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Studies on the Balance of Producers and Decomposers in a Grassland Ecosystem in Obihiro

V. Phosphorus Cycle

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草地生態系における生産および分解の平衡に関する研究

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Introduction

Variation of the amount of demand for available P in establishing and maintaining the high production of grasses is considered to constitute a significant difference between the soil characteristics and the vegetal patterns. Soil inorganic P and fertilizer P usually are the most important P sources in grass growth.

Since most of the volcanic ash soil in Hokkaido is unusually high in active aluminium, soluble P applied in this soil is fixed in an unsoluble state. Hence, OOHARA *et al.* (1963 a, 1963 b, 1969) and DRAKE *et al.* (1968) have demonstrated that on soils low in available P and with a great capacity to fix soluble P, the principle of applying large amounts of fertilizer P in precision bands before planting has been highly effective in establishing and providing P to sustain high yields of improved legume-grass forage.

The importance of soil organic P in plant nutrition has been demonstrated by a number of investigators (ACQUAYE 1963, EID *et al.* 1951, 1954, FRIED *et al.* 1960, and VAN DIEST *et al.* 1959).

Organic P, however, assumes great importance only in situations where it forms the main reserve in various sources of organic matter for replenishing grass available P. In such environments, the significance of the organic P fraction depends on the rate of its mineralization, since grasses obtain their P mainly

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in the inorganic form. The mineralization of soil organic P, principally a microbial phenomenon, is influenced by all factors that affect microbial activity and their count. Of these, temperature, moisture, soil reaction, and supply of energy materials are of special relevance. In this respect soil organic matter is an important energy source for the soil microbial population. The mineralization of organic P from this source depends, among other things, on the organic P content of the organic matter in relation to the microbial demand. In this investigation, the mineralization, accumulation and annual cycle of litter organic P were studied in native grassland ecosystems in volcanic ash soils in Obihiro.

Materials and Methods

The samples of grass-litter were collected from the same habitats as in the previous papers (OOHARA *et al.* 1970 a, b, c, & d). Total C in the samples was determined by a wet combusion method (ENWEZOR and CORNFIELD 1965).

Organic P was estimated as the difference between the inorganic P extracted from comparable ignited (at 550°C) and unignited soil samples (SAUNDER and WILLIAMS 1955). Available P was extracted by shaking each 3.57 g sample in a shaker, for one minute, with 25 m*l*. of 0.03 N NH_4F. The extracted P was determined by the molybdenum blue, stanous chloride method of YUEN and POLLARD (1955). The pH was determined in a 1 : 2.5 (for Ao and H samples) and 1 : 5 (for F or L samples), soil : water suspension, by the use of a glass electrode assembly.

Analysis formulae for mineralization

Since a grass-litter (L) consists of organic matter (Lo) and ash (La), the basic concepts of OOHARA *et al.* (1970 a, b, & c) are defined as follows:

$$\begin{aligned} \mathrm{L} &= \mathrm{Lo} + \mathrm{La} \\ &= (\mathrm{Lpc} + \mathrm{Lfc} + \mathrm{Lbc} + \mathrm{Lnf}) + \mathrm{La} \\ &= (\mathrm{Lpc} + \mathrm{Lfc} + \mathrm{Ls} + \mathrm{L}_{\mathrm{G}} + \mathrm{L}_{\mathrm{H}}) + \mathrm{La} \end{aligned}$$

where Lpc, Lfc, Lbc, Lnf, Ls, L_G, and L_H are crude protein, crude fat, crude fiber, *N*-free extract, cellulose, lignin and other carbohydrates of a grass-litter respectively.

The decay rate of a grass-litter at an instant in time (t) is

$$\begin{aligned} \frac{d\mathrm{L}}{dt} &= \frac{dc}{dt} + \frac{da}{dt} \\ &= \left(\frac{\partial Pc}{\partial t} + \frac{\partial Fc}{\partial t} + \frac{\partial Bc}{\partial t} + \frac{\partial Nf}{\partial t}\right) + \frac{da}{dt} \\ &= \left(\frac{\partial Pc}{\partial t} + \frac{\partial Fc}{\partial t} + \frac{\partial S}{\partial t} + \frac{\partial G}{\partial t} + \frac{\partial H}{\partial t}\right) + \frac{da}{dt} \end{aligned}$$

where $\frac{dc}{dt}$ is the same rate as set forth in the previous papers (OOHARA *et al.* 1970 a, b, & c) and $\frac{da}{dt}$ is the rate of change of mineralization for the grass ash. The ash of a grass-litter is analyzed into various mineral oxides such as P, K, Ca, Mg, Na, Fe, Mn, Cu, Co, Zn, Mo etc. Therefore, the decay rate of ash $\left(\frac{da}{dt}\right)$ holds the following relationship.

