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Post-drainage dynamics of P uptake by trees and ground vegetation in Scots pine dominated peatlands

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We investigated long-term dynamics of phosphorus (P) in ground vegetation, tree stand biomass and litterfall in two undrained and four drained oligotrophic pine fens in southern Finland. The study sites, which encompassed observation periods up to six decades after drainage, were chosen to form a chronosequence of sites initially similar floristically, showing different stages of the forest succession induced by drainage. The pattern of P allocation to above- and below-ground plant biomass followed the changes in growth form dominance from mosses, graminoids and shrubs to trees. Overall, net vascular plant uptake of P increased after drainage and remained on a higher level compared to that in the pristine fen. The amount of P in the drained ecosystem seems to remain high enough to support the uptake and continuing forest succession.

Key words: ecosystem functioning, drainage for forestry, mires, nutrient cycling, nutrient uptake, Pinus sylvestris, secondary succession

Introduction

Peatlands have been drained to improve forest growth in many parts of the Northern Hemisphere. Peat soils are originally formed of partially decomposed, water saturated plant debris. Onset of productive tree growth requires improved aeration of surface peat through lowering of the groundwater level, a change that induces a succession from wetland towards forest vegetation (Laine et al. 1995a, Laiho et al. 2003). At the same time, the surface peat is largely detached from an additional nutrient supply by the groundwater. Sustainability in peatland forestry implies that successive harvest-regeneration cycles do not exhaust the nutrient reserves of the growing media.

Composition and functioning of vegetation regulate the partitioning and cycling of the total element pool between the interactive ecosystem compartments of live biomass and the peat substrate (Aerts et al. 1999). The water level, directly or indirectly, regulates the vegetation composition (Glaser et al. 1990, Jeglum & He 1995), as well as all ecosystem processes (e.g. Funk et al. 1994) in peatlands. Consequently, the conditions for biogeochemical cycles change drastically in response to long-term water level drawdown, leading eventually to a partial re-distribution of nutrients within the compartments of the ecosystem (Westman & Laiho 2003). The drainage-induced changes in plant-mediated element cycles have to be evaluated before we can estimate the long-term sustainability for converting a wetland into a manageable forest.

In peatlands, shortage of phosphorus (P) and/or potassium (K) often directly restrict plant growth and microbial activity (Bedford et al. 1999, Hoosbeek et al. 2002), even if the availability of nitrogen (N) may determine the (potential) level of net primary productivity and tree growth (e.g. Kaunisto & Paavilainen 1988). In Finland, a satisfactory N mineralization level without N fertilizations has been considered a prerequisite for peatland forestry. Soil N pool in a peatland forest is substantially higher than that in a mineral soil site, but the availability of many nutrient species may be low in peat (Westman & Laiho 2003). It has been estimated that a shortage of P is generally limiting tree growth in drained peatlands (e.g., Holmen 1964, Kaunisto 1997, Nieminen 2000). This view has been supported by the positive responses of tree growth to P fertilization found in several experiments (e.g., Dickson 1971, Paavilainen 1990, Moilanen 1993, Silfverberg & Hartman 1999). There are no previous studies on the long-term post-drainage dynamics of P uptake by vegetation and the implications for P pools in the peat soil, however.

Monitoring of the fate of nutrients over the post-drainage forest succession is not easy even within the first cycle of management. There would be changes in above- and belowground biomass of ecosystem compartments, such as mosses, ground vegetation, litter, and trees, and in the respective partitioning of nutrient pools. Samples taken from the different ecosystem compartments at any time only reveal the contemporary nutrient pools of that site. While true repeated sampling over the decades of forest growth is unfeasible, the development history can be derived using stands on sites differing in drainage ages. History of tree growth can be compiled using growth-ring analysis and diameter/biomass functions available for corresponding stands and climatic region. Dynamics of nutrient transport between the compartments, through e.g. uptake and litterfall, has to be indirectly derived via the modelled biomass change. Hence the results cannot entirely be based on statistical analysis, but a reconstruction.

