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Abstract

In general, natural grassland develops even under very low-phosphorus fertility conditions and maintains high dry-matter production. This suggests that natural grassland may have a particular system to utilize phosphorus nutrient effectively. To clarify why such natural grasslands develop under such low phosphorus fertility, we analyzed the characteristics of the phosphorus dynamics in the semi-natural grasslands receiving no fertilizer in comparison with sown grasslands.

1. In two sown grasslands, a perennial ryegrass/white clover-mixed grassland and a Kentucky bluegrass grassland, and three semi-natural grasslands, a azumanezasa-dominant, a Japanese lawngrass-dominant and a silvergrass dominant-grassland, seasonal changes in plant phosphorus concentration in 49 plant species of the grasses including pasture grasses were examined.
2. The amount of phosphorus accumulation in the aboveground shoots in the azumanezasa (*Pleioblastus chino* Makino)-dominant grassland was almost the same as that in the fertilized perennial ryegrass (*Lolium perenne* L.)/white clover (*Trifolium repens* L.)-mixed grassland. The phosphorus accumulation in the silvergrass (*Miscanthus sinesis* Andress.)-dominant grassland was half of that in the perennial ryegrass/white clover grassland, and that in the Japanese lawngrass (*Zoysia japonica* Steud.)-dominant grassland was one-seventh.
3. Semi-natural grasses maintained a considerable amount of dry-matter production even under very low phosphorus fertility conditions. In particular, azumanezasa- and silvergrass-dominant grassland maintained a high shoot biomass equal to or greater than that of the fertilized sown grassland. This fact suggests that the high efficiency of phosphorus utilization in the dry-matter production might be a primary factor in the adaptation of natural grasses to low-phosphorus fertility.
4. Based on model analysis of the phosphorus dynamics in the Japanese lawngrass-dominant grassland without grazing and the silvergrass-dominant grassland, the following characteristics were found; In the Japanese lawngrass-dominant grassland, since the phosphorus translocation from the soil to the root was found, soil phosphorus significantly contributes to the phosphorus dynamics of this grassland, while in the silvergrass-dominant grassland, phosphorus accumulation during the growing season was found not only in the aboveground shoots but also underground. However, soil phosphorus may not be important in the phosphorus dynamics of Japanese lawngrass. Thus, the phosphorus cycle of the grassland significantly depends on the phosphorus translocation between the aboveground parts (shoots, dead shoots and litter) and underground parts (roots) in the silvergrass-dominant grassland.
5. Two general types of phosphorus dynamics in semi-natural grasslands were recognized; 1) Japanese lawngrass-type grassland, which is significantly assisted by available phosphorus in the surface soil layer and phosphorus accumulated in living shoots, dead shoots, litter and roots, and 2) silvergrass-type grassland, which is significantly dependant on the phosphorus translocation between the aboveground and underground parts of the plants except soil parts.

Key words: Semi-natural grassland, Phosphorus dynamics, Japanese lawngrass, Silvergrass, Olsen-P

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Introduction

After the Uruguay Round, it was indicated that agriculture production thereafter should be carried out under environmentally friendly management. In order to achieve this, practical management techniques to bring about the reduction of agricultural chemicals and/or fertilizers are needed.

From the viewpoint of phosphorus resources, Japan depends completely on imports for its entire domestic phosphorus supply. It is a matter of concern that phosphorus resources might be exhausted by the middle of the 21st century. The grassland of Japan is mostly covered by volcanic ash soil that has reduced grass production due to its strong acidity and poor phosphorus fertility. Especially in hay grassland, even though sufficient application of fertilizers or cattle manure has been carried out up to now, the reduction of management costs, which includes soil reclamation materials and fertilizers, is demanded. Furthermore, a physiological obstruction problem has occurred, caused by inappropriate management or productivity reduction.

