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SOIL OXYGEN CONDITIONS IN PALUDIFYING BOREAL FOREST SITES

Maan happiolot soistuvissa havumetsissä

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Soil oxygen conditions were characterized with the help of polycarbonate tubes, which were filled with water and inserted into the soil. The oxygen content of the water inside the tube was measured and compared with that in conditions of full aeration. Five forest sites were studied. Three of them form a moisture gradient — mesophyte spruce forest (MSF), paludifying spruce forest (PSF) and paludified pine forest (PPF). For comparison, three other sites were included: a dry pine forest (DPF), an alder carr mire (ACR) and an ombrotrophic bog. Soil aeration conditions were the most unfavourable at the PSF site at the beginning of June; the lowest values being recorded in depressions with *Sphagnum girgensohnii.* Considering the whole vegetation period, the bog site demonstrated the lowest soil aeration level. At the alder carr site, soil aeration conditions were dependent on precipitation. In forest sites the lowest aeration level was observed at the beginning of June, but in the ACR and bog sites, another minimum occurred in September after heavy rains.

Keywords: Coniferous forest, oxygen conditions, paludification, succession

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INTRODUCTION

Mire formation by the waterlogging of supra-aquatic terrestrial soils (paludification, Versumpfung) represents a transition between two principally different types of ecosystem — from a non-accumulative to a peat-accumulative one. The crucial mechanism of paludification is the slowdown of decomposition. In mire formation the appearance of *Sphagna* is clearly of critical significance, and the further, rapid development towards an ombrogenous bog is irrevocally determined (Gorham 1967, Walker 1970, Barry & Synnott 1984). The appearance of *Sphagna* is associated with an increase in moisture conditions. Once established, *Sphagna* themselves make the local environment more acidic through the release of hydrogen ions and more oligotrophic as microbial decomposition is suppressed in the acidic environment.

The initial establishment of *Sphagna* in paludifying forest takes place preferentially in the wetter environment of depressions (Noble et al. 1984). Wet soil, where the soil pores are filled with water, contains less oxygen. Soil oxygen conditions are better known on paddy soils (cf. Shu-Zheng 1985). There is much less information on the role of the soil aeration regime in determining the processes of forest paludification and mire formation (cf. Sikora & Keeney 1983 for a review). Some authors (Hesselman 1910, Tamm 1950, Pyavchenko 1985) have referred to the lack of oxygen in the soil environment as a crucial factor in mire development.

There is also documented evidence concerning the deterioration of soil aeration conditions with increasing moisture in coniferous forest sites (e.g. Pyatt & Smith 1983). On the other hand, some authors report that the oxygen content of soil water is higher in oligotrophic raised bogs, which represent final stages of mire succession (Yurkevich et al. 1966, Orlov 1958, 1968, Vompersky 1968, Zobel 1987). The content of free oxygen in soil water, however, can not indicate the soil oxygen input but rather the intensity of its consumption. Yet in oligotrophic mires a certain amount of free oxygen remains unused by plant roots and soil organisms.

Here an attempt will be made to describe soil oxygen conditions in the ecotone between boreal forest and mire.

STUDY SITE

The investigation was carried out near Tipu, south-western Estonia, during May–September 1986. Climatically, the Tipu district belongs to the southern boreal zone with an annual mean temperature of +3.1°C, an annual accumulated temperature (≥ 10°C) of 1850 dd and an annual mean precipitation of 650 mm. Ecotone conditions were represented by three forest stands from oligo-mosotrophic site types (types are described by Lõhmus 1984a): spruce forest with mesophyte vegetation (*Oxalis* site type) on a gleic podzol (MSF); spruce forest with pines and some patches of *Sphagna* in depressions (*Myrtillus* site type) on a gleic podzol with a weakly developed peaty layer (paludifying spruce forest — PSF); pine forest with spruce, dwarf shrubs and *Sphagna* (*Vaccinium uliginosum–Myrtillus* site type) on a peaty gleic podzol (paludificated pine forest — PPF). The stands are located within a distance of 100 m, where the parent material (noncalcareous loamy sand) does not change considerably (cf. Fig. 1). Other types of ecosystem were also studied for comparison: alder carr (ACR) on thin alluvial deposits, dry pine forest (*Vaccinium vitis-idaea* site type, DPF) on non-calcareous sand. Hummock (BH) and depression (BD) sites at the adjacent Kikepera bog, where the mean depth of peat deposit is 3 m, were also studied — these data have been published earlier (Zobel 1986).