Development of a tree stand, after a successful drainage, is constrained by the availability of nutrients. Our first aim is to evaluate the long-term capacity of an oligotrophic pine fen to provide an adequate P source needed to reach a harvestable forest ecosystem. We use a chronosequence consisting of undrained and drained oligotrophic fens in southern Finland to model the long-term dynamics of plant-mediated P transport between plant biomass and litter compartments over several decades. Secondly, a hypothesis of parallel turnover of P and N in peatland forest succession is examined. In an earlier study (Laiho et al. 2003), we inspected forest succession initiated by water-level drawdown in these sites. We observed that the total uptake by vascular plants of N, an abundant element in the ecosystem, increased after water-level drawdown and remained at a higher level than in the pristine state. In contrast, the total uptake of K, that is scanty on these sites, initially somewhat decreased. It could be hypothesized that the dynamics of P would resemble those of N (e.g. Kaunisto 1997), because both these elements are largely bound in organic peat matrix, and their compartment-wise concentrations often correlate positively (e.g. Hartman et al. 2001). However, it has been suggested that the N and P turn differently in the ecosystem due to different mechanisms and factors controlling the mineralization (McGill & Cole 1981), and different controls of uptake after mineralization (Bridgham et al. 1998). We presumed that the consequences of dissimilar behaviour of these nutrients should be revealed in our chronosequence data as follows: If the availability of P and N to plants were similar after water-level drawdown, similar nutrient uptake would result in similar dynamics of nutrient partitions in the various ecosystem compartments. Otherwise, a greater demand of P relative to N would lead to a higher increase in the total uptake of P by plants after water level drawdown.

Material and methods

Study sites

The peatlands chosen for this study are situated in southern Finland (61°35' – 61°52'N, 24°05' – 24°25'E). The mean annual temperature in the region is +3°C and that of July is +16 °C. The mean annual temperature sum (accumulated mean daily temperatures ≥ +5°C) varies between 1150 and 1250 degree-days. The annual precipitation is ca. 650 mm, of which ca. 240 mm is snowfall.

Six sites that formed a drainage succession chronosequence were chosen for detailed measurements (Table 1). Two of the sites were undrained, while the rest had been drained 8, 22, 30, and 55 years before the beginning of the investigation period (summer 1992), thus representing different stages of the secondary succession induced by the persistent drawdown of water level by 20–40 cm. All sites represented tall-sedge pine fen communities (*sensu* Laine & Vasander 1996) before drainage. In a pristine state, these fens are characterised by the abundance of sedges (*Carex* spp. L.), and have a sparse stand of pine (*Pinus sylvestris* L.) growing on low hummocks. Dwarf shrubs, especially *Betula nana* L., are abundant but stunted. The moss layer consists of a thick carpet of *Sphagnum* L., mostly of the *S. recurvum* coll. species (see Flatberg 1992). Following drainage, sedges start a steady and rapid decline, while dwarf shrubs increase in cover (Laine et al. 1995a) and, especially, in biomass (Laiho et al. 2003). Following a distinct 'dwarf shrub stage', above ground biomass is increasingly allocated to the tree stand. Along with the increase in the tree stand biomass, shade-tolerant forest shrubs and mosses gain dominance in the ground vegetation (Laine et al. 1995b).

The sites were subjectively selected from the extensive material (84 sites) of an earlier study dealing with the effect of drainage on peat properties and vegetation (Laiho & Laine 1994, 1995, Laine et al. 1995a, Weiss et al. 1998, Laiho et al. 1999). Our target was to select sites which would form a best available post-drainage succession chronosequence of different drainage ages, initially as similar as possible. Ditching had been the only operation done, the original sparse tree stands had formed the basis for productive forest stands.

