distinguishing variable. Plots were established in 82-year-old, single-species, single-layer stands growing on the same soil unit classified as Carbic Podzol (WRB 2015). Sample plots were located within one forest complex and were managed by one owner, the State Forests since World War Two. Because forests were planted in the same year and by the same owner, it could be assumed that the initial spacing was the same. Therefore, current differences in stand densities were due to differences in natural mortality or different thinning intensities. To avoid disturbing the results by recent thinning, selected stands were 5-10 years after last thinning. To confirm the correct selection of plots, the correlation between a stand density and stand biomass was checked.

On the plots, diameter at breast height (DBH) was measured for each tree. The height of 20% of the trees was also measured and Näslund's height curves were developed for each plot separately, which allowed us to calculate the height of each tree.

The dry mass of all trees was estimated with allometric equations. On each plot, 10 model trees were selected, with DBH representing the range of the measured diameters, resulting in 50 model trees in total. Model trees were cut down, delimbed, and divided into defined compartments: stem, dead branches, thick branches (thicker than 5 mm), thin branches and needles. From the stem, samples were taken as 10-cm long cross-sections that were cut every meter along the stem. The fresh mass of a compartment was measured. After weighing the fresh compartments, the samples were dried at 65°C to a constant weight to determine the dry mass. The dry mass

of each compartment of each model tree was calculated using the sample proportion of dry and fresh mass. The 10-cm cut-outs were also used to determine the proportion of dry mass between wood and bark.

Allometric equations were developed based on the data obtained for the 50 model trees across all plots. The best fitting equations to determine the dry mass of each compartment were selected basing on: Akaike's information criterion (AIC), coefficient of determination (R^2) and residual standard error (RSE). These criteria of model fitness were used for: stem wood (AIC = 456, R^2 = 0.936, RSE = 22.19), dead branches (AIC = 268, R^2 = 0.746, RSE = 3.35), thick branches (AIC = 366, R^2 = 0.728, RSE = 8.92), thin branches (AIC = 188, R^2 = 0.674, RSE = 1.53) and needles (AIC = 214, R^2 = 0.750, RSE = 1.98). The estimated allometric equations allowed us to calculate the dry mass of the aboveground compartments of every individual tree, using DBH and height as predictive variables. The results were used to calculate the mass of each individual tree and the collective mass for the sample plots.

Chemical analyses were conducted on a selected number of trees used for biomass estimation. For each sample area, 3 out of the 10 model trees were selected. From a list ordered by increasing DBH, the second, fifth and ninth trees were chosen. Across the whole study area, a total of 15 trees were selected. Materials for the chemical analysis were taken beforehand from the samples used to determine dry mass. Separate samples from the following tree compartments: stem wood, stem bark, dead branches, thick branches, thin branches and needles, were taken for chemical analysis. The material was ground, marked, and sent to the laboratory. Laboratory samples were wet-digested in HNO_3 (concentration) and the content of metals was analysed by Inductively Coupled Plasma - Optical Emission Spectrometer (ICP-OES).

Based on the dry mass of each individual tree and percentage content of the elements, the mass of four micronutrients in each tree compartment was calculated. For these calculations, the percent share of a given macronutrient in the closest model tree (closest DBH) from the same stand was used for each tree.

Statistical analyses were performed using the Multivariate Platform tool in JMP 10.0 statistical software (SAS Institute Inc., Cary, NC, USA). The results consisted of the Pearson correlation coefficients (r) and the corresponding levels of significance. On this basis, an assessment of the correlations between the density of the stands and (1) the micronutrient stock, (2) the aboveground biomass, (3) the mean DBH, (4) the mean tree high (5) the stand volume and (6) the basal area was performed.

RESULTS

For 15 model Scots pine trees from 5 stands of different densities, the content of 4 micronutrients in the dry mass of various tree compartments (stem wood, stem bark, thick branches, thin branches and needles – Table 2) was analysed. The content of Fe and Mn was the highest in dry biomass of needles, while Zn was the richest in the stem bark and Cu was most abundant in thin branches. All analysed micronutrients had the lowest content in the stem wood (Table 2).

