The effect of botanical composition of vegetation cover and peat-forming species on the concentration of indole-3-acetic acid and chemical compounds in peat

L.W. Szajdak, M. Szczepański, T. Meysner

Institute for Agricultural and Forest Environment, Polish Academy of Sciences, Poznań, Poland

SUMMARY

Indole-3-acetic acid (IAA) is one of the most important auxin/phytohormones for plant growth. The effect of peat botanical composition of various vegetation cover and peat-forming species at 13 sampling points located in fens, bogs and drained peatlands on the content of IAA, hot water extractable organic carbon (C_{HWE}), total organic carbon (TOC), total nitrogen (TN) and C/N quotient was assessed. The objective of this study was to analyse comparatively the quantities of IAA, TOC, C_{HWE}, TN and C/N in peats of varying genesis with respect to the peculiarities of their origin due to the botanical composition of vegetation cover and peat-forming species. A high content of IAA, C_{HWE} and TN was found in the top layers of the peatlands, indicating the formation of IAA mainly by the roots of peat-forming species and rhizosphere bacteria, because of the rich supplies of chemical and biochemical compounds exuded from the roots. Drainage of the peatlands did not have a significant effect on the amounts of IAA and TOC, but contributed to the release of large amounts of C_{HWE} (mainly representative of labile carbon). High TOC contents and C/N quotients in deeper layers of the peat deposits indicated a decline in the rate of soil organic matter (SOM) mineralisation and accumulation of the recalcitrant fraction. Varying C/N quotients of peat-forming species may reflect the initial botanical composition of the vegetation cover or peat-forming species, or differences in the degree of decomposition and/or TN content of the peats.

KEY WORDS: bog peat, hot water extractable organic carbon, IAA, total nitrogen, total organic carbon

INTRODUCTION

Peat is a raw material with a high level of biologically active organic substances which is used for soil improvement, landscape projects, organic fertiliser, and is a common component of the growing media used in the production of horticultural plants (Picken & Reinikainen 2009, Naumova *et al.* 2015). The importance of plant community composition as a factor controlling biogeochemical cycles in soils is widely recognised across a range of ecosystems and is often attributed to functional traits of the dominant plant species and groups present (Andriesse 1988, Ward *et al.* 2009). The composition of peat material is predominantly influenced by the parent vegetation, the degree of decomposition, and the original chemical and biochemical environment (e.g. underlying geology). Plants tend to release a wide spectrum of biologically active substances (Smith 1976). *Sphagnum* peat, rich in biologically active compounds, has been the most important growing medium constituent for many decades. It contains a complex variety of biologically active substances, which are available for cultivated plants. *Sphagnum* spp. does not contain 'true' lignin but rather a chemically different polymeric phenolic network and lipid surface coating (containing C_{14}-C_{26} hydroxy acids, C_{20}-C_{24} dicarboxylic acids, fatty alcohols and fatty acids) (van Breemen 1995). These phenolic polymers, tannins and waxes may also form complexes with cellulose or hemicellulose, making them less accessible for microbial enzymes and thus decreasing their decomposability. Moreover, fresh *Sphagnum* litter, which lacks lignin and is rich in easily degradable soluble carbohydrates, decomposes more slowly than lignin-rich vascular plants such as *Carex* spp. (Verhoeven & Toth 1995, Szumigalski & Bayley 1996, Inisheva & Dementieva 2000, Williams *et al.* 2000, Scheffer *et al.* 2001, Williams & Yavitt 2003). Also, the content of Klason lignin (fraction of lignin extracted from cell wall tissue by 72 % H_2SO_4) in *Sphagnum* moss ranges from 18 to 29 % (Ringqvist & Öborn 2002). Ringqvist & Öborn (2002) also showed the following elemental composition in *Sphagnum* species: Fe_{total} 31 mmol kg^{-1}, Ca 41 mmol kg^{-1}, Cu < 0.13 mmol kg^{-1}, Zn 0.09 mmol kg^{-1}, S (% of organic matter) 0.08, N (% of organic matter) 0.7, and P 25 mmol kg^{-1}. These substances are available for cultivated plants and affect seed germination and root growth. Currently, the use of other organic and mineral-organic materials is being forced ahead by research and development against a background of public preference for peat replacement, recycling and re-use of biodegradable waste. The spectrum of biologically active substances in peat is quite broad and heterogeneous, and depends on many interacting geobotanical, physicochemical and environmental factors: these include botanical composition of vegetation cover, peat-forming species, the thickness of the peat layer, and its degree of decomposition (Belkevich *et al.* 1989, Zaitseva 2008, Zaitseva *et al.* 2010, Stepchenko & Syedykh 2012). Due to these factors, biologically active organic components of low molecular weight (Indole-3-acetic acid (IAA), amino acids, phenolic compounds, derivatives of coumarin, flavonoids, alkaloids, glycosides, phytoalexins, purine and pyrimidine bases, fatty acids, antibiotics, waxes/bitumens, carbohydrates, sugars, vitamins, steroids, triterpenoids, β-sitosterol) and high molecular weight (humic and fulvic acids and their salts as well as cellulose, lignite, bitumens, peptides, enzymes and fats) now occurring in peats are predictors for those which may be released from peats in horticultural applications (Bambalov *et al.* 2000, Dundek *et al.* 2011, Szajdak *et al.* 2017). The application of chemical compounds that induce hormonal or hormonal-like effects has become important practice in agricultural production, particularly in horticulture, agriculture, fruit production and floriculture as well as for growing media (Kamnev *et al.* 2001, Halda-Alija 2003, Martinez-Morales *et al.* 2003). Auxins represent a wide group of such compounds. IAA affects plant development; especially cell elongation, apical dominance, root initiation, parthenocarpy, abscission callus formation and respiration (Gravel *et al.* 2007). IAA-like substances have been found in some species of green, brown and red algae, which are regarded as a less advanced group of organisms than higher plants (Mazur 1998). IAA, present at very low concentrations (10–100 ng g^{-1} fresh mass), is formed in soils from tryptophan by enzymatic conversion (Arshad & Frankenberger 1991, Sarwar *et al.* 1992, Wöhler 1997, Beyeler *et al.* 1999, Kamnev *et al.* 2001, Halda-Alija 2003, Neşe-Çokuğraş & Bodur 2003, Szajdak 2004, Szajdak & Maryganova 2007, Tsavkelova *et al.* 2007, Szajdak & Maryganova 2009, Lenin 2012). Higher amounts of IAA can be observed in rhizosphere environments than in non-rhizosphere ones. Thus, the most likely cause of auxin production in rhizosphere soil is the abundance of both microorganisms and organic compounds that are metabolically converted into IAA (Narayanaswami & Veerraju 1969, Rossi *et al.* 1984, Szajdak & Maryganova 2009, Ueda *et al.* 2016). Because plants take up auxin released into the rhizosphere soil from microorganisms, plant growth is positively modulated by IAA (Arshad & Frankenberger 1991, Ueda *et al.* 2016). Wöhler (1997) has also shown that tryptophan concentration, glucose, pH, temperature, redox potential, ionic strength, kind of soils and their properties stimulate the growth of microorganisms and can, therefore, be used as indicators for promoting the formation of auxins.