P pools in plant biomass and litterfall

Partitioning of the total P pool was inspected in the above- and belowground components of plants and, in larger scale, compartments in the ecosystem consisting of mosses, groups of ground vegetation and trees. Twenty systematically chosen locations relative to the whole plot area, 600–1200 m^2, were sampled on each site for ground vegetation biomass. Sampling was done at the time of maximum biomass. A detailed description of the sampling method can be found in Laiho (1996). Total P concentrations were measured for the shrub, graminoid, and moss compartments separately using an ICP analyzer (ARL 3580) after nitric acid-perchloric acid digestion. These concentrations were used as "unit concentrations" with the parameters of respective compartments measured at the chronosequence sites as described below.

Table 1. General features of the study sites.

Taulukko 1. Poikkileikkausaineiston muodostavien koealojen yleistiedot.

Site	1	2	3	4	5	6
Year of drainage	-	-	1984	1970	1961	1937
Stand volume, m^3 ha^{-1}	6	35	10	76	102	150
GWT[a], cm	10	10	20	50	50	60
P[b], ppm in dry mass	458	626	685	650	693	835

[a] Average water table depth during growing season

[b] Total concentration in the 0–20 cm peat layer

All trees on the sample plots were tallied for DBH (diameter at 1.3 m). Tree stand biomass measurements that were based on harvesting sample trees have been described by Laiho and Laine (1997). Phosphorus concentrations were measured for each biomass component (wood, bark, live branches, dead branches, and needles/leaves) in each sample tree, using the same method as for ground vegetation. Equations were developed to estimate the total above-ground biomass and P content of a single pine or birch tree (Table 2) using DBH as an independent variable (Laiho et al. 2003), and the P content of the whole tree stand at the time of measurements was obtained by applying these equations to the tally tree data.

The tree compartment was divided into its above- and belowground components. The aboveground changes in the P pool were estimated over time for each site using dendrochronological growth analysis. The past annual stem diameters without bark at 11 heights (base, 5%, 10%, 20% …90% of height) were reconstructed for each sample tree back to five years before drainage using their annual ring data. The previous year's diameter increment at breast height was then regressed against the current DBH. Applying the regression to the recorded diameters at breast height produced the DBH of each tree a year earlier. This procedure was repeated either until the fifth pre-drainage year or until the tree's DBH became zero. The reconstructed annual tree data were divided by tree species into 1-cm DBH classes. The mean of each DBH class was fitted into the P content equation. The P contents thus obtained for each DBH class were then multiplied by the number of trees in that DBH class. These values were summed up to give the total P pools of the tree stands each year since the fifth pre-drainage year.

Fine root (diameter ≤10 mm) biomass in the beginning of the investigation period was measured and reported by Laiho & Finér (1996). Sixteen to twenty peat cores were systematically taken on each plot from the 0–30 cm peat layer. Roots were extracted by hand from the cores. The root fraction included both the morphological roots and the rhizomes. Living roots were separated into compartments using three species

Table 2. Parameters for equations $Ci = p1 \text{ DBH}^{p2}$ for estimation of aboveground and coarse root (dry) biomass (BM), and P content of single trees. The dimension of the estimate C_i is kg for biomass and g for P, asymptotic standard errors of estimates are given in parentheses. Equations for abovegound BM and P were obtained from Laiho et al. (2003), and those for coarse root BM (same for undrained and drained sites) were obtained for Scots pine from Laiho & Finér (1996) and for Birch [$\ln Ci = \ln p1 + p2 \ln \text{DBH}$] as corrected from Finér (1989).

Taulukko 2. Yhtälöt maanpäällisen sekä paksujuurten biomassan (kg kuiva-ainetta) sekä P-sisällön (g) estimointiin männyllä ja koivulla. Suluissa estimaattien asymptoottiset keskivirheet. Lähteet: Maanpäällinen biomassa ja P: Laiho et al. (2003); paksujuuret: mänty: Laiho & Finér (1996), koivu: Finér (1989; Appendix 19, yhtälö korjattu).