$$\frac{da}{dt}=\frac{\partial \mathrm{P}}{\partial t}+\frac{\partial \mathrm{K}}{\partial t}+\frac{\partial \mathrm{Ca}}{\partial t}+\frac{\partial \mathrm{Mg}}{\partial t}+\frac{\partial \mathrm{Na}}{\partial t}+\cdots\cdots \tag{1}$$

The models of the accumulation and decomposition on the grassland floor are expressed by the same principles as in the previous papers (OOHARA *et al.* 1970 a, b, c, & d). However, since the litter ash in samples of F, H, and Ao horizons can not be analyzed, each mineral nutrient must be considered separately. Thus each mineral nutrient of organic form and inorganic form are determined by chemical methods and then the respective mineralization is analyzed by the following theoretical models. The mineralization for the litter under a grassland ecosystem of a steady state condition is derived from the basic concept of decomposition (OOHARA *et al.* 1970 a).

$$\frac{dM}{dt}=-rM \tag{2}$$

where M is the weight of mineral nutrient per unit area in soil sampled at depth d, and r is the constant of mineral nutrient mineralized per year. The integrated equation (2) is

$$M=\mathrm{Mo}\,e^{-rt} \tag{3}$$

where Mo is the weight of mineral nutrient in the soil initially. In the case of a steady state grassland, the characteristics of the soils for a regular annual cycle of mineral nutrients are shown.

The yield of mineralization or annual cycle $\mathrm{M_Y}$ of ash constituents at an instant in time is defined as the equation for the annual peak values Fm minus the annual accumulative values Ma.

$$\mathrm{M_Y}=\mathrm{Fm}-\mathrm{Ma} \tag{4}$$

The equation (4) is calculated at

$$\mathrm{M_Y}=\mathrm{Lm}\left(\frac{1-e^{-r't}}{r'}-\frac{1-e^{-rt}}{r}\right) \tag{5}$$

where r' is the constant for the theoretical limiting values of the annual peak values.

When the time t limits ∞, $e^{-r't}$ and e^{-rt} aproach zero and thus is

$$M_Y = Lm\left(\frac{1}{r'} - \frac{1}{r}\right)$$

Therefore, in steady state grassland the annual cycle of mineral nutrient is

$$M_Y = Lm \tag{6}$$

where Lm is the mineral production due to the annual litter addition.

Results and Discussion

(1) Characteristics of the surface soils

Organic P content in surface soils of *Phragmites longivalvis*, *Reynoutria sachalinensis* and *Sasa purpurascens* grasslands varied from 0.1187 to 0.1421 percent in L horizons, from 0.1214 to 0.1542 percent in F horizons, from 0.0118 to 0.0261 percent in H horizons, and from 0.0079 to 0.0132 percent in Ao horizons. The other soil characteristics are shown in Table 1.

There was a highly significant relationship between total C and organic P ($r=0.9723$, $n=24$ & t value$=19.446$). This is in agreement with the results of KAILA (1963), ACQUAYE (1963) and SHARMA *et al.* (1963). These results show that total C and organic P varied together in the soils. The wide range of values for the C : organic P ratio indicates that this covariance did not necessarily mean a proportionality in C and organic P content of the organic matter.