For some of the compartments the nutrient content was correlated with the tree size (Figure 1). Correlations between DBH and the content of a micro-

Table 2

Mean (±SD) content of elements in dry biomass for all (N = 15) sampled Scots pine model trees

Element	Stem wood	Stem bark	Thick branches	Thin branches	Dead branches	Needles
Cu (mg kg^{-1})	0.94±0.95	2.39±0.87	1.48±0.78	3.60±1.35	1.44±1.28	2.67±0.96
Fe (mg kg^{-1})	13.4±11.1	22.2±7.1	23.3±19.9	32.7±16.4	21.9±11.5	34.2±16.3
Zn (mg kg^{-1})	11.7±3.2	66.6±19.4	34.7±6.6	45.0±13.6	25.7±7.8	47.4±7.2
Mn (mg kg^{-1})	154±55	654±157	315±66	341±66	217±77	1127±215

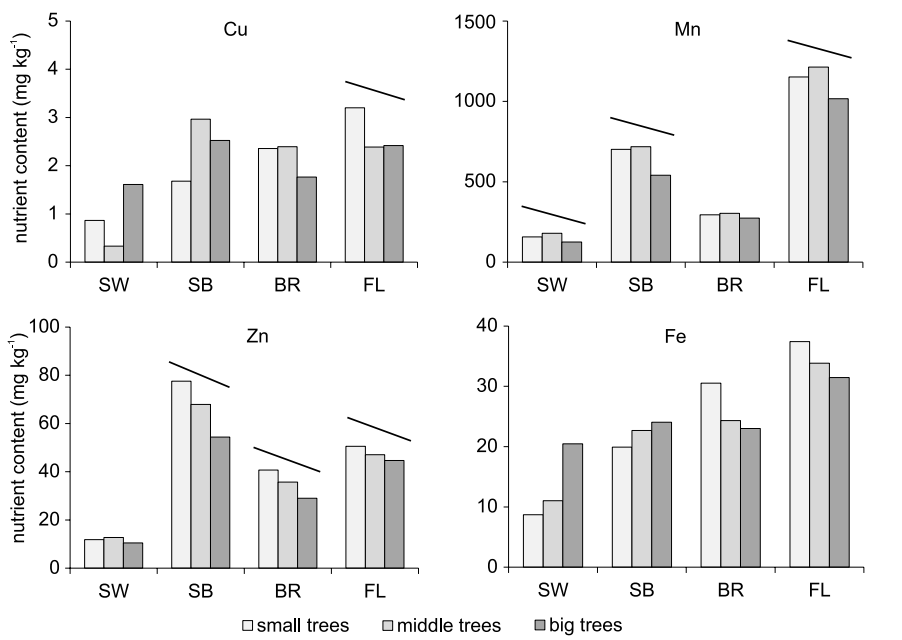

Fig. 1. Mean micronutrient content (mg kg^{-1}) in dry biomass for tree compartments of all model trees (N = 15) divided into three groups of different DBH (small, middle and big trees). Statistically significant correlations at $p < 0.05$ between the tree DBH and the micronutrient content are marked with an oblique line. Tree compartments: SW – stem wood, SB – stem bark, BR – branches and FL – foliage.

nutrient were statistically significant (at $p < 0.05$) for stem wood (Mn), stem bark (Mn and Zn), branches (Zn) and needles (Cu, Mn and Zn). All correlations were negative, which means that bigger trees had a lower content of micronutrients.

The amount of stored micronutrients in the aboveground biomass of Scots pine stands of different densities is shown in Table 3. Manganese was the most abundant element in the aboveground biomass (30.9-47.1 kg ha^{-1}). The second most abundant micronutrient in the aboveground biomass was zinc (2.6-3.2 kg ha^{-1}), followed by iron (1.4-3.8 kg ha^{-1}) and copper (0.1-0.3 kg ha^{-1}).