C_i	$p1$ or ln $p1$*	$p2$	r^2	s.e.e.	n
	Pine: Undrained sites				
Aboveground BM	0.094 (0.043)	2.255 (0.170)	0.986	3.2	14
Coarse root BM	0.013	2.740	0.989	0.5	20
P	0.017 (0.009)	2.237 (0.198)	0.987	0.6	9
	Pine: Drained sites				
Aboveground BM	0.106 (0.028)	2.369 (0.083)	0.987	14.8	38
Coarse root BM	0.013	2.740	0.989	0.5	20
P	0.202 (0.120)	1.547 (0.191)	0.931	5.4	33
	Birch				
Aboveground BM	0.155 (0.071)	2.226 (0.191)	0.983	2.9	15
Coarse root BM	–5.3806*	3.0861	0.991		8
P	0.151 (0.126)	1.677 (0.332)	0.922	2.2	11

* ln$p1$ only for birch coarse roots; see table text.

groups: Scots pine, shrubs and birch, and graminoids (mostly sedges and cottongrass, *Eriophorum vaginatum* L.). The P concentrations were measured with the same methods as described before.

Coarse root biomass of the tree stands was estimated using equations related to DBH, developed by Laiho & Finér (1996) for Scots pine, and by Finér (1989, Appendix 19, see Table 2). Coarse root P concentration was estimated using measured stem P concentration corrected by the ratio of coarse root vs. stem P concentration derived from Finér (1989), who measured the same tree species and site type as ours. The below ground change in tree stand P pools was reconstructed using the dendrochronological growth analysis described above.

Aboveground tree stand litterfall was measured during five consecutive years (1 June 1993–31 May 1998) on sites 2, 4 and 5, and during two years on site 6 that was later harvested. The sampling methods have been described in more detail by Laiho et al. (2003). Total P concentrations in the litter materials were determined with the same methods as those in plant biomass. The litterfall of other vegetation components was estimated using our maximum annual biomass values and earlier data on turnover coefficients (see Laiho et al. 2003 for details).

Phosphorus uptake

The annual net uptake of P from soil was estimated by adding P returned to the soil in annual litterfall to the annual change in the biomass P pools. The nutrient content of litterfall has often been used as a surrogate measure for nutrient uptake (Pastor & Bridgham 1999) on the basis that the nutrients in litterfall must have been taken up by the plants first. With perennial plants, such as trees and shrubs, that retain a major biomass and nutrient reserve over winter, we face a conceptual problem of timing. The nutrients returned to soil in litterfall in a certain year may actually have been taken up during several earlier years. We assumed that this would be irrelevant in our analysis, where the focus is on longer-term trends and most annual variation is averaged out on purpose.

Results

On undrained sites, most of the plant biomass P was found in field layer (graminoids and shrubs) and mosses, but within two decades the P pool in trees exceeded that in the ground vegetation (Fig. 1). The growth rate of the tree stand determined the range over time of this change. Above-ground, the first reaction of all vegetation layers was an increase in biomass P pool, sustained in the tree layer, but reducing in other layers where it finally turned to net loss (Fig. 2). As for below-ground,