The objective of this study was to quantitatively compare IAA, TOC, C_{HWE}, TN and C/N quotient in peats collected from three drained and undrained peatlands of varying genesis in Russia and Poland, with regard to the peculiarities of their origins due to the botanical composition of vegetation cover and peat-forming species.

METHODS

Study area

For the purposes of the present study, 13 sampling points were chosen located on three different peatlands, each with varying peat types and botanical composition (Figure 1). Sampling points were recorded via GPS (TRIMBLE GeoExplorer 3 with accuracy 1–3 m).

Great Batorowskie Bog is located in the Stołowe Mountains National Park (6340 ha) in the Central Sudetes (southwest Poland). The mean annual air temperature (MAAT) is 4.8 °C, the warmest month is July (16.9 °C) and the coldest is January (-7.3 °C). Mean annual precipitation (MAP) increases with altitude from 750 to 920 mm and the wettest month is July (mean rainfall >1150 mm) (Gałka *et al.* 2014). The total area of organic soils in the National Park is about 100 ha, located at altitudes ranging from 500 to 900 m a.s.l. The development of organic soils has been largely influenced by various hydrological conditions on the top plateau, slopes, foothills and in the river valley (Bogacz & Glina 2015, Glina *et al.* 2019). At the turn of the 19th and 20th centuries, peatland ecosystems in the Stołowe Mountains were drained to obtain a new area for afforestation by spruce monoculture. Due to artificial drainage, a rapid drop of the water table has been observed relative to the pre-disturbance condition (Glina *et al.* 2017). The thickness of the peat deposit in drained and undrained parts of Great Batorowskie Bog is 1.2 m and 4.4 m, respectively.

Zieleniec Mire is located in the Kłodzka Valley (750–764 m a.s.l.), south of Duszniki Zdrój, in the watershed flattening of the Bystrzyckie Mountains, and ranks among the largest (about 160 ha) raised bogs of the Sudety Mountains. MAAT is 6.4 °C, the coldest month is January (-4.2 °C) and the warmest is July (15.0 °C). MAP is 665 mm. The growing season

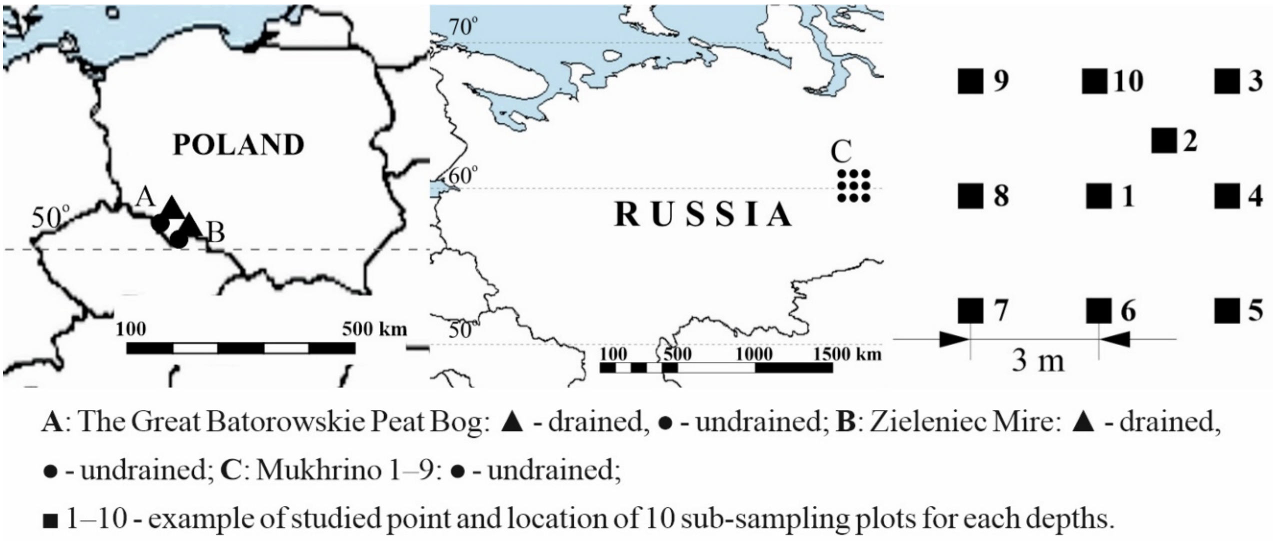

Figure 1. Locations of the 13 sampling points on three different peatlands in Poland and Russia.

is 210–215 days at lower altitudes and 170 days in areas above 900 m a.s.l. (Sobik & Miszuk 2005). Zieleniec Mire resembles the arctic tundra with small water bodies. The peatland includes a nature reserve (area 232 ha) with a raised bog, transitional bog and fens (Madeyska 2005, Bogacz & Glina 2015). The thickness of the peat deposits of drained and undrained parts of Zieleniec Mire is 6.0 m and 6.8 m, respectively.