Relative nutrient stocks per hectare in the specific tree compartments were similar for all micronutrients (Figure 2). All of the micronutrients were

Table 3

Micronutrient stock (kg ha^{-1}) in stem wood, stem bark, branches, needles and total (all aboveground biomass) for Scots pine stands of different densities

Tree parts	Sample plots - Scots pine stands of different densities				
	SP1 476 trees ha^{-1}	SP2 590 trees ha^{-1}	SP3 672 trees ha^{-1}	SP4 756 trees ha^{-1}	SP5 824 trees ha^{-1}
Cu (copper)					
Stem wood	0.20	0.07	0.01	0.19	0.07
Stem bark	0.02	0.03	0.02	0.03	0.02
Branches	0.04	0.04	0.03	0.04	0.04
Needles	0.01	0.01	0.01	0.01	0.01
Total	0.27	0.15	0.07	0.27	0.14
Fe (iron)					
Stem wood	3.09	1.75	0.67	0.99	0.96
Stem bark	0.25	0.22	0.17	0.27	0.20
Branches	0.35	0.74	0.36	0.51	0.58
Needles	0.14	0.10	0.21	0.11	0.27
Total	3.83	2.81	1.41	1.88	2.01
Zn (zinc)					
Stem wood	1.30	1.12	1.17	1.62	1.24
Stem bark	0.59	0.62	0.61	0.63	0.69
Branches	0.63	0.68	0.79	0.73	0.86
Needles	0.22	0.21	0.23	0.26	0.20
Total	2.74	2.63	2.80	3.24	2.99
Mn (manganese)					
Stem wood	14.92	12.96	14.32	26.54	15.93
Stem bark	5.48	6.34	6.52	6.63	5.75
Branches	6.40	6.86	6.18	7.87	5.53
Needles	5.09	4.70	5.66	6.02	5.09
Total	31.89	30.86	32.68	47.06	32.30

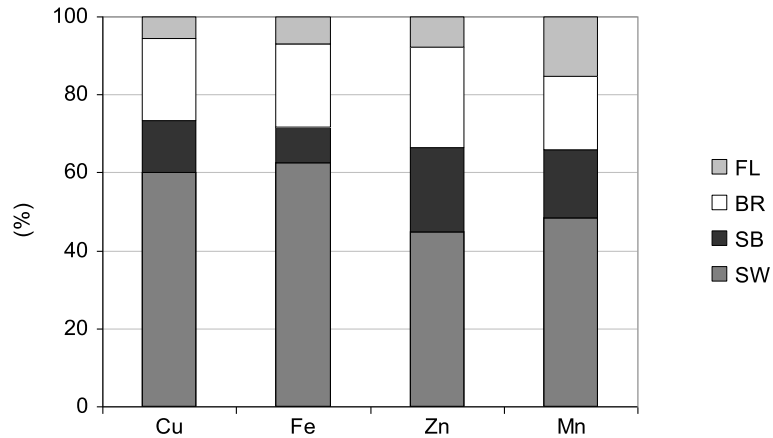

Fig. 2. Proportions of micronutrient (Cu, Fe, Zn and Mn) stock per hectare in tree compartments (FL – foliage, BR – branches, SB – stem bark, SW – stem wood) for all sampled stands

stored mostly in the stem wood (Cu – 60%, Fe – 62%, Zn – 45% and Mn – 48%), and in the smallest amounts in the needles (Cu – 6%, Fe – 7%, Zn – 8% and Mn – 15%).

The analysis of correlations showed no statistically significant relationship between the total micronutrient stock per hectare and stand density for any of the micronutrients (Table 4). A correlation for the nutrient stock per

Table 4

Pearson's correlation coefficients (r) between stand density and nutrient stock in different tree parts of the sampled Scots pine stands ($N = 5$).