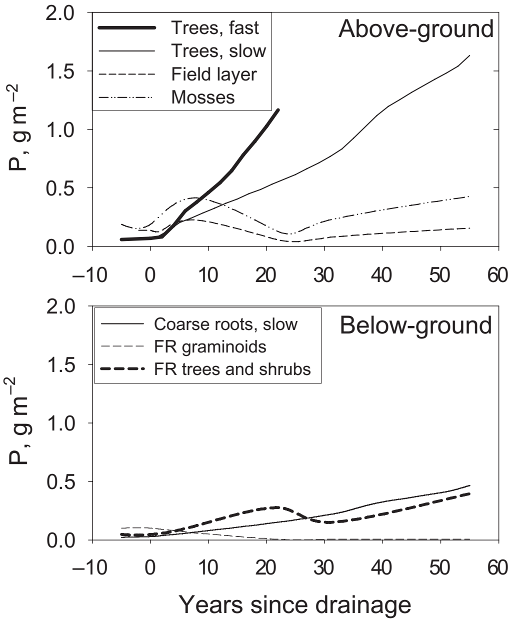

Fig. 1. Evolution of the P pools in the plant biomass, smoothed from raw data using cubic spline interpolation. Tree stand values are from the dendrochronological growth analysis of the study sites drained in 1970 (faster-growing; volume increment 6 m^3 ha^{-1} $year^{-1}$ at 20 years since drainage) and 1937 (slower-growing; volume increment 2 m^3 ha^{-1} $year^{-1}$ at 20 years since drainage). Ground vegetation values are from the chronosequence data. FR = fine roots.

Kuva 1. Kasvillisuuden biomassaan sitoutuneen fosforimäärän kehitys kuutiosplini-interpoloinnilla tasoitettuna. Puuston arvot perustuvat v. 1970 ja v. 1937 ojitettujen koealojen dendrokronologiseen analyysiin (v. 1970 ojitetun koealan puusto oli nopeakasvuisempi: sen tilavuuskasvu oli 6 m^3 ha^{-1} *vuodessa 20 vuoden kuluttua ojituksesta; v. 1937 ojitetun koealan puuston vastaava kasvuluku oli 2* m^3 ha^{-1}*). Pintakasvillisuuden arvot perustuvat poikkileikkausaineistoon. FR = ohutjuuret.*

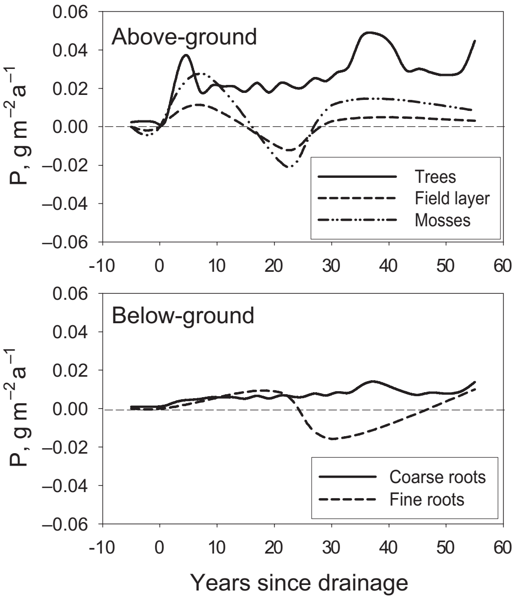

Fig. 2. Estimated annual changes in the plant biomass P pools. Tree stand values (aboveground and coarse roots) are from the dendrochronological growth analysis of the study site drained in 1937. Other values are from the chronosequence data.

Kuva 2. Vuotuiset muutokset kasvillisuuden biomassaan sitoutuneissa fosforimäärissä. Puuston arvot (maanpäällinen osa ja paksujuuret) perustuvat v. 1937 ojitetun koealan dendrokronologiseen analyysiin. Muut arvot perustuvat poikkileikkausaineistoon.

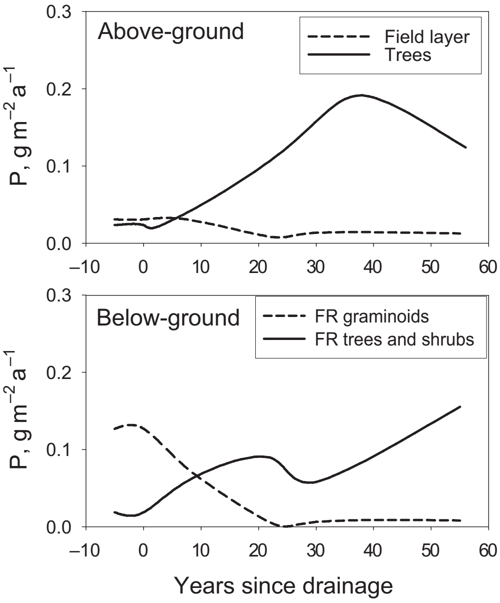

Fig. 3. Evolution of the estimated amount of P in annual litterfall from vascular plants. Aboveground tree litterfall has been measured; other components have been estimated using measured maximum biomass values from the chronosequence data, measured P concentrations, and turnover coefficients. FR = fine root litter.