There was also a significant positive correlation ($r=0.5875$, $n=24$ & t value $=3.4038$) between organic P and available P. This suggests that available P is

Table 1. Mineralized phosphorus and some characteristics of the soil samples used

Grasslands	Horizon	pH*	Organic phosphorus (%)	Available phosphorus (ppm)	Total carbon (%)	C : Org. P ratio (Average)
Phragmites longivalvis	L	6.11	0.1225±0.00372	14.93±0.825	54.024±1.7099	440.87
	F	5.79	0.1254±0.00398	15.75±0.735	43.693±1.7193	348.30
	H	6.18	0.0149±0.00312	9.53±1.080	10.663±1.7985	715.89
	Ao	6.21	0.0088±0.00089	10.37±1.583	8.448±1.942	957.23
Reynoutria sachalinensis	L	6.75	0.1382±0.00391	13.65±2.025	51.909±1.8341	375.59
	F	6.38	0.1436±0.01055	17.48±2.625	48.696±2.6234	339.14
	H	6.47	0.0194±0.00668	11.63±0.930	13.652±1.7492	703.65
	Ao	6.64	0.0126±0.00264	14.14±1.988	6.901±0.0864	549.51
Sasa purpurascens	L	6.55	0.1287±0.01994	14.13±0.910	47.073±1.3964	365.71
	F	6.17	0.1332±0.00310	16.65±0.450	46.578±1.3991	349.70
	H	6.07	0.0172±0.00074	5.19±0.212	16.165±1.9464	941.79
	Ao	6.23	0.0131±0.00011	3.04±0.147	7.998±1.2975	611.25

* Medians instead of arithmatic averages are given for all pH values because of the logarithmic nature of this factor.

increased by the mineralization of organic P and utilized by the grass, while the soluble erosion by rain water decreases the content of available P in surface soils.

(2) Phosphorus mobilization

The estimates for the C : organic P ratio correlated very highly and negatively ($r = -0.7133$, $n = 24$ & t value $= 4.7767$) with total C. This means an inverse proportionality in C and organic P content of the decaying organic matter. Thus it shows that the decomposition of P compounds is more rapid than C compounds. However, the C : organic P ratio of F samples, shown in Table 1, was lower than L and the soil pH showed the same tendency. This indicates that the P compounds of organic matters are decomposed more slowly than C compounds in this stage.

A very highly significant negative correlation ($r = -0.7995$, $n = 24$ & t value $= 6.2461$) existed between organic P and the C : organic P ratio and also between available P and the C : organic P ratio ($r = -0.5566$, $n = 24$ & t value$=3.1411$). This suggests that these relationships are in agreement with the total C. The very low estimates of available P content for the H horizons as compared with L and F, in the absence of parallel changes in mineralized C, indicate that there was a luxurious absorption of P by plant and microorganisms where available P levels were high.

(3) The production of organic phosphorus

As shown in Table 2 and Fig. 1, organic P production is high amounting to 0.6985～0.9193 g/m^2, in *P. longivalvis* and *R. sachalinensis* grasslands but sometimes below 0.6500 g/m^2 in the former and seldom above 1.0000 g/m^2 in the latter. It is as low as 0.1339～0.1983 g/m^2 in *S. purpurascens* grasslands.

Table 2. The estimates of the production and accumulation of organic phosphorus for the surface soils under the three grassland ecosystems in Obihiro

Grasslands	Horizon	Air dry weight (g/m^2)	Water content (%)	Organic phosphorus (g/m^2)
Phragmites longivalvis	L	620.6 ± 44.63	4.189 ± 0.2438	0.7269 ± 0.02836
	F	1101.0 ± 31.03	4.902 ± 0.3267	1.3143 ± 0.07418
	H	2044.2 ± 223.08	3.657 ± 0.2886	0.2812 ± 0.01121
	Ao	2922.1 ± 209.98	2.211 ± 0.4993	0.2545 ± 0.05126
Reynoutria sachalinensis	L	649.0 ± 35.04	5.121 ± 0.3075	0.8521 ± 0.06718
	F	695.6 ± 5.61	6.329 ± 0.5071	0.9347 ± 0.05612
	H	1460.2 ± 123.03	5.428 ± 0.2398	0.2655 ± 0.05512
	Ao	2807.0 ± 201.06	4.384 ± 0.3211	0.3457 ± 0.02621
Sasa purpurascens	L	135.0 ± 5.09	5.025 ± 0.2878	0.1661 ± 0.03218
	F	367.6 ± 16.42	5.514 ± 0.2452	0.4627 ± 0.02403
	H	541.2 ± 28.05	5.119 ± 0.3400	0.0889 ± 0.00371
	Ao	1675.6 ± 152.41	4.124 ± 0.4697	0.2101 ± 0.01834