Tree part	Cu	Fe	Mn	Zn
Stem wood	-0.287	-0.852	0.459	0.299
Stem bark	-0.002	-0.193	0.344	0.837
Branches	-0.091	0.249	-0.081	**0.895***
Needles	0.549	0.531	0.414	0.200
Total	-0.276	-0.799	0.416	0.736

* significant at $p < 0.05$

hectare in a specific tree compartment was significant only for Zn stored in branches ($r = 0.895$, $p < 0.05$). Statistically significant, negative correlations between the stand density and average DBH ($r = -0.850$, $p < 0.001$) and average tree height ($r = -0.497$, $p < 0.05$) were found. No correlations between the stand density and total aboveground biomass, stand volume or basal area were found.

DISCUSSION

The results corroborate the generally known fact that there are significant differences in nutrient content in different tree compartments. The nutrient content is usually the highest in stem bark and tree crowns (mostly needles) and lowest in stem wood (Saur et al. 1992, Barron-Gafford et al. 2003, Augusto et al. 2008). According to our results, the amounts of micronutrients in the aboveground biomass of Scots pine stands can be ordered as Mn>Fe>Zn>Cu. The results obtained by other authors usually show a different order, namely Fe>Mn>Zn>Cu (Merino et al. 2005, Dogan et al. 2010, Yan et al. 2017). In our study, the content of Mn was higher than that of Fe in all tree compartments. This is in line with results obtained by Beaton et al. (1965). Our results show that the content of Fe, Zn and Cu was similar to values given by other authors for Scots pine, but the content of Mn was higher (Helmisaari 1992, Rautio et al. 1998, Olsson et al. 2000, Saarela et al. 2005, Saarsalmi et al. 2010).

In managed forests, harvesting is the main factor that causes nutrient losses. Nutrients removed from forest ecosystems by harvesting can be compensated for by inputs from atmospheric deposition and, in mineral soils, by weathering (Merino et al. 2005, Palviainen, Finér 2012). Maintaining a positive nutrient balance is essential to achieving sustainable forestry (Paré, Thiffault 2016). As forests are harvested more intensively, nutrient export from the ecosystem also increases (Blanco et al. 2005, Węgiel et al. 2018*b*). However, the magnitude of nutrient removal depends on the harvesting method because the nutrient content differs between tree compartments. Usually, branches and needles have a higher content of nutrients than the stem (Merino et al. 2005, Helmisaari et al. 2011, Palviainen, Finér 2012). Our results prove that this is also true for the four assessed micronutrients (Table 2).

In conventional stem-only harvesting (SOH), branches and needles constitute logging residues and are left on the site. In contrast, whole-tree harvesting (WTH), especially for bioenergy purposes, includes the removal of these residues from the site. Nutrient balance calculations indicate that in many cases nutrient removals by WTH exceed the replenishment rate of plant-available nutrient pools in soil by mineral weathering and atmospheric deposition (Olsson et al. 2000, Wall 2008, Achat et al. 2015, Vangansbeke et al. 2015).

When analyzing the relationship between the stand density and the amount of stored nutrients, two situations should be distinguished: (1) when differences in densities are a consequence of different ages, and (2) when stands of different densities are of similar ages. In the first case, changes in density result from the stand's age, when the number of trees decreases but the overall biomass increases, along with the amount of stored nutrients. In this case, the relationships are rather obvious – the amounts

of stored nutrients should be positively correlated with biomass growth and stand age and negatively correlated with density (Barron-Gafford et al. 2003).

The situation is not so obvious when analyzing relationships between the nutrient stock and stand density in even-aged stands, where biomass is not correlated with the stand density.

In our stands, DBH was negatively correlated with the stand density. Lower density means a lower number of trees, but of bigger dimensions (Del Rio et al. 2001). Furthermore, for Cu, Zn and Mn, negative correlations between the micronutrient content in some compartments and DBH were found (Figure 1). The same was also found for some macronutrients (Skonieczna et al. 2014).

It could be therefore expected that if the nutrient content is correlated with the size of a tree, the nutrient stock will also correlate with the stand density. In spite of this assumption, no correlation between the stand density and micronutrient stock was found in this study. This could be explained by a low number of analyzed stands ($N = 5$) or too few model trees in each stand ($N = 3$).