Kuva 3. Putkilokasvikarikkeen mukana maahan tulevan fosforimäärän ojituksenjälkeinen kehitys. Puuston maanpäällisen karikkeen määrä on mitattu, muiden ositteiden määrät on arvioitu poikkileikkausaineistosta saatujen biomassatunnusten ja kirjallisuudesta saatujen kuolleisuustunnusten avulla. FR = ohutjuurikarike.

a steady P accumulation in coarse roots occurred following the water level drawdown, while the pattern for fine roots resembled that of the ground vegetation (Fig. 2).

Clear changes in the amount of P in annual litterfall (Figs 3 and 4), as well as the quantity and allocation of the total annual P uptake (Figs 4 and 5) occurred with the change in growth form dominance. The total uptake by vascular plants of P increased after water-level drawdown and remained at a higher level than in the pristine state. The patterns of P allocation to above- and below-ground plant biomass varied in the course of the forest succession, depending on plant species and growth form dynamics. In the P cycle through mosses, there was a distinctive but temporary recession in conjunction with the major species change 20–30 years following water-level drawdown.

Discussion

Generally, the dynamics of plant-mediated P flows after water level drawdown resembled those of N (see Laiho et al. 2003), supporting the hypothesis of parallel P and N dynamics. Within two decades, the P cycle shifted from ground vegetation dominance, typical of wet pristine peatlands (Bernard & Hankinson 1979, Urban & Eisenreich 1988, Verry & Urban 1992), to dominance of arboreal vegetation. Net uptake of P by plants clearly increased after water level drawdown. At first, this was caused by the buildup of biomass in shrubs, then in the tree layer. There were differences in the dynamics, however. The increase of net uptake of P was even more pronounced than that of N (see Laiho et al. 2003).

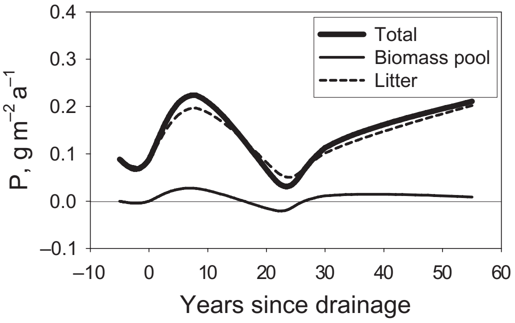

Fig. 4. Evolution of the estimated total annual P uptake by mosses, and its components, i.e. estimated annual changes of P in moss biomass (same as in Fig. 2), and P in moss litter.

Kuva 4. Sammalkerroksen vuotuisen fosforinkulutuksen sekä sen osatekijöiden (biomassan fosforisisällön vuotuiset muutokset ja sammalkarikkeen fosforimäärä) ojituksenjälkeinen kehitys.

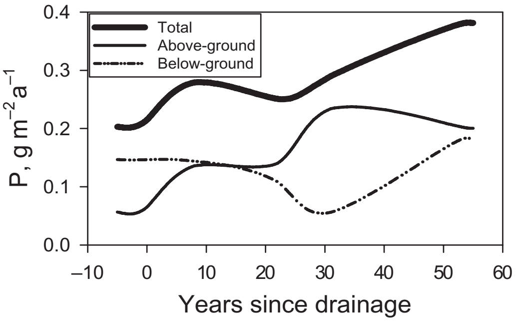

Fig. 5. Evolution of the estimated net annual uptake of P by vascular plants, and its allocation between above- and belowground biomass.

Kuva 5. Putkilokasvien vuotuinen fosforinkulutus sekä sen jakautuminen maanpäällisiin ja maanalaisiin kasvinosiin.