An effective nutrient-cycle system establishes itself in grassland under low soil fertility conditions. Natural grassland is able to maintain considerably high grass production even under very low-phosphorus fertility conditions, which means very little phosphorus is available in the soil. Some papers reported on phosphorus concentrations of the natural grasses in Japan (Ichikawa[6]), but they did not indicate seasonal changes. Palatability is an important factor considering the practical use of natural grasses. Sato and Hayakawa[11] and Green *et al.*[3] have shown the higher palatability of the grasses under higher phosphorus concentration. A study of root systems of silvergrass was conducted by Yano *et al.*[15], who reported that the subterranean stem of grass that lied mainly between 0 to 20 cm deep plays a role in nutrient accumulation. Honda[5] presented the morphological study of silvergrass root systems, and suggested the importance of the shallow part of the root system in nutrient uptake. Kondo *et al.*[7] measured the nutrient absorption ability of grass roots by using the actival tracer method for orchardgrass-dominant grassland, and found that 80% of total absorption was occupied by the root layer from 0 to 5 cm deep. Kondo *et al.*[8] also showed an effective phosphorus cycle in grazing pasture. Harada *et al.*[4] compared phosphorus uptake abilities under low phosphorus fertility conditions among several pasture grasses.

In this study, we investigated (1) characteristics of phosphorus status both in plants and soil in five different grasslands, (2) characteristics of dry matter and phosphorus accumulation in relation to soil phosphorus in these grasslands, and (3) characteristics of phosphorus dynamics in semi-natural grasslands. Based on the series of the investigations, we aim to prove the mechanisms of low-phosphorus tolerance of natural grasses.

Materials and Methods

Experiment site

All experiments in this study were carried out at Fujinitayama experiment field of the National Grassland Research Institute, Nishinasuno, Tochigi, Japan, which is situated at lat. 36° 55' N. and long. 139° 58' E. The average annual temperature is 12.0℃ and the average annual precipitation is 1,561 mm.

Sown grassland surveyed

Perennial ryegrass (*Lolium perenne* L.) and white clover (*Trifolium repens* L.)-mixed grassland (A), and Kentucky bluegrass (*Poa pratensis* L.)-dominant grassland (B) were treated as representatives of sown grasslands. The soils of these two fields were classified as gray lowland soil. Chemical fertilizer was applied at 94 kg N, 102 kg P_2O_5 and 94 kg K_2O per ha annually in grassland (A), and 65 kg N, 70 kg P_2O_5 and 65 kg K_2O per ha annually in grassland (B).

Semi-natural grassland surveyed

Three semi-natural grasslands were used as experiment sites. Japanese lawngrass (*Zoysia japonica* Steud.)-dominant grassland (C) was reclaimed in around 1980 on the sublayer field of andosol after earthwork for highway construction, and has been managed through grazing of 100 head-day per year by Japanese Black cattle. An unknown amount of chemical fertilizer was applied at reclamation, after which no fertilizer was applied. Grazing was stopped at the experiment year during 1997 and 1999. In a part of this field, azumanezasa (*Pleioblastus chino* Makino) invaded and composed almost all of the vegetation. This grassland was treated as azumanezasa grassland, (D). Silvergrass (*Miscanthus sinesis* Andress.)-dominant grassland (E) was managed through grazing of 100 head-day per year by Japanese Black cattle during 1970 and 1989, but after 1990 it was managed exclusively by cutting every fall season. Chemical fertilizer was not applied. These three semi-natural grasslands had andosol soil sublayers.

Phosphorus analysis for the plants and soils of sown/semi-natural grasslands

Square frames 1 m in size were set at three sites for sampling in each plot. The top part of vegetation was harvested at the ground surface of the frames, and the plants were separated by species. Plants were divided into three parts; living shoots, dead shoots and dead stands. When necessary, the underground parts were collected, and they were divided into roots and subterranean stems. Plant samples were oven dried at 70℃ for 4 to 7 days, and phosphorus concentrations were analyzed by the conventional method (Harada *et al.*[4]). Soil samples were collected from three layers of 0-2.5 cm, 2.5-5.0 cm and 5.0-10.0 cm, from each sampling frame. Soil samples were air dried in dark conditions, and the available phosphorus (Truog-P by Truog[14] and Olsen-P by Olsen and Sommers[10]), total phosphorus and total inorganic phosphorus by burning (Egawa and Nonaka[2]) were analyzed. Truog-P and Olsen-P have been commonly used as available phosphorus. They generally show high correlations with the amount of plant nutrient uptake. In the soils in which Truog-P were too low to be analyzed, Olsen-P was found to be a good parameter of the available soil phosphorus pool, which is closely related to microbial activities (Kondo *et al.*[10]). Therefore, Olsen-P is expected to present valuable data concerning phosphorus cycling between soils and plants.