MATERIAL AND METHODS

Soil oxygen conditions were characterized by the original method of Rogers and King (1972), with which the oxygen content is not determined directly from soil water but from polycarbonate centrifuge tubes filled with water. Molecular oxygen in soil environment is able to diffuse through the membrane in both directions, an equilibrium being attained when the partial pressure within the tube is equal to that on the outside of the membrane, both in the gaseous and solution phase (for more details of the method see Zobel 1986). According to Lõhmus (1984b) the water oxygen content in polycarbonate tubes is an inert parameter when compared to redox potential. Together with the oxygen content, the temperature of the water in polycarbonate tubes was also measured.

The soil profile was described in the three forest stands; in the alder carr site only the upper organic layer was studied.

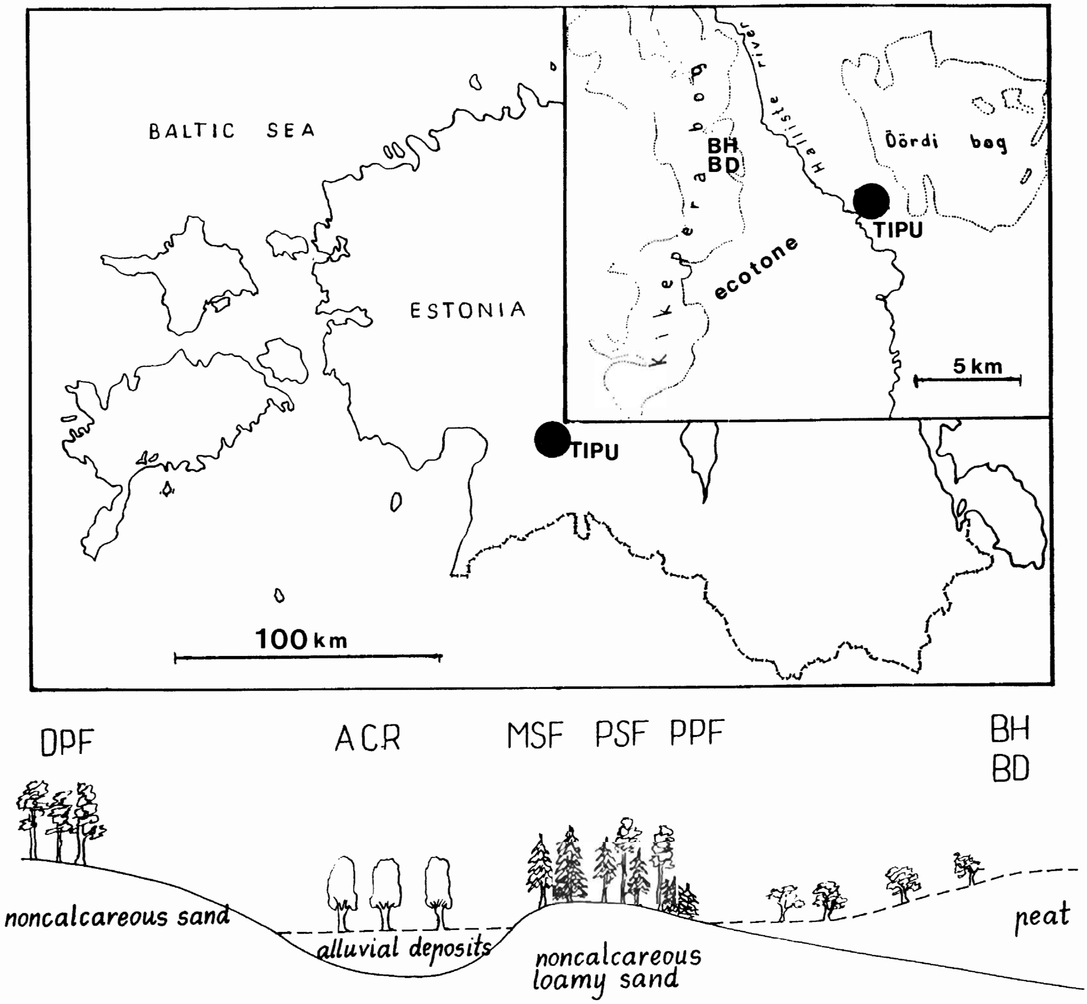

Fig. 1. General location of the study area (upper) with the sites. BD and BH refer to the bog depression and bog hummock, ecotone to the other sites. Lower figure describes the sequence of the sites.