For our sample stands, a positive correlation between the stand density and the amount of stored nutrients was found for 3 out of the 7 macronutrients. These were the most abundant elements: N, P and K (Węgiel et al. 2018*a*). There are few studies concerning the relationship between the stand density and macronutrient stock (Barron-Gafford et al. 2003, Fang et al. 2016). In the case of micronutrients – no such studies are available.

CONCLUSIONS

Forest utilization methods focusing on preserving a positive macronutrient balance could be also beneficial for micronutrients. More intensive utilization could cause excessive export of some elements from forest environment. Less intensive utilization is much safer for a positive balance of both micro- and macronutrients.

Our results show that the stock of Cu, Fe, Mn and Zn in the aboveground biomass of Scots pine stands was not correlated with the stand density. This could mean that thinnings of various intensity do not affect the stock of micronutrients either. More intensive thinning increase the biomass utilization and facilitates making a better profit from the final felling of a less dense stand (Bembenek et al. 2014). The results, however, need to be treated with caution because of the small size of the analyzed material and different results obtained for macronutrients.

ACKNOWLEDGEMENTS

The authors would like to thank the participants of the International Scientific Camps for Forestry Students ForseenPOMERANIA, for their valuable contribution to the laborious field studies on sample stands in Drawno Forest District (Pomerania Region, Poland).

REFERENCES

Achat D.L., Deleuze C., Landmann G., Pousse N., Ranger J., Augusto L. 2015. *Quantifying consequences of removing harvesting residues on forest soils and tree growth - A meta-analysis*. Forest Ecol. Manage., 348: 124-141. DOI: 10.1016/j.foreco.2015.03.042

Akselsson C., Westling O., Sverdrup H., Holmqvist J., Thelin G., Uggla E., Malm G. 2007. *Impact of harvest intensity on long-term base cation budgets in Swedish forest soils*. Water Air Soil Pollution: Focus, 7: 201-210.

Augusto L., Meredieu C., Bert D., Trichet P., Porté A., Bosc A., Lagane F., Loustau D., Pellerin S., Danjon F. et al. 2008. *Improving models of forest nutrient export with equations that predict the nutrient concentration of tree compartments*. Ann Forest Sci, 65.

Augusto L., Ranger J., Ponette Q., Rapp M. 2000. *Relationships between forest tree species, stand production and stand nutrient amount*. Ann Forest Sci, 57: 313-324.

Barron-Gafford G.A., Will R.E., Burkes E.C., Shiver B., Teskey R.O. 2003. *Nutrient concentrations and contents, and their relation to stem growth, of intensively managed Pinus taeda and Pinus elliottii stands of different planting densities*. Forest Sci, 49: 291-300.

Beaton J.D., Brown G., Speer R.C., MacRae I., McGhee W.P.T., Moss A., Kosick R. 1965. *Concentration of micronutrients in foliage of three coniferous tree species in British Columbia*. Soil Sci Soc Am J, 29: 299-302. DOI: 10.2136/sssaj1965.03615995002900030022x

Bembenek M., Karaszewski Z., Kondracki K., Łacka A., Mederski P.S., Skorupski M., Strzeliński P., Sułkowski S., Węgiel A. 2014. *Value of merchantable timber in Scots pine stands of different densities*. Drewno, 57: 133-142. DOI: 10.12841/wood.1644-3985.S14.09

Blanco J.A., Imbert J.B., Castillo F.J. 2006. *Effects of thinning on nutrient content pools in two Pinus sylvestris forests in the western Pyrenees*. Scandinavian J Forest Res, 21: 143-150. DOI: 10.1080/02827580600559726

Blanco J.A., Zavala M.A., Imbert J.B., Castillo F.J. 2005. *Sustainability of forest management practices: Evaluation through a simulation model of nutrient cycling*. Forest Ecol Manage, 213: 209-228.