Time of surveying plants and roots

Dates of survey for vegetation (only in 1997) and the underground parts are as follows:

Sown grassland (A) (Perennial ryegrass and white clover-mixed grassland): May 27 and October 23, 1997.

Sown grassland (B) (Kentucky bluegrass-dominant grassland): May 27, 1997.

Semi-natural grassland (C)(Japanese lawngrass-dominant grassland): May 21 and August 21, 1997; April 1, May 21, July 1, September 20 and November 4, 1998; and March 17, April 7, May 18, July 6, September 30 and November 4, 1999.

Semi-natural grassland (D)(azumanezasa grassland): June 18 and August 21, 1997.

Semi-natural grassland (E)(Silvergrass-dominant grassland): July 18, and September 10, 1997; March 30, May 20, July 21, September 30 and November 9, 1998; and March 23, July 21 and November 4, 1999.

Time of surveying soil phosphorus

Soil samples were taken and analyzed at the time of surveying plants and roots, but available phosphorus in 1997 was analyzed only for Truog-P.

Results and Discussion

1. Characteristics in vegetation and phosphorus concentration of soil and shoots

In the sown grasslands (A) and (B), the dominant grass species occupied more than 80% in crown coverage. Over 95% of the crown coverage in semi-natural grassland (C), (D) and (E) was occupied by Japanese lawngrass, azumanezasa and silvergrass, respectively. Other primary species present were: sweet vernalgrass (*Anthoxanthum odoratum* L.): 9-15%, and birdsfoot trefoil (*Lotus corniculatus* L. var. *japonicus* Regel): 5-13%, in semi-natural grassland (C); Kudzu (Pueraria lobata (Willd.) Ohwi): 2-12%, and *Arumdinella hirta* (Thunb.) C. Tanaka: 5-11%, in semi-natural grassland (E). Almost 100% of the area was occupied by the dominant species in semi-natural grassland (D).

Table 1 shows the total phosphorus, total inorganic phosphorus and available phosphorus of the surface soil layer (0-5 cm) of the grasslands. Sown grasslands (A) and (B) showed a high phosphorus fertility because of the chemical fertilization. Semi-natural grasslands (C), (D) and (E), however, showed rather low phosphorus fertility, since they were managed by grazing without fertilizer application for many years.

Table 2 shows the list of natural grass species including sown species observed in the grasslands (A), (B), (C), (D) and (E), and the typical phosphorus concentration of the plant shoots in the order of the sampling time. There were 49 plant species observed. Plant phosphorus concentrations were considerably high in *Ophioglossum petiolathum* (Hanayasuri) 3.38 gkg^{-1} in grassland (C) and *Oenothera striata* (Matsuyoigusa) 2.64 gkg^{-1} in grassland (E), but those of most other natural species were rather low compared with sown species of perennial ryegrass: 2.70 gkg^{-1}, Kentucky bluegrass: 3.16 gkg^{-1}, or white clover: 3.75 gkg^{-1}.

Figure 1 shows the frequency distribution for annual mean shoot phosphorus concentrations of each

Table 1. Soil phosphorus content in different grasslands (1997) ($mgPkg^{-1}$dry soil, 0-5cm)

Grassland type		Dominant species	Date of sampling		Total-P	Inorganic-P	Available-P (Truog-P)
Sown grasslands	(A)	Perennial ryegrass	May	1997	1638	1297	114
			October	1997	861	484	41
	(B)	Kentucky bluegrass	May	1997	1139	983	117
Semi-natural grasslands	(C)	Japanese lawngrass	May	1997	302	100	2
			August	1997	336	116	1>
	(D)	Azumanezasa	June	1997	419	144	1>
			August	1997	432	144	1>
	(E)	Silvergrass	June	1997	323	86	1>
			September	1997	271	65	1