Kuva 1. Tutkimusalueen sijainti (yläkuva), johon on merkitty keidassuokohteet (BD, BH) ja muiden kohteiden tutkimuslinja (ecotone, yläkuvassa). Alakuva havainnollistaa kohteiden sijoittumista toisiinsa nähden.

Soils were sampled by horizon from the pits and analysed for bulk density, pH KCl, humus content, content of P (flame-photometrically), Ca, Mg, K (colorimetrically) from a 1N HCl extraction, and specific surface area by the vapour absorption method. Field moisture capacity was computed from the regression equations of Kitse (1978), using bulk density and specific surface area as arguments. According to Kitse (1978) field moisture capacity is significantly correlated with aeration porosity, which is correlated with the rate of oxygen flux (Wilson et al. 1985).

The differences in aeration conditions between the study sites were evaluated with the help of discriminant analysis (DA). DA may be used to evaluate the discreteness of different sets of samples (representing soil conditions, vegetation structure, etc.). A stepwise procedure for the separation of group means was used to select variables for analysis (for more details see Williams 1983).

One task of so-called descriptive discriminant analysis is to exhibit optimal separation of groups, based on certain linear transformations of the measurement variables. If the separation of sites into groups, called site-types is optimal using soil aeration level as the discriminating variable, there should be no 'misclassifications'. If there is a more optimal way of group separation, some sites (or more precisely, aeration levels characterizing these sites) are considered to be 'misclassified' and will be included in some other group.

RESULTS

Aeration conditions

Soil aeration conditions were characterized by relative values (Table 1). An analysis of variance showed that the influence of all three factors: site, depth and time were significant at $P<0.01$.

Table 1. Aeration conditions in soil environment as percentage from mean oxygen saturation level in condition of full aeration. The numbers are means of three replications, the numbers in parentheses represent small depression with invading *Sphagnum girgensohnii* in paludifying spruce forest. – = no data. Abbreviations: DPF = dry pine forest, MSF = mesophyte spruce forest, PSF = paludifying spruce forest, PPF = paludified pine forest, ACR = alder carr mire.

Taulukko 1. Happiolot tutkittujen kohteiden maaperässä prosentteina vertailuna maan pinnalla olleisiin putkiin. Arvot ovat kolmen toiston keskiarvoja. Sulkumerkeissä olevat arvot on saatu korpirahkasammallaikuista soistuvassa MT-metsikössä. – = ei mitattu.

Month *Kuukausi*	Depth (cm) *Syvyys*	DPF *VT*	MSF *OMT*	PSF *MT*	PPF *KgR*	ACR *TIK*
May – *Toukokuu*	3–10	92.1	78.5	40.6 (32.6)	56.8	30.4
	13–20	94.8	67.2	30.9 (24.4)	30.4	24.0
	28–35	89.1	51.9	27.3 (26.6)	41.6	22.1
June – *Kesäkuu*	3–10	–	34.3	13.4 (9.7)	65.5	25.5
	13–20	88.3	28.4	7.5 (6.0)	37.5	7.3
	28–35	79.1	11.2	4.6 (2.3)	9.3	10.5
July – *Heinäkuu*	3–10	80.8	85.0	76.1 (68.5)	80.7	83.1
	13–20	78.0	69.4	67.0 (42.4)	57.1	53.1
	28–35	79.5	68.5	30.2 (18.1)	47.6	31.0
August – *Elokuu*	3–10	71.2	64.4	71.1 (76.1)	64.0	72.2
	13–20	69.5	63.7	63.4 (46.7)	66.7	45.2
	28–35	79.4	32.8	13.4 (12.4)	44.3	23.9
September – *Syyskuu*	3–10	93.6	75.8	69.1 (–)	74.5	12.8
	13–20	87.8	70.7	35.4 (14.7)	66.6	11.4
	28–35	79.4	55.4	29.1 (14.7)	46.0	16.8