This suggests that P rather than N restricted tree growth in our sites, as is often the case in forested oligotrophic fens (Kaunisto 1997, Hökkä et al. 1996). Even though much of the P in peat is in organic form (e.g., Kaila 1956), it seems that shrubs and trees can at least to some extent access this pool, probably through mycorrhizae.

The P pools in the surface soils of oligotrophic fens (Fig. 6) are rather large relative to the accumulation in the tree stand. This means that the shortage of P for tree growth may be caused by low availability rather than a small soil pool as such. Thus, the increased uptake of P by the trees is not likely to lead to a rapid decline in the soil pool that would hamper tree growth and the forest succession (also Kaunisto & Paavilainen 1988, Laiho & Laine 1994, Westman & Laiho 2003). The same applies to N, as well (Laiho & Laine 1994, 1995, Laiho et al. 1999, Westman & Laiho 2003). Because a well-developed tree layer maintains an efficient drainage by evapotranspiration, the conditions for succession are self-sustained. Secondary succession will proceed until a new equilibrium between the new hydrology and vegetation composition and physiognomy is reached. Estimated on the basis of tree stand development data from mineral soil sites (Ilvessalo & Ilvessalo 1975), we assume that the new equilibrium will be reached after a century at the earliest.

Organic soil is a highly dynamic system, affected by the ratio between litter inputs and decomposition. During the first two decades after water level drawdown, both the content and the concentration of P increase in surface peat. The total P pool within the rooting zone is affected by subsidence of peat surface and the compaction of peat following water-level drawdown (Rothwell et al. 1996, Minkkinen & Laine 1998). The peat P concentration is affected by mineralization and uptake. Later in the forest succession, the amount of litterfall increases, but the litter accumulating on the ‘old’ peat surface is relatively poor in P (Kaunisto & Paavilainen 1988). Some decades after water level drawdown such a secondary ‘raw humus’ layer is probably substantial enough to explain the decreasing trend in the P concentration observed in the surface peat at that time (Fig. 6). The static content of P in the 30-cm peat layer is caused by the continued compaction of the surface peat, compensating for the decreasing mass-based concentration.

The P uptake dynamics of vegetation suggest one phase in the succession that may allow some P leaching. Such a situation occurs in our sites two decades after water level drawdown, when the tree layer canopy closes. This causes a steep decline in light-demanding original mire vegetation, and a decline in the total ground vegetation cover, as the shade-tolerant forest species have not yet gained dominance (Laine et al. 1995b). The rapid turn of a live biomass compartment into

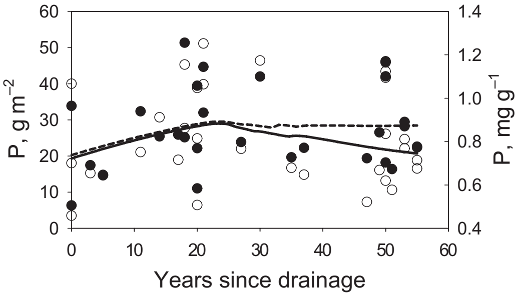

Fig. 6. Total P concentrations (mg g^{-1} dry mass, scale right, open circles, solid line) and total P pools per unit area (g m^{-2}, scale left, filled circles, dashed line) in a 0–30 cm peat layer in the chronosequence material of Laiho & Laine (1994). Only tall-sedge pine fen sites are included, and values have been summed up for the 0–30 cm layer that forms the major rooting zone in these sites (Laiho & Finér, 1996). Trends are indicated by a robust locally weighted regression with an 80% estimation window.