Table 2. Phosphorus concentration of sown and semi-natural grasslands; typical data of 4 years during 1997 and 2000 ($gPkg^{-1}$ in dry matter)

Common name (Japanese)	Common name (English)	Scientific name	May	Jun	Sep	Nov	Mean
Perennial ryegrass-dominant grassland (A)							
Hosomugi	Perennial ryegrass	*Lolium perenne* L.	2.69			2.78	2.74
Shirotsumekusa	White clover	*Trifolium repens* L.				3.75	3.75
Kentucky bluegrass-dominant grassland (B)							
Nagahagusa	Kentucky bluegrass	*Poa pratensis* L.	2.50			3.82	3.16
Japanese lawngrass dominant grassland (C)							
Shiba	Japanese lawngrass	*Zoysia japonica* Steud.	1.66	1.24	1.26	1.50	1.42
Chigaya	Needlegrass	*Imperata cylindrica* (L) Beauv. var. *koenigii* (Retz.) Durand et Schinz.		0.97		0.52	0.75
Yotsubamugura	Bedstrow	*Galium trachyspermum* A. Gray		0.79			0.79
Himekugu	Green kyllinga	*Cyperus brevifolius* (Rottb.) Hassk. var. *leiolepis* (Fr.et Sav.)T. Koyama			0.95		0.95
Susuki	Silvergrass	*Miscanthus sinensis* Anderss.		0.99	1.19	0.95	1.04
Noazami	Common thistle	*Cirsium japonicum* DC.				1.06	1.06
Shibasuge	Sedge	*Carex nervata* Franch. et Savat.	1.23	0.96	1.03	1.14	1.09
Mitsubatsuchiguri	Cinquefoil	*Potentilla freyniana* Bomm.	1.46		0.79		1.13
Oniushinokegusa	Tall fescue	*Festuca arundinacea* Schreb.		0.90	1.43		1.17
Suzumenoyari	Wood rush	*Luzula capitata* (Miq.) Miq.	1.05	0.93	1.53		1.17
Nekohagi	Bush-clover	*Lespedeza pilosa* (Thunb.) Sieb. et Zucc.		0.99	1.27	1.25	1.17
Nagahagusa	Kentucky bluegrass	*Poa pratensis* L.	1.25	1.04	1.37		1.22
Medohagi	Sericea lespedeza	*Lespedeza cuneata* (Du Mont. Cours.) G. Don		0.99	1.41	1.30	1.23
Chikarashiba	Fountain grass	*Pennisetum alopecuroides* (L.) Spreng.			1.25		1.25
Yahazusou	Common lespedeza	*Lespedeza striata* (Thunb.) Schindler		1.26			1.26
Miyakogusa	Birdsfoot trefoil	*Lotus corniculatus* L. var. *japonicus* Regel	1.40	1.02	1.38	1.28	1.27
Himeyaburan	Lily-turf	*Liriope minor* (Maxim.) Makino	1.76	0.81			1.29
Suzumenohie	Knotgrass	*Paspalum thunbergii* Kunth	2.06	1.23	1.03	0.88	1.30
Harugaya	Sweet vernalgrass	*Anthoxanthum odoratum* L.	1.16	1.11	1.41	1.65	1.33
Orandamiminagusa	Sticky mouse-ear	*Cerastium glomeratum* Thuill.	1.41				1.41
Yamanukabo	Bentgrass	*Agrostis clavata* Trin.	1.45				1.45
Himehagi	Polygala	*Polygala japonica* Houtt.		1.62		1.28	1.45
Sumire	Violet	*Viola mandshurica* W. Becker		1.35	1.89		1.62
Oochidome	Water-pennywort	*Hydrocotyle ramiflora* Maxim.	1.80		2.17	2.20	1.80
Konasubi	Loosatrife	*Lysimachia japonica* Thunb.			2.04		2.04
Takanekoubou	Vernalgrass	*Anthoxanthum japonicum* Maxim. Hack.	2.04			2.04	2.04
Miminagusa	Mouse-ear	*Cerastium holosteoides* Fries var. *angustifolium* (Franch) Mizushima			2.08		2.08
Fuyunohanawarabi	American temate grape fer	*Botrychium tematum* Swartz		0.84	3.03	3.71	2.53