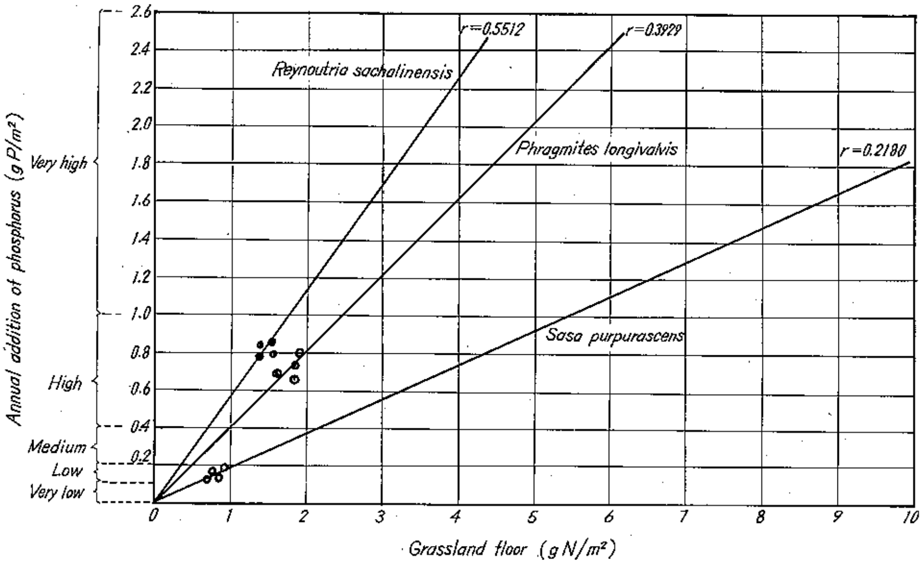

Fig. 1. Estimates of mineralization rate factor r for P in *P. longivalvis*, *R. sachalinensis* and *S. purpurascens* grasslands, from the ratio of annual addition of P to a steady state accumulation of the grassland floor

The scattering in any one portion of Fig. 1 indicates that the production and storage of organic phosphorus are not closely related. In fact, the diagram as a whole demonstrates an inverse relation. Low storage of P in the highly productive grasslands contrasts with high levels of organic P accumulation in the relatively unproductive grasslands. A major reason for this inverse relation clearly involves rates at which dead organic matter is broken down or incorporated into the mineral soil by microorganisms.

(4) Phosphorus mineralization

As shown in Table 3 the estimates of r or r' ranges and durations of accumulation or mineralization of organic P for the grass-litter were determined

Table 3. Parameters for exponential accumulation and mineralization of organic phosphorus in grassland ecosystems with a steady litter fall rate

Grasslands	Constants	r and r'	$1/r$ and $1/r'$	Half time (years)	95% time (years)	99% time (years)
P. longivalvis	r	0.3929 ± 0.01451	2.54517	1.7638	7.6355	12.7259
	r'	0.2821	3.54482	2.4566	10.6345	17.7242
R. sachalinensis	r	0.5512 ± 0.08341	1.81422	1.2573	5.4427	9.0711
	r'	0.3553	2.81452	1.9505	8.4436	14.0726
S. purpurascens	r	0.2180 ± 0.04554	4.58715	3.1789	13.7615	22.9358
	r'	0.1790	5.58659	3.8715	16.7598	27.9330

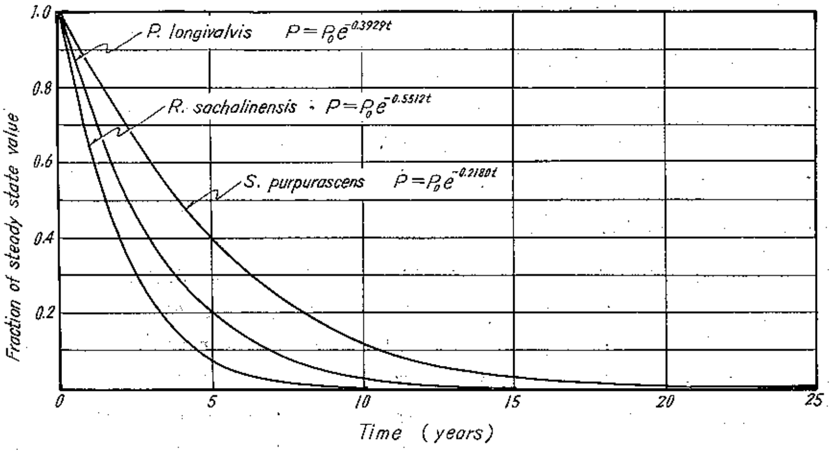

Fig. 2. Exponential curves for mineralization of organic P of grass-litter under the grassland ecosystems of *P. longivalvis*, *R. sachalinensis* and *S. purpurascens* in Obihiro