Sites. It is apparent from Table 2 that the extremes of the moisture gradient (from dry pine forest to *Sphagnum* bog) were well differentiated by soil aeration conditions. However, the differences in aeration conditions between site types representing the ecotone were not always clear; discriminant analysis indicated a relatively high number of 'misclassifications' (Table 2). For example, the soil aeration conditions in the MSF site were frequently similar to those of the DPF site. Sometimes, however, the aeration conditions in the MSF site were quite unfavourable and resembled those of the bog.

In the PSF site the oxygen conditions were also quite variable, but generally the aeration conditions there were less favourable than it could be expected from plant community composition and soil morphology. Within the PSF site there did exist a definitive microvariation. One of the sample points represented a local depression with a patch of *Sphagnum girgensohnii* (Table 1). In such locuses, *Sphagna* invade first. With two exceptions — the deeper layer in July and the upper layer in August — the aeration conditions in the depressions of the PSF site were the least favourable among all the forest sites studied.

The number of 'misclassifications' in Table 2 is highest in the case of the PPF site. It indicates that the position of PPF along the moisture gradient is the most unclear; the soil aeration level was sometimes similar to that of the driest site (DPF), but sometimes to the bog.

Soil aeration level in the ACR site was comparable with that in the PPF site, but this is probably more due to precipitation as the surface in ACR became quickly inundated during rainy periods.

Time. The temporal variation in soil aeration conditions differed between sites. In forest soil sites (except DPF) minimal aeration was observed at the beginning of

Table 2. The results of discriminant analysis. Sites (more precisely, data set describing this site) were arranged by increasing moisture level — abbreviations cf. Table 1. Then the optimality of such an arrangement of site types was controlled, while soil aeration level was used as site characteristic. When the separation is optimal, figures from each site are included in the right group. When the aeration level in the site differs too much from the group mean, it is included in another group (i.e. 'misclassified').

Taulukko 2. Diskriminanttianalyysin (DA) tulokset. Kasvupaikat järjestettiin ensin kosteuden mukaiseen järjestykseen. Tämän jälkeen järjestyksen optimaalisuus määritettiin DA:n avulla käyttäen mitattua happipitoisuutta apuna. Kun järjestys on optimaalinen, sijoittuvat kasvupaikan luvut oikeaan ryhmään (esim. VT). Mikäli kasvupaikan happiolot eroavat liikaa keskiarvosta, se "luokitellaan väärin".

	Numbers of cases classified into group – *Ryhmiteltyjen tapausten lukumäärä*					
Site – *Kasvupaikka*	DPF – *VT*	MSF – *OMT*	PSF – *MT*	PPF – *KgR*	BH – *KeRm*	BD – *KeRk*
DPF – *VT*	15	0	0	0	0	0
MSF – *OMT*	6	3	3	0	1	2
PSF – *MT*	1	0	4	2	4	4
PPF – *KgR*	3	4	2	3	1	2
BH – *KeRm*	1	0	0	0	7	7
BD – *KeRk*	0	0	0	0	2	13

June, despite only moderate precipitation in May (precipitation data are given in Zobel 1986). The strongest seasonal variation appeared at the depth of 28–35 cm. In the ACR site the soil aeration conditions were more dependent on precipitation — after heavy rains in August a significant decrease in the aeration level was observed.

Depth. Generally the deeper layers were weakly aerated. There were a few exceptions, however, where aeration of the deeper layers was better. Most of such exceptions were associated with the DPF site, where the soils are well aerated all through the 35 cm layer. These exceptions probably arose due to random differences in the local texture of the soil.

Bog sites (both BD and BH) were characterized by the highest temperatures. Of the mineral soil sites DPF had the highest temperatures and the lowest temperatures were measured in the soil of spruce forest sites, both MSF and PSF. In case of the ACR and PPF sites, the soil temperatures were somewhat higher than in the spruce forests.