Kuva 6. Fosforin kokonaispitoisuus (mg g^{-1} kuivamassassa, asteikko oikealla, avoympyrät, yhtenäinen viiva) sekä pinta-alayksikköä kohti ilmaistu fosforimäärä (g m^{-2}, asteikko vasemmalla, umpiympyrät, katkoviiva) 0–30 cm turvekerroksessa Laihon & Laineen (1994) poikkileikkausaineistossa. Mukana on vain varsinaisia sararämeitä (ojitettuina puolukkaturvekangas(II)), ja tunnukset on esitetty 0–30 cm turvekerrokselle, jossa lähes kaikki juuret näillä kohteilla sijaitsevat (Laiho & Finér 1996).

litter during that phase may give rise to a temporary excess of P that may not be readily turned back to the new growth but leaches out of the system. Assuming that the decomposition of this emerging litter (Fig. 4) liberates soluble P, and at the same time the total P uptake is not increasing (Fig. 5), we may approximate a maximal potential leaching of 0.2 g P $m^{-2}a^{-1}$ using Figures 4 and 5. This potential loss would not be significant for the forest ecosystem, compared to the remaining soil P pool (Fig. 6), but may be considerable for recipient watercourses. Actually our estimate is high, because a large proportion of P is inert in organic soil. In practice, most P leaching from drained peatlands occurs soon after drainage, when both dissolved and particulate P are exported with the outflow. Later on, the leaching rates of P reported for unfertilized drained peatlands are small (e.g., Sallantaus 1992). Fertilization is a common measure for increasing tree growth in drained peatlands. On the basis of our results we suggest not to apply P fertilizer before the phase of reduced uptake, and the potential risk for leaching, approximately 30 years after drainage has passed. Later, the increasing demand by the tree stand would appear to be able to fix a standard dose of 45 kg ha^{-1} P (Hyvän metsänhoidon...2001) in approximately 10–15 years (Fig. 5).

Climate change scenarios predict warmer temperatures and lowered growing season precipitation in parts of the boreal zone (Gitay et al. 2001), likely leading to a natural drawdown of the water level of peatlands (Gorham 1991, Roulet et al. 1992). The initial lowering in the water level in our chronosequence study sites 1–3, caused by ditching, was 15–20 cm (Table 1). Later on in the forest succession, increased evapotranspiration has induced a further lowering of the water levels down to 50–70 cm during the growing seasons in our older drained sites 4–6. Roulet et al. (1992) predicted climatic warming to lead to a lowering of 14–22 cm for fens in northern Canada. Dry summers have actually been observed to cause a similar or even greater drop in the water level of undrained peatlands (Waddington & Roulet 1996, Carroll & Crill 1997, Alm et al. 1999). Thus, we may expect that the changes in P flows, described here, could be induced not only by artificial drainage, but also by the predicted climatic change.

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Tiivistelmä:

Fosforin ainekierto rämemännikön puustossa ja pintakasvillisuudessa ojituksen jälkeen

Pintakasvillisuuden, puuston ja karikkeen kautta tapahtuvan fosforin ainekierron kehittymistä tarkasteltiin eteläsuomalaisten niukkaravinteisen nevarämeiden ojitusikäsarjassa. Kasvillisuudeltaan alun perin samanlaisista kohteista 2 oli ojittamattomia ja 4 oli ojitettu eri aikoina kuuden vuosikymmenen kuluessa. Metsäkasvillisuuden sukkessio oli eri kohteissa ojitusiästä riippuen eri vaiheessa. Yleispiirteisesti fosforin nettositoutuminen kasvillisuuteen lisääntyi ojituksen jälkeen ja pysytteli ojitussukkession kaikissa vaiheissa ojittamattoman nevarämeen tasoa korkeammalla. Kasvillisuuden käytössä oleva fosforimäärä näytti riittävän ylläpitämään jatkuvaa metsäsukkessiota. Latvuspeitteen sulkeutuessa fosforin nettositouminen kasvillisuuteen aleni tilapäisesti alkuperäisen sammallajiston ja muiden valoa vaativien lajien taantuessa, aineistossamme noin parin vuosikymmenen kuluttua ojituksesta. Siten puuston kasvua voimistavasta fosforilannoituksesta tulisi pidättyä vesistöhaittojen välttämiseksi, kunnes sulkeutuneen metsän varjoa sietävä kasvipeite on korvannut alkuperäisen suolajiston.

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