in the three grassland ecosystems used. The *P. longivalvis* grasslands have values scattered around the line for $r=0.393$ and $r'=0.282$, while *R. sachalinensis* grasslands range down toward the line for $r=0.551$ and $r'=0.355$. This parameter fraction r of *S. purpurascens* grasslands varied from 0.264 to 0.173 and the average value of r' was 0.179 too. This suggests that, of the threegrasslands the mineralization of organic P was most rapid in *R. sachalinensis*, while this was more rapid in *P. longivalvis* than in *S. purpurascens*.

From equations (2) and (3), the theoretical curves of mineralization of organic P for the grass-litter in the present grassland ecosytems are shown Fig. 2. These models for *P. longivalvis*, *R. sachalinensis* and *S. purpurascens* grasslands are given by

$$\mathrm{P}=\mathrm{Po}\,e^{-0.3929t}, \tag{7}$$

$$\mathrm{P}=\mathrm{Po}\,e^{-0.5512t} \tag{8}$$

and

$$\mathrm{P}=\mathrm{Po}\,e^{-0.2180t} \tag{9}$$

where P is the organic P content of the remainder for the grass-litter and Po is the level of the initial organic P.

Since P is Po=0 at $t=0$, the models of organic P accumulation on the grassland floors are as follows:

in *P. longivalvis* grassland

$$\mathrm{P_A}=1.8500\,(1-e^{-0.3929t}), \tag{10}$$

in *R. sachalinensis* grassland

$$\mathrm{P_A}=1.5459\,(1-e^{-0.5512t}) \tag{11}$$

and in *S. purpurascens* grassland

$$P = 0.7617\,(1 - e^{-0.2180t}) \tag{12}$$

where P is the accumulation of organic P. Thus mineralization of organic P seems to depend on the phosphorus in the organic form according to the grass species rather than on the C : organic P ratio.

(5) Annual cycle of phosphorus

The time required for a cycle to be completed from organic P to inorganic P of 50, 95, and 99% are given by the solution of the exponential model (7), (8) and (9). Table 3 presents these data for the grass-litter which are accumulated and decomposed in the three grassland ecosystems respectively.

The important differences among the years for the mineralization of organic P are illustrated by the jagged curves, Figs. 3～5, with peaks and valleys. There is no longer a steady replacement of the P mineralizing between pulses of annual addition by litter fall and the remainder of the steady amount after 1 year of mineralization is less than the amount which had accumulated after either 1 or 2 years of steady addition and mineralization. This deficit below the theoretical level for steady accumulation is then made up by the second sudden autumn litter fall.