Soil parameters

Some soil parameters are presented in Table 3. Except for the ACR site, the soil of which was richer in nutrients, soil fertility is quite similar. The differences in field moisture capacity between similar horizons of different sites are negligible. The main difference is created by the increase in the thickness of peat (and peaty) layers, which are characterized by high moisture capacities.

DISCUSSION

The forest sites MSF, PSF and PPF form a topographic sequence along a moisture gradient. There are considerable differences between plant communities of these stands. However, there is no simple correlation to moisture conditions, characterized by, for example, field capacity, and soil aeration conditions. An oxygen deficiency can be observed in the soil of dry pine forest sites, while the lowest values were measured in the soil of paludifying spruce forest in June. Soil aeration conditions do not depend only on input; the rate of oxygen consumption in soil also influences the aeration regime (Urquhart & Gore 1973, Sidorenko et al. 1986). In the PPF site, the thick organic layer indicates a lower decomposition rate than in the PSF site. More intensive oxygen consumption in the PSF site could be the reason why minimal aeration levels were observed there even though the field capacity was high.

Soil microbial activity is dependent on temperature (Jansson & Berg 1985), but in paludifying forest sites the correlation between soil temperature and aeration level was negligible. The minimum in June could not be explained by the relatively higher rate of oxygen consumption but rather by the saturation of the soil with melting waters during May.

Soil aeration levels in the paludifying forest sites were not correlated with precipitation; towards the end of summer aeration conditions after heavy rainfalls were even better. Another type of seasonal pattern in aeration conditions could be observed in the bog sites (cf. Zobel 1986) and alder carr site, where aeration conditions deteriorated after heavy rains.

The results indicate that pronounced oxygen deficiencies in the soil can arise, even during the initial stages of forest paludification. Further, acidification of the upper horizons is induced by *Sphagna*, which are able to invade as nutrition conditions gradually become less favourable. However, aeration conditions can temporarily even be improved; probably due to the decrease of the microbial oxygen consumption. In general, the deterioration in aeration conditions in water-logged soil

Table 3. Soil parameters in four forest sites; mesophyte spruce forest (MSF), paludifying spruce forest (PSF), paludified pine forest (PPF), alder carr mire (ACR). FMS = field moisture capacity, O = raw humus, P = peat horizon, A = humus horizon, E = eluvial podzolic horizon, B = illuvial horizon, C = parent material.

Taulukko 3. Maaperän ominaisuudet neljässä tutkitussa kohteessa. O = raakahumuskerros, A = humuskerros, E = huuhtoutumiskerros, B = rikastumiskerros, C = pohjamaa, P = turvekerros, FMS = kenttäkapasiteetti.

Site *Kohde*	Horizon *Kerros*	Thickness, cm *Paksuus*	Carbon, % *Hiili*	pH KCl	FMS, % volume *– tilavuudesta*	Ca	Mg	P
							mg l^{-1}	
MSF	O	3	51.3	3.7	83.0	483.3	48.0	11.3
OMT	OA	7	40.1	3.1	83.4	266.7	59.7	3.0
	A	15	1.3	4.2	31.2	33.3	15.0	1.0
	E	7	0.6	4.8	18.9	33.3	16.7	1.0
	B	40	0.7	5.5	21.1	33.3	21.7	18.3
	C		0.3	5.7	15.4	33.3	15.0	28.3
PSF	P	8	51.7	3.0	85.7	183.3	29.7	5.3
MT	AP	3	17.5	3.0	79.1	50.0	21.5	5.0
	A	20	2.3	3.7	22.2	33.3	11.0	1.7
	E	10	0.6	4.3	19.4	33.3	11.0	1.7
	B_1	12	2.7	4.5	31.4	38.3	48.7	57.7
	B_2	16	0.7	4.7	20.8	37.5	14.0	3.5
	C		0.3	4.9	18.4	33.3	11.0	24.7
PPF	P	17	51.6	2.7	89.7	216.7	40.3	5.7
KgR	AP	13	37.8	2.9	74.7	50.0	12.3	1.0
	E	7	0.75	3.9	18.2	33.3	9.0	0.5
	B_1	20	1.45	4.4	26.4	25.0	23.3	16.3
	B_2	20	1.2	4.6	23.6	33.3	21.7	19.0
	C		0.5	4.6	17.4	25.0	16.0	26.7
ACR	AP	17	11.8	5.1	69.7	313.3	69.3	13.3
TlK	A	20	3.9	5.6	48.0	156.7	41.7	16.7

seems to be among the most important factors triggering forest paludification, while other factors (e.g. low pH, shortage of nutrients) gradually become more important as the succession proceeds.