Peat samples were also taken from the Mukhrino peatland located on the east bank of the Irtysh River near its confluence with the Ob River in the central taiga subzone of Western Siberia (Russia), 26 km west of the town of Khanty-Mansiysk. The environmental conditions of the Murkhrino mire are comparable with the sub-arctic zone of Northern Europe. MAP amounts to 530.6 mm and MAAT is -1.1 °C. This peatland is a representative large natural mire complex consisting of ombrotrophic raised bog, patterned bog with ridges and hollows, poor fen and shallow water tracks. So far, it has largely escaped human disturbance. Peat thickness varies between 2 m and 4.5 m. Water table depth is strongly correlated with rainfall, microtopography, temperature, hydraulic conductivity and subsurface flow; during summer, it can reach depths of 5–20 cm below the moss surface in poor fen and hollow habitats but up to 40–80 cm below the surface in *Sphagnum* hummocks (Bleuten & Filippov 2008, Lamentowicz *et al.* 2015, Blanchet *et al.* 2017).

Fieldwork and sub-sampling

Peat samples were collected in triplicate from the field using a 6 cm diameter Instorf peat auger, at different depths ranging from 0 to 100 cm, and divided up according to the visible stratigraphy in the profile of each peat deposit. Samples were transported to the laboratory at around 4 °C and stored at -20 °C (Horawski 1987). The samples were dried at 20 °C, homogenised in a grinder after removal of any visible live plant material, then passed through a 1 mm sieve to remove rock fragments and large organic debris. Botanical composition of peat was analysed by the microscopic method and subsequently classified according to the Polish standard PN-76/G-02501 1977. Degree of peat decomposition was estimated by von Post's method (von Post 1922). This method identifies ten classes of decomposition, with H1 being undecomposed peat and H10 completely decomposed peat.

Chemical analysis

IAA has been determined fluorometrically using a method developed by Szajdak & Maryganova (2009) and Szajdak (2016). The concentration of IAA was quantified at $\lambda_{excitation}$= 290 nm and $\lambda_{emission}$= 368 nm. The IAA amount was calculated from an analytical curve covering the range of IAA content 50–300 ng ml^{-1}, prepared similarly to the investigated soil samples. The pH was measured potentiometrically by adding peats to 1M KCl at a ratio of 1:2.5(v/v) (Sapek & Sapek 1997). C_{HWE} and TOC were measured by TOC 5050A, Shimadzu, Japan. For the investigation of C_{HWE}, soil samples were heated in deionised water at 100 °C for two hours under a reflux condenser. Extracts were separated using a medium porosity filter paper and analysed using a Shimadzu TOC 5050A (Smolander & Kitunen 2002). TN was evaluated by the Kjeldahl method on Vapodest 10, Gerhardt, Germany and the C/N quotients were calculated by measuring the carbon and nitrogen concentrations.

Satisfactory precisions, based on replicate analyses, were: 3.0 % for IAA, ± 0.01 for pH measurements, 3.4 % for C_{HWE}, 3.5 % for TOC and 4.3 % for TN.

Statistical analysis
All chemical and biochemical analyses were run in triplicate and the results were averaged. Confidence intervals for the mean were calculated using the following formula: $\bar{x} \pm t_{\alpha(n-1)}$ SE, where $\bar{x}$ is the mean, $t_{\alpha(n-1)}$ is the value of the Student test for $\alpha = 0.05$ and (n - 1) degrees of freedom, and SE is the standard error. Linear correlations between the values were calculated. Normal distribution of results and homogeneous variances were checked before statistical analysis.

RESULTS

Characteristics of peat deposits
Differences in peat-forming species down-core in the peat profiles can be found. The following nine peat types were determined amongst all of the sites: *Eriophoro-Sphagneti*, *Sphagno-Cariceti*, *Cariceti*, woody-sedge, wood-cottongrass, *Sphagnum*, sedge-*Sphagnum*, herbaceous (*Equisetum*), sedge-*Scheuchzeria* (Tables 1 and 2).

In Zieleniec Mire (drained and undrained), *Eriophoro-Sphagneti* was found through the peat profile with degree of decomposition H2 to H6 (weakly and moderately decomposed) (Table 1). In Great Batorowskie Bog the drained area consisted entirely of *Eriophoro-Sphagneti* (from 0 to 100 cm) and the undrained area had two assemblages down-core, one dominated by *Sphagno-Cariceti* (0–32 cm) and the second one by *Cariceti* (32–100 cm). The degree of decomposition of this peat ranged from H2 to H6 (Table 1). Decomposition was affected by drainage, which resulted in higher von Post decomposition values in drained than in undrained areas of Great Batorowskie Bog and Zieleniec Mire. Also, degree of decomposition increased with increasing depth in the profiles of undrained peat, and decreased with increasing depth in the profiles of drained peat (Table 1).

The Mukhrino peat samples were dominated by woody-sedge (Mukhrino 1; 0–50 cm and Mukhrino 6; 0–100 cm), wood-cottongrass (Mukhrino 1; 50–100 cm), *Sphagnum* (Mukhrino 2, Mukhrino 3, Mukhrino 4, Mukhrino 5, Mukhrino 9 and Mukhrino 8; 0–50 cm), sedge-*Sphagnum*, (Mukhrino 7; 0–50 cm), herbaceous (*Equisetum*) (Mukhrino 7; 50–100 cm) and sedge-*Scheuchzeria* (Mukhrino 8; 50–100 cm). The degree of decomposition ranged from H1 to H6 (Table 2).

IAA analysis
Statistically higher IAA contents were found in peat belonging to the classes *Sphagno-Cariceti* (sedge-*Sphagnum*) (337–356 µg kg^{-1}) and sedge-*Scheuchzeria* (325 µg kg^{-1}) than in *Sphagnum* (100–200 µg kg^{-1}), *Cariceti* (182–200 µg kg^{-1}), woody-sedge (146–222 µg kg^{-1}) and herbaceous (*Equisetum*) (162 µg kg^{-1}) peats (Tables 3 and 4).