Briat J.F., FobisLoisy I., Grignon N., Lobréaux S., Pascal N., Savino G., Thoiron S., von Wirén N., Van Wuytswinkel O. 1995. *Cellular and molecular aspects of iron metabolism in plants*. Biol Cell, 84: 69-81. DOI: 10.1016/0248-4900(96)81320-7

Broadley M.R., White P.J., Hammond J.P., Zelko I., Lux A. 2007. *Zinc in plants*. New Phytologist, 173: 677-702. DOI: 10.1111/j.1469-8137.2007.01996.x

Burkhead J.L., Reynolds K.A.G., Abdel-Ghany S.E., Cohu C.M., Pilon M. 2009. *Copper homeostasis*. New Phytologist, 182: 799-816. DOI: 10.1111/j.1469-8137.2009.02846.x

del Rio M., Montero G., Bravo F. 2001. *Analysis of diameter-density relationships and self -thinning in non-thinned even-aged Scots pine stands*. Forest Ecol Manage, 142: 79-87. DOI: 10.1016/s0378-1127(00)00341-8

Diatta J., Nawracała J., Andrzejewska A., Chudzińska E., Duczmal-Czernikiewicz A. 2016. *Biogeochemical assessment of a Zn-contaminated site using Scots pine (Pinus sylvestris* L.*) needles as phytoindicators*. Pol J Environ Stud, 25: 2315-2325. DOI: 10.15244/pjoes/63413

Dogan Y., Ugulu I., Baslar S. 2010. *Turkish red pine as a biomonitor: a comparative study of the accumulation of trace elements in the needles and bark*. Ekoloji, 19: 88-96. DOI: 10.5053/ /ekoloji.2010.7512

Dučić T., Polle A. 2005. *Transport and detoxification of manganese and copper in plants*. Braz J Plant Physiol, 17: 103-112.

Egnell G., Valinger E. 2003. *Survival, growth, and growth allocation of planted Scots pine trees after different levels of biomass removal in clear-felling*. Forest Ecol Manage, 177: 65-74.

Fang X.M., Christenson L.M., Wang F.C., Zeng J.P., Chen F.S. 2016. *Pine caterpillar outbreak and stand density impacts on nitrogen and phosphorus dynamics and their stoichiometry in Masson pine (Pinus massoniana) plantations in subtropical China*. Can J Forest Res, 46: 601-609. DOI: 10.1139/cjfr-2015-0357

Gielen S., Batlle J.V.I., Vincke C., Van Hees M., Vandenhove H. 2016. *Concentrations and distributions of Al, Ca, Cl, K, Mg and Mn in a Scots pine forest in Belgium*. Ecol Modelling, 324: 1-10. DOI: 10.1016/j.ecolmodel.2015.12.015

Hell R., Stephan U.W. 2003. *Iron uptake, trafficking and homeostasis in plants*. Planta, 216: 541-551. DOI: 10.1007/s00425-002-0920-4

Helmisaari H.S. 1992. *Nutrient retranslocation within the foliage of Pinus sylvestris*. Tree Physiol, 10: 45-58.

Helmisaari H.S., Hanssen K.H., Jacobson S., Kukkola M., Luiro J., Saarsalmi A., Tamminen P., Tveite B. 2011. *Logging residue removal after thinning in Nordic boreal forests: Long-term impact on tree growth*. Forest Ecol Manage, 261: 1919-1927.

Ivanov Y.V., Kartashov A.V., Ivanova A.I., Savochkin Y.V., Kuznetsov V.V. 2016. *Effects of copper deficiency and copper toxicity on organogenesis and some physiological and biochemical responses of Scots pine (Pinus sylvestris* L.*) seedlings grown in hydroculture*. Environ Sci Pollut Res, 23: 17332-17344. DOI: 10.1007/s11356-016-6929-1

Ivanova E.M., Kholodova V.P., Kuznetsov V.V. 2010. *Biological effects of high copper and zinc concentrations and their interaction in rapeseed plants*. Russ J Plant Physiol, 57: 806-814. DOI: 10.1134/s1021443710060099

Jacobson S., Kukkola M., Mälkönen E., Tveite B. 2000. *Impact of whole-tree harvesting and compensatory fertilization on growth of coniferous thinning stands*. Forest Ecol Manage, 129: 41-51.