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TIIVISTELMÄ:

MAAN HAPPIOLOT SOISTUVISSA HAVUMETSISSÄ

Eri kasvupaikkojen happioloja tutkittiin Tipun alueella Lounais-Eestissä kasvupaikoilla, jotka muodostavat ravinteisuus- ja kosteussarjan savisella podsolimaannoksella: OMT (taulukoissa ja kuvassa 1 MSF), MT-soistuma (PSF), KgR (PPF), VT (DPF), TlK (ACR). Vertailuksi tutkittiin lisäksi rahkasuon mätäs- (BH) ja painannepintoja (BD), joiden tulokset on julkaistu aikaisemmin (Zobel 1986).

Kokeissa käytettiin 7 cm:n pituisia polykarbonaatista valmistettuja sentrifuugiputkia (Rogers & King 1972). Happimolekyylit pystyvät diffuntoitumaan putken ohuen membraanin lävitse. Hapen määrä mitattiin Tarton yliopistossa kehitetyllä sähkökemiallisella mittauslaitteella ja arvot suhteutettiin ilmassa olleista putkista mitattuihin. Menetelmä on hitaampi kuin redox-potentiaalin mittaus. Eräänä käytännön vaikeutena on ohuiden polykarbonaattikalvojen helppo rikkoontuminen maassa.

Sentrifuugiputket täytettiin vedellä ja asetettiin kasvupaikoille kolmelle eri syvyydelle: 3–10, 13–20 ja 28–35 cm. Tutkimus tehtiin kasvukauden 1986 aikana n. kuukauden välein siten, että ensimmäiset mittaukset olivat kesäkuussa ja viimeiset syyskuussa. Myös veden lämpötila mitattiin koeputkista. Maannosprofiilit kuvattiin ja analysoitiin fysikaalis–kemiallisesti kerroksittain. Kohteiden happiolojen eroja analysoitiin diskriminanttianalyysillä. Mikäli happiolot kuvaavat kasvupaikkojen eroja optimaalisesti, pitäisi samojen kohteiden eri aikoina ryhmittyä samaan ryhmään, eikä "väärin luokitteluja" tapahtua.

Varianssianalyysin perusteella voitiin todeta kaikkien kolmen tutkittavan tekijän, kasvupaikan, syvyyden ja ajan, vaikuttavan erittäin merkitsevästi hapen määrään maaperässä. Tutkituista metsätyypeistä olivat happipitoisuudet yleensä alhaisimmat soistuvassa mustikkatyypin kuusikossa. Tosin kasvupaikan vaikutus ei aina ollut selkeä kosteusakselin suhteen (taulukko 1), ja niinpä diskriminanttianalyysi antoi usein tulokseksi "väärin luokitteluja" (taulukko 2). Happiolot tervaleppäkorvessa muistuttivat usein kangasrämeen happioloja, mutta niissä näkyi selvemmin sateiden nopea vaikutus hapen määrän vähenemiseen. Siellä myös happiolojen ajallinen ja syvyyden mukainen vaihtelu oli selvintä. Veden lämpötila oli korkein keidassuokohteissa ja alhaisin kuusimetsissä.

Vaikkakaan yhteydet kasvupaikan, ajan ja sateiden välillä eivät aina olleet selkeitä, todettiin, että jo soistumisen alkuvaiheissa voi kasvupaikalla ilmetä selvää hapen puutetta. Joissakin tapauksissa voi rahkasammalten jo ilmestyttyä ilmetä happiolojen paranemistakin, ilmeisesti mikrobien hapen kulutuksen vähentyessä, mikä johtaa vähentyvään hajotustoimintaan. Yleisesti voidaan kuitenkin todeta hapen puutteen maassa olevan tärkeä laukaisin soistumiselle. Muiden tekijöiden, kuten happamuus ja ravinteiden puute, merkitys nousee tärkeäksi vasta soistumisen myöhemmissä vaiheissa.

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