There were no significant differences in IAA concentrations between drained and undrained Great Batorowskie Bog, nor between drained and undrained Zieleniec Mire (Table 3). Moreover, the contents of IAA decreased with increasing depth, except in Mukhrino 1 and Mukhrino 8 (Table 4). We suggest that, except in Mukhrino 1 and Mukhrino 8, the observed variations in IAA content with depth were caused by changes in the rhizosphere associated with botanical composition of the present vegetation. Endogenous IAA is found naturally in plants and can be produced by microorganisms, whereas exogenous IAA is associated with fungus obtained from the rhizosphere. Endogenous IAA is produced by plants in limited amounts and is not used directly by plants, whereas IAA obtained from fungus isolation can be applied for optimal results as an additive in biological fertilisers. Fungi that can produce auxin in different concentrations are *Aspergillus* spp., *Trichoderma* spp., *Penicillium* spp., *Rhizopus* and *Fusarium* spp. Moreover, the fact that IAA and C_{HWE} were observed to be directly proportional to one another also clearly suggests that both IAA and C_{HWE} decrease with increasing depth.

Chemical analysis
The peats showed acidic pH values, ranging from 2.40 to 4.43 (Tables 3 and 4). The pH values were lower in *Eriophoro-Sphagneti* (2.60–2.88), wood-cottongrass (2.75), *Sphagnum* (2.40–3.28), and *Sphagno-Cariceti* (sedge-*Sphagnum*) (from 3.21 to 3.43) than in woody-sedge (2.75–4.43) and herbaceous (*Equisetum*) (4.33) peats (Tables 3 and 4). Soil acidification is a consequence of organic matter development and is strongly dependent on the N, S, and P cycles and the conversion of organic and mineral anions in the soil. Acidity in peatlands is a by-product of microbial degradation processes, cation exchange and input of acids from the atmosphere. In the first case, bacteria and fungi break down dead plant and animal material, and the humic acids resulting from the decay process are released into the surrounding environment.

Table 1. Sampling locations for Great Batorowskie Bog and Zieleniec Mire (Poland), including botanical composition of vegetation cover and peat stratigraphy.

Place of sampling	Coordinates WSG 84 (N/E)	Botanical species present at sampling point	Depth (cm)	Peat types based on macrofossil analysis	Degree of decomposition (von Post)
Great Batorowskie Bog drained	50° 27' 28.56'' N 16° 23' 14.07'' E	*Pinus sylvestris*, *Picea abies*, *Betula pubescens*, *Vaccinium myrtillus*, *Calamagrostis villosa*, *Deschampsia flexuosa*, *Polytrichum commune*, *P. formosum*, *Sphagnum girgensohnii*, *S. magellanicum*, *S. palustre* (Potocka 1999).	0–8	*Eriophoro-Sphagneti*	-
			8–18	*Eriophoro-Sphagneti*	H6
			18–35	*Eriophoro-Sphagneti*	H5
			35–43	*Eriophoro-Sphagneti*	H5
			43–50	*Eriophoro-Sphagneti*	H5
			50–68	*Eriophoro-Sphagneti*	H5
			68–82	*Eriophoro-Sphagneti*	H4
			82–100	*Eriophoro-Sphagneti*	H5
Great Batorowskie Bog undrained	50° 27' 31.47'' N 16° 22' 50.62'' E	*Picea abies*, *Betula pubescens*, *Pinus × rhaetica*, *Eriophorum vaginatum*, *Vaccinium myrtillus*, *Oxycoccus palustris* (Potocka 1999).	0–13	*Sphagno-Cariceti*	H2
			13–32	*Sphagno-Cariceti*	H4
			32–56	*Cariceti*	H5
			56–75	*Cariceti*	H3
			75–100	*Cariceti*	H5
Zieleniec Mire drained	50° 20' 48.64'' N 16° 24' 41.92'' E	*Pinus sylvestris*, *Betula pubescens*, *Vaccinium myrtillus*, *V. uliginosum*, *Calluna* spp., *Sphagnum palustre* (Smoczyk 2011).	0–7	*Eriophoro-Sphagneti*	-
			7–15	*Eriophoro-Sphagneti*	H6
			15–30	*Eriophoro-Sphagneti*	H4
			30–42	*Eriophoro-Sphagneti*	H4
			42–52	*Eriophoro-Sphagneti*	H4
			52–72	*Eriophoro-Sphagneti*	H3
			72–88	*Eriophoro-Sphagneti*	H4
			88–100	*Eriophoro-Sphagneti*	H3
Zieleniec Mire undrained	50° 20' 53.47'' N 16° 24' 37.71'' E	*Pinus × rhaetica (Pinus sylvestris × P. mugo)*, *Betula pubescens*, *Pinus mugo*, *Betula nana*, *Carex limosa*, *C. nigra*, *Drosera rotundifolia*, *Sphagnum magellanicum*, *Eriophorum vaginatum*, *Andromeda polifolia*, *Oxycoccus palustris* (Smoczyk 2011).	0–26	*Eriophoro-Sphagneti*	H2
			26–37	*Eriophoro-Sphagneti*	H3
			37–50	*Eriophoro-Sphagneti*	H5
			50–65	*Eriophoro-Sphagneti*	H3
			65–83	*Eriophoro-Sphagneti*	H4
			83–100	*Eriophoro-Sphagneti*	H3

Table 2. Sampling locations for Mukhrino peatland (Russia), including botanical composition of vegetation cover and peat stratigraphy.