Jeong J., Guerinot M.L. 2009. *Homing in on iron homeostasis in plants*. Trends Plant Sci, 14: 280-285. DOI: 10.1016/j.tplants.2009.02.006

Joki-Heiskala P., Johansson M., Holmberg M., Mattsson T., Forsius M., Kortelainen P., Hallin L. 2003. *Long-term base cation balances of forest mineral soils in Finland*. Water Air Soil Pollut, 150: 255-273.

Kosiorek M., Modrzewska B., Wyszkowski M. 2016. *Levels of selected trace elements in Scots pine (Pinus sylvestris* L.*), silver birch (Betula pendula* L.*), and Norway maple (Acer platanoides* L.*) in an urbanized environment*. Environ. Monit Assess, 188. DOI: 10.1007/s10661-016-5600-0

Krutul D., Zielenkiewicz T., Radomski A., Zawadzki J., Antczak A., Drożdżek M., Makowski T. 2017. *Metals accumulation in Scots pine (Pinus sylvestris* L.*) wood and bark affected with environmental pollution*. Wood Res, 62: 353-364.

Küpper H., Andresen E. 2016. *Mechanisms of metal toxicity in plants*. Metallomics, 8: 269-285. DOI: 10.1039/c5mt00244c

Maksymiec W. 1997. *Effect of copper on cellular processes in higher plants*. Photosynthetica, 34: 321-342. DOI: 10.1023/a:1006818815528

Mandre M., Lukjanova A., Pärn H., Kõresaar K. 2010. *State of Scots pine (Pinus sylvestris* L.*) under nutrient and water deficit on coastal dunes of the Baltic Sea*. Trees - Structure and Function, 24: 1073-1085.

Merino A., Balboa M.A., Rodríguez Soalleiro R., González J.G.A. 2005. *Nutrient exports under different harvesting regimes in fast-growing forest plantations in southern Europe*. Forest Ecol Manage, 207: 325-339.

Millaleo R., Reyes-Diaz M., Ivanov A.G., Mora M.L., Alberdi M. 2010. *Manganese as essential and toxic element for plants: transport, accumulation and resistance mechanisms*. J Soil Sci Plant Nutrit, 10: 476-494. DOI: 10.4067/s0718-95162010000200008

Modrzewska B., Kosiorek M., Wyszkowski M. 2016. *Content of some nutrients in Scots pine, silver birch and Norway maple in an urbanized environment*. J Elem, 21: 149-157. DOI: 10.5601/ /jelem.2015.20.2.845

Możdżeń K., Wanic T., Rut G., Łaciak T., Rzepka A. 2017. *Toxic effects of high copper content on physiological processes in Pinus sylvestris* L. Photosynthetica, 55: 193-200. DOI: 10.1007/ /s11099-016-0229-3

Mukhopadhyay M.J., Sharma A. 1991. *Manganese in cell metabolism of higher-plants*. Bot Rev, 57: 117-149.

Nagajyoti P.C., Lee K.D., Sreekanth T.V.M. 2010. *Heavy metals, occurrence and toxicity for plants: a review*. Environ Chem Lett, 8: 199-216. DOI: 10.1007/s10311-010-0297-8

Noh N.J., Kim C., Bae S.W., Lee W.K., Yoon T.K., Muraoka H., Son Y. 2013. *Carbon and nitrogen dynamics in a Pinus densiflora forest with low and high stand densities*. J Plant Ecol, 6: 368-379. DOI: 10.1093/jpe/rtt007

Olsson B.A., Lundkvist H., Staaf H. 2000. *Nutrient status in needles of Norway spruce and Scots pine following harvesting of logging residues*. Plant Soil, 223: 161-173.

Palviainen M., Finér L. 2012. *Estimation of nutrient removals in stem-only and whole-tree harvesting of Scots pine, Norway spruce, and birch stands with generalized nutrient equations*. Europ J Forest Res, 131: 945-964.