An equation for the annual peak values which occur right after the t-th

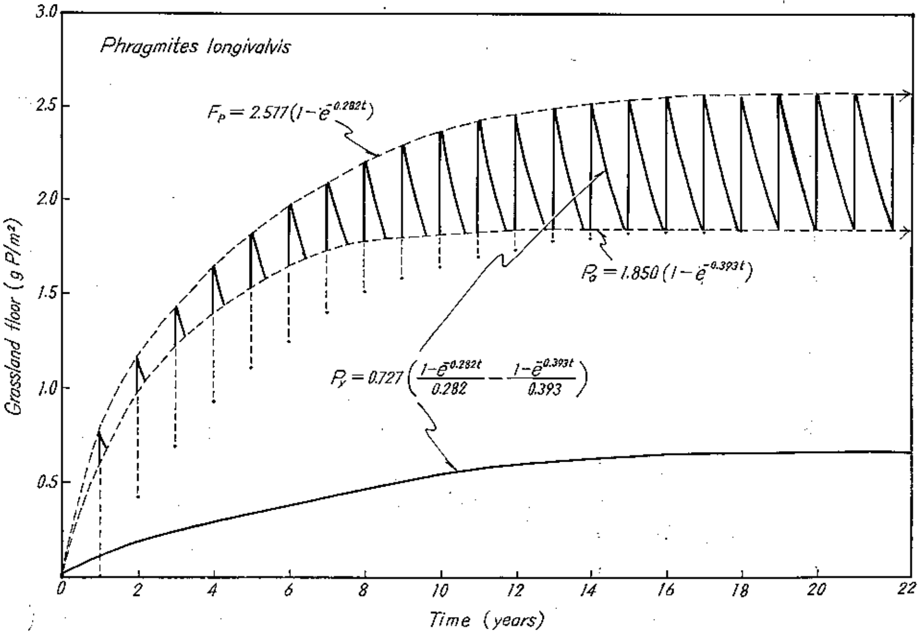

Fig. 3. The annual P cycle for mineralization of grass-litter in *P. longivalvis* grasslands on the Satsunai River banks in Obihiro

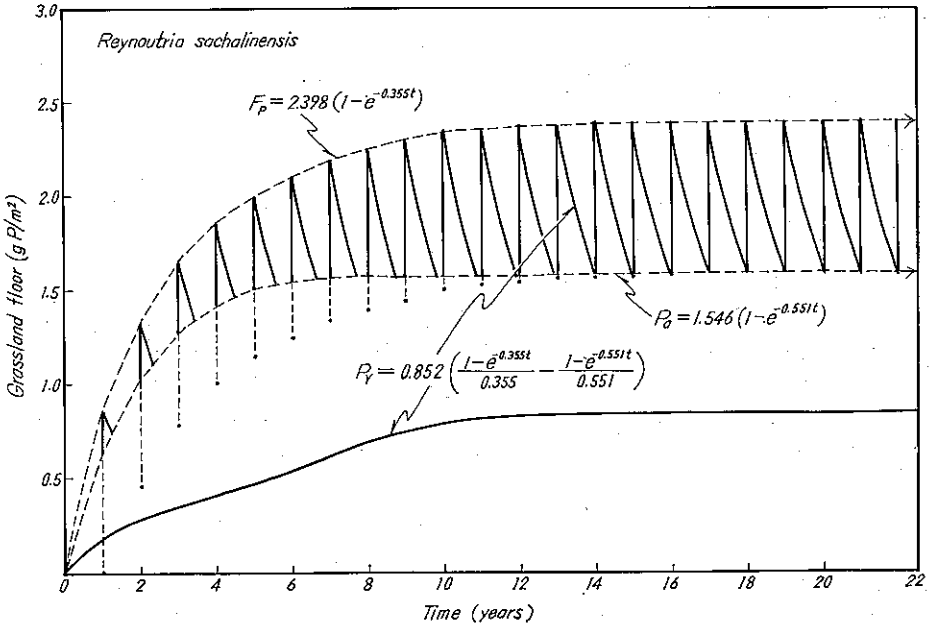

Fig. 4. The annual P cycle for mineralization of grass-litter in *R. sachalinensis* grasslands on the Satsunai River banks in Obihiro

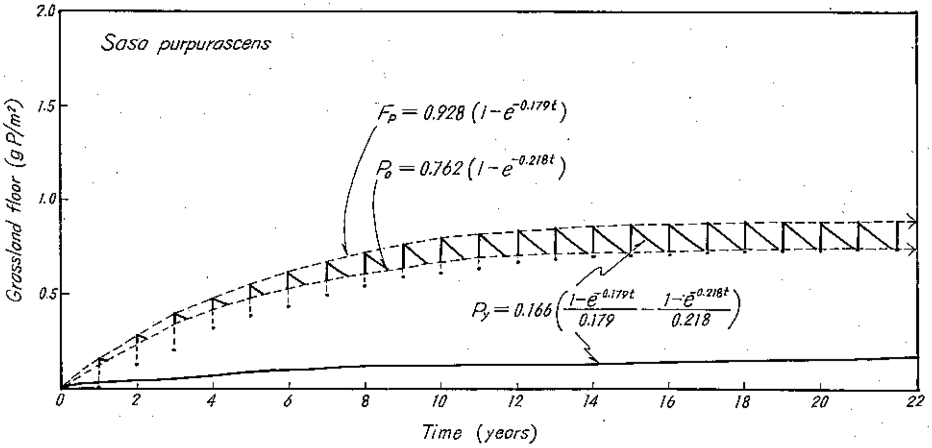

Fig. 5. The annual P cycle for mineralization of grass-litter in *S. purpurascens* grasslands on the Satsunai River banks in Obihiro