Place of sampling	Coordinates WSG 84 (N/E)	Botanical species present at sampling point	Depth (cm)	Peat types based on macrofossil analysis	Degree of decomposition (von Post)
Mukhrino 1	60° 53' 41.6" N 68° 41' 51.9" E	*Sphagnum fuscum, S. fallax, S. magellanicum, S. angustifolium, Ledum palustre, Rubus chamaemorus, Carex globularis, Chamaedaphne calyculata, Vaccinium vitis-idaea, V. myrtillus, Oxycoccus microcarpus, Pleurozium schreberi, Polytrichum strictum, Dicranum polysetum, Aulacomnium palustre, Pinus sylvestris, P. sibirica, Betula pendula.*	0–50	woody-sedge	H2
			50–100	wood-cottongrass	H3/H4
Mukhrino 2	60° 89' 50.5" N 68° 69' 20.9" E	*Sphagnum angustifolium, S. fuscum, S. magellanicum, Ledum palustre, Rubus chamaemorus, Chamaedaphne calyculata, Betula nana, Pinus sylvestris, P. sibirica.*	0–50	*Sphagnum*	H1
			50–100	*Sphagnum*	H2
Mukhrino 3	60° 53' 43.9" N 68° 40' 46.8" E	*Sphagnum fuscum, Ledum palustre, Chamaedaphne calyculata, Cladonia* spp.*, Rubus chamaemorus, Pinus sylvestris, Betula nana.*	0–50	*Sphagnum*	H1
			50–100	*Sphagnum*	H2
Mukhrino 4	60° 53' 44.2" N 68° 40' 12.5" E	*Sphagnum fuscum, Ledum palustre, Chamaedaphne calyculata, Rubus chamaemorus, Oxycoccus palustris, Pinus sylvestris.*	0–50	*Sphagnum*	H1
			50–100	*Sphagnum*	H1
Mukhrino 5	60° 53' 29.1" N 68° 41' 33.5" E	*Sphagnum capillifolium, S. fallax, S. fuscum, Ledum palustre, Chamaedaphne calyculata, Oxycoccus microcarpus, Vaccinium uliginosum, V. vitis-idaea, Rubus chamaemorus, Pinus sylvestris, P. sibirica, Betula nana.*	0–50	*Sphagnum*	H1
			50–100	*Sphagnum*	H2
Mukhrino 6	60° 53' 55.2" N 68° 44' 59.9" E	*Carex juncea, Comarum palustre, Phalaris arundinacea, Lactuca sibirica, Calamagrostis stricta* (*C. neglecta*)*, C. phragmitoides, Lythrum salicaria, Lysimachia thyrsiflora, L. vulgaris, Rumex aquatilis, Galium ruprechtii, Lathyrus palustris, Anemone dichotoma, Betula pubescens, Salix pentandra, S. cinerea.*	0–50	woody-sedge	H5
			50–100	woody - sedge	H6
Mukhrino 7	60° 52' 35.9" N 68° 36' 46.7" E	*Carex rostrata, C. lasiocarpa, C. limosa, Sphagnum riparium, Menyanthes trifoliata, Lysimachia thyrsiflora, Eriophorum vaginatum, Betula pendula, B. pubescens.*	0–50	sedge-*Sphagnum*	H2
			50–100	herbaceous (*Equisetum*)	H2
Mukhrino 8	60° 52' 33.1" N 68° 36' 55.3" E	*Sphagnum magellanicum, S. fallax, Chamaedaphne calyculata, Oxycoccus palustris, Andromeda polifolia, Eriophorum vaginatum, Betula pendula.*	0–50	*Sphagnum*	H1
			50–100	sedge-*Scheuchzeria*	H1
Mukhrino 9	60° 53' 43.5" N 68° 38' 20.4" E	*Sphagnum papillosum, Carex pauciflora, Rhynchospora alba, Drosera anglica, Scheuchzeria palustre, Menyanthes trifoliata, Oxycoccus microcarpus, Eriophorum gracile, Andromeda polifolia.*	0–50	*Sphagnum*	H1
			50–100	*Sphagnum*	H1

Table 3. Mean contents of chemical compounds and physical factors in the investigated soils (Polish site). IAA = indole-3-acetic acid, C_{HWE} = hot water extractable organic carbon, TOC = total organic carbon, TN = total nitrogen, C/N = C/N quotient, $x \pm \Delta x$ = confidence interval of average at confidence level $\alpha = 0.05$ for (n - 1) degrees of freedom.

Place of sampling	Depth (cm)	pH	IAA (µg kg^{-1})	C_{HWE} (g kg^{-1})	TOC (g kg^{-1})	TN (g kg^{-1})	C/N
Great Batorowskie Bog drained	0–8	2.61	333±*14*	25.2±*2.5*	452±*22*	16.0±*1.3*	28.3±*2.6*
	8–18	2.60	325±*13*	23.2±*2.2*	475±*27*	15.0±*0.9*	31.8±*3.0*
	18–35	2.60	309±*12*	18.8±*1.9*	488±*23*	12.6±*1.3*	38.8±*3.8*
	35–43	2.56	293±*11*	16.8±*1.7*	490±*23*	10.2±*1.1*	47.8±*4.7*
	43–50	2.62	294±*12*	17.0±*1.4*	491±*24*	9.4±*0.9*	52.4±*5.1*
	50–68	2.64	238±*10*	16.6±*1.7*	496±*24*	9.3±*0.7*	53.1±*5.3*
	68–82	2.69	236±*9*	16.2±*1.5*	500±*24*	8.8±*0.5*	56.7±*5.6*
	82–100	2.70	218±*7*	16.0±*1.6*	511±*22*	9.2±*0.4*	55.6±*5.5*
Great Batorowskie Bog undrained	0–13	3.21	356±*15*	13.3±*1.3*	452±*23*	18.0±*1.7*	25.2±*2.4*
	13–32	3.26	337±*14*	12.2±*1.2*	468±*29*	17.5±*1.2*	26.8±*2.6*
	32–56	3.22	200±*10*	9.8±*1.0*	493±*23*	16.6±*1.0*	29.7±*2.9*
	56–75	3.21	198±*8*	9.0±*0.9*	500±*23*	15.4±*1.3*	32.5±*3.2*
	75–100	3.28	182±*8*	8.7±*0.8*	514±*27*	12.5± *0.9*	41.0±*4.0*
Zieleniec Mire drained	0–7	2.66	245±*10*	20.5±*2.0*	457±*22*	16.5±*1.0*	27.7±*2.7*
	7–15	2.71	236±*10*	17.6±*1.4*	464±*20*	14.8±*1.4*	31.5±*3.0*
	15–30	2.63	214±*9*	13.6±*1.2*	475±*23*	11.7±*0.9*	40.6±*4.1*
	30–42	2.70	209±*8*	11.9±*1.1*	483±*24*	10.7±*1.1*	45.1±*4.5*
	42–52	2.74	203±*8*	11.4±*0.9*	484±*24*	10.7±*1.1*	45.1±*4.6*
	52–72	2.81	206±*8*	11.4±*1.2*	489±*29*	10.3±*1.0*	47.7±*4.7*
	72–88	2.85	182±*7*	11.3±*1.0*	497±*29*	9.9±*1.0*	50.2±*5.0*
	88–100	2.84	176±*7*	10.9±*1.2*	503±*29*	9.4±*0.8*	53.4±*5.3*
Zieleniec Mire undrained	0–26	2.88	230±*9*	13.8±*1.4*	463±*21*	15.0±*1.4*	30.8±*3.1*
	26–37	2.86	216±*8*	12.4±*1.2*	491±*28*	14.7±*1.4*	33.5±*3.3*
	37–50	2.76	213±*7*	10.8±*1.0*	491±*28*	12.6±*1.1*	38.9±*3.8*
	50–65	2.82	215±*8*	10.4±*1.0*	497±*22*	11.7±*1.0*	42.3±*4.2*
	65–83	2.83	198±*7*	10.1±*1.0*	503±*20*	11.2±*1.0*	45.0±*4.5*
	83–100	2.86	190±*7*	10.0±*0.9*	502±*29*	11.3±*1.1*	44.2±*4.4*