Paré D., Thiffault E. 2016. *Nutrient budgets in forests under increased biomass harvesting scenarios*. Curr Forestry Reports, 2: 81-91. DOI: 10.1007/s40725-016-0030-3

Ranger J., Turpault M.P. 1999. *Input-output nutrient budgets as a diagnostic tool for sustainable forest management*. Forest Ecol Manage, 122: 139-154. DOI: 10.1016/s0378-1127(99)00038-9

Rautio P., Huttunen S., Lamppu J. 1998. *Element concentrations in Scots pine needles on radial transects across a subarctic area*. Water Air Soil Pollut, 102: 389-405. DOI: 10.1023/ /a:1004940627740

Roitto M., Rautio P., Julkunen-Tiitto R., Kukkola E., Huttunen S. 2005. *Changes in the concentrations of phenolics and photosynthates in Scots pine (Pinus sylvestris* L.*) seedlings exposed to nickel and copper*. Environ Pollut, 137: 603-609. DOI: 10.1016/j.envpol.2005.01.046

Saarela K.E., Harju L., Rajander J., Lill J.O., Heselius S.J., Lindroos A., Mattsson K. 2005. *Elemental analyses of pine bark and wood in an environmental study*. Sci Total Environ, 343: 231-241. DOI: 10.1016/j.scitotenv.2004.09.043

Saarsalmi A., Tamminen P., Kukkola M., Hautajärvi R. 2010. *Whole-tree harvesting at clear-felling: Impact on soil chemistry, needle nutrient concentrations and growth of Scots pine*. Scand. J Forest Res, 25: 148-156.

Saur E., Ranger J., Lemoine B., Gelpe J. 1992. *Micronutrient distribution in 16-year-old maritime pine*. Tree Physiol, 10: 307-316. DOI: 10.1093/treephys/10.3.307

Skonieczna J., Małek S., Polowy K., Węgiel A. 2014. *Element content of Scots pine (Pinus sylvestris L.) stands of different densities*. Drewno, 57: 77-87. DOI: 10.12841/wood.1644- -3985.S13.05

Tahvonen O., Pihlainen S., Niinimäki S. 2013. *On the economics of optimal timber production in boreal Scots pine stands*. Can J Forest Res, 43: 719-730. DOI: 10.1139/cjfr-2012-0494

Vangansbeke P., De Schrijver A., De Frenne P., Verstraeten A., Gorissen L., Verheyen K. 2015. *Strong negative impacts of whole tree harvesting in pine stands on poor, sandy soils: A long-term nutrient budget modelling approach*. Forest Ecol Manage, 356: 101-111. DOI: 10.1016/j. foreco.2015.07.028

Wall A. 2008. *Effect of removal of logging residue on nutrient leaching and nutrient pools in the soil after clearcutting in a Norway spruce stand*. Forest Ecol Manage, 256: 1372-1383.

Węgiel A., Bielinis E., Polowy K. 2018a. *Macronutrient stocks in Scots pine stands of different densities*. Forests, 9. DOI: 10.3390/f9100593

Węgiel A., Małek S., Bielinis E., Grebner D.L., Polowy K., Skonieczna J. 2018b. *Determination of elements removal in different harvesting scenarios of Scots pine (Pinus sylvestris L.) stands*. Scand J Forest Res, 33: 261-270. DOI: 10.1080/02827581.2017.1352019

WRB, 2015. *World Reference Base for Soil Resources 2014, update 2015. International soil classification system for naming soils and creating legends for soil maps*. World Soil Resources Reports No. 106. FAO, Rome.

Yan T., Zhu J.J., Yang K., Yu L.Z., Zhang J.X. 2017. *Nutrient removal under different harvesting scenarios for larch plantations in northeast China: Implications for nutrient conservation and management*. Forest Ecol Manage, 400: 150-158. DOI: 10.1016/j.foreco.2017.06.004

Yruela I. 2009. *Copper in plants: acquisition, transport and interactions*. Functional Plant Biol, 36: 409-430. DOI: 10.1071/fp08288

Zeide B. 2004. *Optimal stand density: A solution*. Can J Forest Res, 34: 846-854. DOI: 10.1139/ /x03-258