year's annual addition includes the annual yield of mineralization with accumulation. Therefore, the annual cycle (from the equation 5) is given in *P. longivalvis* grassland by

$$P_Y = 727\left(\frac{1-e^{-0.282t}}{282} - \frac{1-e^{-0.393t}}{393}\right) \qquad (13)$$

in *R. sachalinensis* grassland

$$P_Y = 852\left(\frac{1-e^{-0.355t}}{355} - \frac{1-e^{-0.551t}}{551}\right) \tag{14}$$

and in *S. purpurascens* grassland

$$P_Y = 166\left(\frac{1-e^{-0.179t}}{179} - \frac{1-e^{-0.218t}}{218}\right) \tag{15}$$

These equations indicate that annual yields of minearlization for organic P in steady state grasslands of *P. longivalvis*, *R. sachalinensis* and *S. purpurascens* are 0.727, 0.852 and 0.166 g/m^2 respectively. It is expected that if and when these grasslands are subjected to a complete removal of the accumulated grass-litter the same amount as that of the annual yield of mineralized P must be supplied to maintain the steady state conditions of these grasslands.

Summary

1. In this investigation, the accumulation, mineralization and annual cycle of litter organic P has been studied in native grassland ecosystems of *P. longivalvis*, *R. sachalinensis* and *S. purpurascens* on the volcanic ash soils in Obihiro.

2. The basic models of the accumulation and mineralization for ash components of a grass-litter have been presented as equations (1), (2) and (3). The equations (7)~(12) for organic P are derived from these basic concepts.

3. There was a highly significant relationship between total C and organic P. The estimates for the C/organic P ratio correlated very highly and negatively with total C but the C/organic P ratio of F samples was lower than L.

4. The parameter factors r or r' of mineralization of organic P for *P. longivalvis*, *R. sachalinensis* and *S. purpurascens* grasslands were $r=0.393$ or $r'=0.282$, $r=0.551$ or $r'=0.355$, and $r=0.218$ or $r'=0.179$ respectively.

5. The time required for a cycle to be completed from organic P to inorganic P of 50, 95 and 99% are 1.764, 7.636 and 12.726 years in *P. longivalvis*, grassland 1.257, 5.443 and 9.071 years in *R. sachalinensis*, grassland and 3.179, 13.762 and 22.936 years in *S. purpurascens* grassland respectively.

6. The annual P cycle formulae for mineralization were based on the equations (5), (13), (14) and (15). Annual yields of mineralization for organic P in the steady state grasslands of *P. longivalvis*, *R. sachalinensis* and *S. purpurascens* are 0.727, 0.852 and 0.166 g/m^2 respectively.

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要約

1. 帯広札内川辺のヨシ，オオイタドリおよびササの草地生態系における有機燐の蓄積，無機化およびその年循環を検討した。

2. 落葉の諸灰分の蓄積と無機化を分析する基礎的なモデルは (1), (2) および (3) 式であり，これらの基礎式によって誘導した燐の場合の式は (7)~(12) に示される。

3. 有機炭素の全量と有機燐の間には高い有意性が認められ，その炭素量と有機燐の割合 (C/P) は炭素の全量と高度の負の相関を示したが F 層の供試材料では L 層のそれぞれの割合より低い。

4. 有機燐の無機化恒数はヨシ群落で $r=0.393$ および $r'=0.282$，オオイタドリ群落で $r=0.551$ および $r'=0.355$，ササ群落において $r=0.218$ および $r'=0.179$ であった。

5. ヨシ群落の生態系における落葉の有機燐から 50% の無機燐に変化するには 1.764 年，その 90% では 7.636 年，99% では 12.726 年を要し，オオイタドリ群落では 50% で 1.257 年，95% で 5.443 年，99% で 9.071 年であり，またササ群落では 50% で 3.179 年，95% で 13.762 年，99% で 22.936 年を要することが認められた。

6. 無機化における年間燐の循環は (5), (3), (14), および (15) 式で示され，平衡状態にあるヨシ群落では 0.729 g/m^2 の燐量が毎年循環し，オオイタドリ群落では 0.852 g/m^2，ササ群落の場合には 0.166 g/m^2 である。