The amounts of C_{HWE} were significantly higher in the *Eriophoro-Sphagneti* (10.0–25.2 g kg^{-1}), *Sphagnum* (10.7–18.1 g kg^{-1}) and *Sphagno-Cariceti* (sedge-*Sphagnum*) (12.2–14.7 g kg^{-1}) peats than in the herbaceous peat types *Equisetum* (7.3 g kg^{-1}), wood-cottongrass (7.7 g kg^{-1}) and woody-sedge (5.6–9.6 g kg^{-1}) (Tables 3 and 4).

C_{HWE} concentrations varied significantly with the depth change between drained and undrained parts of Great Batorowskie Bog and Zieleniec Mire (Table 3), and decreased with increasing depth in the peat profile (Tables 3 and 4). A greater decrease in C_{HWE} content with depth was observed in Great Batorowskie Bog (25.2–8.7 g kg^{-1}) than in Zieleniec Mire (20.5–10.0 g kg^{-1}) and the Mukhrino peatland (18.0–5.6 g kg^{-1}), although the distribution of IAA down the peat profile was similar and there was a significant correlation between IAA content and C_{HWE} ($r = 0.315$, $P < 0.05$) (Table 5).

TOC content differed significantly between vegetation types and sampling depths. The TOC concentration was much lower in the herbaceous (*Equisetum*; 378 g kg^{-1}), *Sphagnum* (408–451 g kg^{-1}) and *Sphagno-Cariceti* (sedge-*Sphagnum*) (353–468 g kg^{-1}) peats than in the *Cariceti* (493–514 g kg^{-1}), *Eriophoro-Sphagneti* (452–511 g kg^{1}) and wood-

Table 4. Mean contents of chemical compounds and physical factors in the investigated soils (Russian site). Explanation of column headings as for Table 3.

Place of sampling	Depth (cm)	pH	IAA (μg kg^{-1})	C_{HWE} (g kg^{-1})	TOC (g kg^{-1})	TN (g kg^{-1})	C/N
Mukhrino 1	0–50	2.72	222±*8*	9.6±*1.0*	461±*45*	15.0±*1.5*	30.7±*3.00*
	50–100	2.75	265±*11*	7.7±*0.7*	499±*48*	19.7±*1.9*	25.4±*2.6*
Mukhrino 2	0–50	2.40	146±*6*	17.6±*1.6*	408±*39*	11.7±*1.1*	35.0±*3.4*
	50–100	2.67	105±*4*	13.4±*1.4*	437±*43*	4.7±*0.5*	92.9±*9.2*
Mukhrino 3	0–50	2.42	190±*8*	18.1±*1.8*	410±*40*	9.9±*1.0*	41.6±*4.0*
	50–100	2.63	166±*7*	13.4±*1.3*	437±*42*	5.4±*0.5*	81.4±*8.2*
Mukhrino 4	0–50	2.40	111±*4*	18.0±*1.8*	421±*38*	6.7±*0.7*	62.7±*6.3*
	50–100	2.41	100±*4*	13.7±*1.3*	438±*42*	6.1±*0.6*	72.4±*7.5*
Mukhrino 5	0–50	2.46	170±*7*	17.9±*1.7*	427±*42*	10.8±*1.0*	39.7±*3.9*
	50–100	2.65	127±5	17.5±1.8	451±*43*	6.5±0.5	69.4±*7.0*
Mukhrino 6	0–50	4.43	158±*6*	7.5±*0.7*	442±*46*	15.5±*1.5*	28.6±*2.9*
	50–100	4.30	146±*6*	5.6±*0.5*	477±*49*	15.0±*1.4*	31.9±*3.1*
Mukhrino 7	0–50	3.43	356±*14*	14.7±*1.3*	353±*35*	17.1±*1.7*	20.7±*2.2*
	50–100	4.33	162±*6*	7.3±*0.8*	378±*37*	17.0±*1.7*	22.2±*2.2*
Mukhrino 8	0–50	2.77	150±*6*	12.3±*1.2*	420±*40*	8.7±*0.9*	48.0±*4.9*
	50–100	3.17	325±*13*	10.9±*1.0*	470±*48*	20.4±*2.0*	23.1±*2.3*
Mukhrino 9	0–50	3.28	200±*8*	12.6±*1.3*	412±*40*	11.8±*1.1*	34.9±*3.4*
	50–100	2.77	173±*7*	10.7±*1.1*	442±*42*	4.5±*0.4*	98.6±*9.8*

Table 5. Correlation coefficients of the relationships between IAA content and other investigated factors in different peat-forming species (*significance level $p < 0.05$). IAA = indole-3-acetic acid, C_{HWE} = hot water extractable organic carbon, TOC = total organic carbon, TN = total nitrogen, C/N = C/N quotient.

Relationship	Correlation coefficients (r)
IAA = f(C_{HWE})	0.315*
IAA = f(TOC)	0.138
IAA = f(TN)	0.609*
IAA = f(C/N)	-0.538*

cottongrass (499 g kg^{-1}) peats. The concentration of TOC in samples from drained and undrained sites was found to be similar, and TOC increased with depth down-core in all cases (Tables 3 and 4).

The TN content was significantly higher in sedge-*Scheuchzeria* (20.4 g kg^{-1}), wood-cottongrass (19.7 g kg^{-1}), *Sphagno-Cariceti* (sedge-*Sphagnum*) (17.1–18.0 g kg^{-1}) and *Caricetii* (12.5–16.6 g kg^{-1}) than in *Sphagnum* community (4.5–11.8 g kg^{-1}) (Tables 3 and 4). No differences in TN concentration were observed between the drained soils of Great Batorowskie Bog and undrained and drained soils of Zieleniec Mire, but a larger amount of TN was observed in the undrained core from Great Batorowskie Bog. TN decreased with increasing depth; except at Mukhrino 1 and Mukhrino 8, where the TN and IAA contents decreased in parallel and significant correlation coefficients between them were calculated ($r = 0.61$, $P < 0.05$) (Table 5).

A higher C/N quotient was calculated in *Sphagnum* community peat (34.9–98.6) than in herbaceous (*Equisetum*) (22.2), sedge-*Scheuchzeria* (23.1), wood-cottongrass (25.4) and *Sphagno-Cariceti* peat (sedge-*Sphagnum*) (20.7–26.8) (Tables 3 and 4). C/N quotient did not differ significantly between drained and undrained peatland. The decline of C/N quotient in the upper layers of most of the peat profiles is equivalent to a loss of TOC content. Contrary results were obtained for Mukhrino 1 and Mukhrino 8, where there was a significant negative correlation ($r = -0.54$, $P < 0.05$) between C/N quotient and IAA across the vegetation types (Table 5).

DISCUSSION

A large number of plant species occurring in mires including sedges, grasses, *Sphagnum*, *Carex* and woody plants contribute to peat formation. The botanical composition of the main plant species or species groups strongly influences the nature and the biochemical (activity of enzymes), chemical, physical (class of fibre content, degree of decomposition, acidity, ash content, bulk density, porosity, moisture, hydraulic conductivity, shrinkage) and biological properties of the peats in this area, and the species composition is in turn the result of the oligotrophic conditions. We found in peats contrasting amounts of IAA, C_{HWE}, TOC, TN and value of C/N quotient, which were associated with different peat-forming species (Tables 1–4).

The IAA represents free amino acid in the soil participating in biochemical conversions and is responsible for physiological and biological effects (Szajdak & Maryganova 2007). Therefore we used IAA as an important proxy for determining the productivity and biological activity of peats (Narayanaswami & Veerraju 1969, Rossi *et al*. 1984, Szajdak & Maryganova 2009, Szajdak *et al*. 2016, Ueda *et al*. 2016). In particular, the highest content of IAA in *Sphagno-Cariceti* (sedge-*Sphagnum*) and sedge-*Scheuchzeria* peats with degree of decomposition from H1 to H4 corresponded to higher amounts of TN and C_{HWE} (Tables 1–4).

Based on the quantity of IAA, the investigated peats can be divided into two groups:

- high concentrations of IAA (> 200 µg kg^{-1}) determined in: *Eriophoro-Sphagneti*, *Sphagno-Cariceti*, *Cariceti*, woody-sedge, wood-cottongrass, sedge-*Sphagnum*, *Sphagnum*; and
- low amounts of IAA (< 200 µg kg^{-1}) measured in: *Sphagnum*, wood-sedge, sedge-*Schauchzeria*, herbaceous (*Equisetum*).

In addition, significant differences in the quantity of IAA were observed for *Sphagnum* in Mukhrino 2, 3, 4, 5, 9 (Tables 2 and 4). In these sampling locations different botanical composition of vegetation cover was detected, probably arising from the same cause as the differences in IAA content in peats.

Parallel high content of IAA with TOC, C_{HWE}, TN and value of C/N quotient in peats of sedge-*Sphagnum*, *Eriophoro-Sphagneti* and *Sphagno-Cariceti*, and sedge-*Scheuchzeria* with degree of decomposition from H2 to H6, might be caused by changes in the composition of peat-forming species and degree of decomposition affecting IAA production and changing the contents of C_{HWE}, TOC, TN and C/N quotient. These findings suggest that the chemical composition of peat-forming species and the factors controlling biogeochemical cycles may influence IAA synthesis in the peat deposit. Our findings are in line with other chemistry and biochemistry studies in peat-forming species such as *Sphagnum* and *Carex* (Nichols-Orians 1991, Painter 1991, Williams *et al*. 2000, Bragazza & Freeman 2007). The amounts of IAA were positively correlated to the contents of C_{HWE} and TN in peats ($r = 0.315$ and $r = 0.609$, respectively). IAA formation tended to increase with increasing concentrations of these compounds in peats. These findings indicate some importance of available amounts of C_{HWE} and TN for IAA synthesis in various peat-forming species and in the deeper layers of peat deposits.

Besides the chemistry and biochemistry data for peat-forming species, many reports show a relationship between IAA production and the contents of chemical compounds in soils (Narayanaswami & Veerraju 1969, Rossi *et al*. 1984, Szajdak & Maryganova 2009, Szajdak *et al*. 2016, Ueda *et al*. 2016). Szajdak & Maryganova (2009) and Szajdak *et al*. (2016) showed beneficial effects of C_{HWE} and TN on IAA content, estimating a significant relationship between IAA, C_{HWE}, TOC and TN in soils of adjoining cultivated fields and old shelterbelts, suggesting that very high IAA content in the peat types may be due to high concentrations of SOM and dissolved organic matter (DOM), large amounts of TN and its inorganic forms as well as high microbial activity.

In addition, our data showed the same overall pattern for the contents of IAA and C_{HWE} in the top layers of peat deposits. This may indicate that the IAA is produced mainly by the roots of peatland plants, as well as by the bacteria inhabiting the rhizosphere in the presence of organic matter. Our suggestions are in accord with Arshad & Frankenberger (1991), Shahab *et al*. (2009) and Lenin & Jayanthi (2012), who postulated that microorganisms inhabiting the rhizosphere of various plants are likely to synthesise and release auxins as secondary metabolites because of the rich supplies of substrates exuded from the roots compared with non-rhizospheric soils. In addition, Shahab *et al*. (2009) and Lenin & Jayanthi (2012) suggested that plant morphogenic effects may also be a result of different ratios of plant hormones produced by roots as well as by the rhizosphere. The quantitative and qualitative composition of root exudates varies depending on plant species, type of soil and the physical properties of the environment such as land use, the degree of decomposition, pH, ionic strength, humidity, and temperature (Arshad & Frankenberger 1991, Szajdak & Maryganova 2007, Shahab *et al*. 2009, Szajdak 2016).

Drainage of peatland did not significantly affect IAA and TOC amounts but significantly contributed to the release of a large amount of labile C (carbon) from drained peats. Investigated C_{HWE} represents a labile form of C and the assimilative component of the total organic matter (OM) that could contain readily available nutrients for plant growth. The obtained fraction of organic carbon makes up only a small percentage of the soil OM and directly reflects the changes in the rhizosphere. The C_{HWE} is a component of the labile SOM and, also being closely related to soil microbial biomass and micro aggregation, could be used as one of the soil quality indicators in soil-plant ecosystems. The present study found that changes in the degree of decomposition caused by previous long-term historical exposure to drainage for afforestation has effected a greater release of labile C in the mires of the Sudety Mountains. Our observations are likely to be due to changes in the water table, and in microbial activity during drainage. Our finding for C_{HWE} amounts within the peat profile is in agreement with other authors (Kalbitz *et al.* 2003, Fröberg *et al.* 2007). They reported that root-derived C represents an alternative source of labile C in the peat soil deposit and explained that this form of carbon decreases with depth due to retention by soil surfaces and is considered to be mostly derived from old organic matter with a slow incorporation rate from recently-deposited sources.

In contrast to C_{HWE} amounts, higher TOC contents and C/N quotients was measured in the bottom than in the top layers of the peat deposits (Tables 3 and 4). These results are probably explained by resistant and mature SOM fractions accumulated deeper in the soil profile, whereas the majority of the labile compounds in the soil surface decomposed within several months (Fenner *et al*. 2004, Bonnett *et al.* 2006, Fenner *et al.* 2007, Bernal & Mitsch 2008, Clark *et al.* 2008). The investigations of Szajdak & Styła (2011) and Szajdak *et al.* (2015, 2016) showed higher enzyme activity in surface peat layers relative to deeper ones. This activity is indicative of higher biological activity closer to the surface and higher rate of organic matter decomposition resulting in an increased labile SOM fraction. Our observations might reflect a lack of decomposition of organic matter related to TOC accumulation in deeper layers and the reduction of TN.

Peatlands are a major source of C for aquatic ecosystems. Naturally, increased labile C in peatlands may be the result of drainage (Frank *et al.* 2017). Great Batorowskie Bog and Zieleniec Mire share similar climatic conditions and peat species, but the release of labile C differs due to their contrasting degree of decomposition. In addition, the results reported a significant release of large amounts of C from drained areas of peatlands, particularly in Great Batorowskie Bog compared to Zieleniec Mire. These bogs were characterised by a higher degree of decomposition, especially in the upper layers. This suggests a destabilisation of the peat bog structure and functioning due to previous long-term historical exposure to drainage for afforestation. Müller *et al.* (1997) reported an increase of labile C release from drained peatlands, postulating that rising DOM could be due to microbial or root necromass, and also result from uncommonly dry conditions in the acrotelm. These elevated C concentrations showed DOM release due to an ‘ecosystem disturbance’ and indicated continued decomposition and labile C release (Müller *et al.* 1997, Glatzel *et al.* 2006, Frank *et al.* 2014). Thus, drying accelerates the rate of organic matter decomposition, thereby releasing previously locked-up C and turning peatlands from C sinks into C sources (Davidson & Janssens 2006, Fenner & Freeman 2011).

By contrast, a negative relationship between IAA and C/N quotient ($r = -0.538$) confirmed the greatest concentrations of IAA in peat-forming species characterised by a lower C/N quotient with degree of decomposition H1–H4. The observations could have resulted from differences in botanical composition and degree of decomposition of the peats. The peat-forming species in the peat profile are related to the C/N quotient (Tables 3 and 4). A higher C/N quotient in the *Sphagnum* derived peat compared to the herbaceous (*Equisetum*), sedge-*Scheuchzeria*, wood-cottongrass and *Sphagno-Cariceti* (sedge-*Sphagnum*) derived peats indicates a lower availability of carbon in organic compounds to the microorganisms. These results are in line with the observations of Scheffer *et al.* (2001), who found slower degradation of litter in *Sphagnum* than in *Carex* caused by intrinsic differences in litter quality, not simply environmental conditions. A high soil C/N quotient can slow down the decomposition rate of organic matter and organic nitrogen compounds by limiting soil microbial activity, whereas a low soil C/N quotient could accelerate the process of microbial decomposition of organic matter and organic nitrogen compounds, which is not conducive for carbon sequestration (Lucas 1982, Wu 2001).

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AUTHOR CONTRIBUTIONS

LWS, MS and TM performed the field measurements and laboratory analysis. MS and TM conducted the statistical data calculations. LWS, MS and TM drafted the manuscript and designed the Tables. LWS wrote the manuscript with input from all authors. All authors discussed the results and commented on the manuscript.

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Author for correspondence:
Professor Lech Wojciech Szajdak, Institute for Agricultural and Forest Environment, Polish Academy of Sciences, Bukowska 19, 60-809 Poznań, Poland. Tel: +48618475601; E-mail: lech.szajdak@isrl.poznan.pl