Hanayasuri	Stalked adders tongue	*Ophioglossum petiolatum* Hook.			3.38		3.38
Azumanezasa-dominant grassland (D)							
Azumanezasa	**Azumanezasa**	*Pleioblastus chino* (Franch. et Savat.) Makino		0.56	0.42		0.49
Silvergrass dominant grassland (E)							
Susuki	**Silvergrass**	*Miscanthus sinensis* Anderss.	1.30	1.54	0.59	0.28	0.93
Yamahagi	Bicolor lespedeza	*Lespedeza bicolor* Turcz.				0.28	0.28
Sarutoriibara	Greenbrier	*Smilax china* L.	0.63				0.63
Himeyaburan	Lily-turf	*Liriope minor* (Maxim.) Makino	0.63				0.63
Merikenkarugaya	Broomsedge	*Andropogon virginicus* L.		0.98	0.44		0.71
Gamazumi	Viburnum	*Viburnum dilatatum* Thunb.			0.72		0.72
Yahazusou	Common lespedeza	*Lespedeza striata* (Thunb.) Schindler			0.74		0.74
Todashiba		*Arundinella hirta* (Thunb.) C. Tanaka	1.26	0.92	0.48	0.32	0.75
Hekusokazura	Skunk vine	*Paederia scandens* (Lour.) Merrill var. mairei (Leveille) Hara	1.31		0.25		0.78
Mitsumatsuchiguri	Cinquefoil	*Potentilla freyniana* Bornm.	0.64	0.89	1.02	0.77	0.83
Kuzu	Kudzu	*Pueraria lobata* (Willd.) Ohwi	0.85	1.19	0.80	0.75	0.90
Yomogi	Mugwort	*Artemisia princeps* Pampan.	0.97		1.03		1.00
Medohagi	Sericea lespedeza	*Lespedeza cuneata* (Du Mont.d.Cours.) G. Don		1.09			1.09
Yamanukabo	Bentgrass	*Agrostis clavata* Trin.			1.20		1.20
Harujion	Common fleabane	*Erigeron philadelphicus* L.	1.28				1.28
Oochidome	Water-pennywort	*Hydrocotyle ramiflora* Maxim.	1.29				1.29
Nokongiku	Starwort	*Aster ageratoides* Turcz. var. *ovatus* (Franch.et Savat.)Nakai	1.29				1.29
Harugaya	Sweet vernalgrass	*Anthoxanthum odoratum* L.	1.31	1.27			1.29
Kijimusiro	Cinquefoil	*Potentilla fragarioides* L. var. major Maxim.	1.33				1.33
Nohara-azami	Common thistle	*Cirsium tanakae* (Franch. et Savat.) Matsum.		1.33			1.33
Sumire	Violet	*Viola mandshurica* W. Becker		1.20	1.48		1.34
Tachisubosumire	Violet	*Viola grypoceras* A. Gray	2.08		1.12	1.00	1.40
Matsuyoigusa	Evening primrose	*Oenothera striata* Ledeb. ex Link			2.64		2.64

species. Semi-natural grassland (C) (Japanese lawngrass-dominant grassland) had 29 species, showing an average of 14.6 mgPkg^{-1} in concentration, and a standard deviation of 0.054, while semi-natural grassland (E) (silvergrass-dominant grassland) had 24 species, 10.6 mgPkg^{-1} average concentrations, and a standard deviation of 0.045. Semi-natural grassland D (azumanezasa-dominant grassland) had 1 species, which showed 4.9 mgPkg^{-1}.

2. Accumulation of phosphorus in shoots compared with soil phosphorus

Table 3 shows aboveground biomass, which means dry-matter accumulation in aboveground parts, phosphorus concentration and accumulation of aboveground plant parts including dead shoots, and available soil phosphorus (Truog-P) of sown grassland (A), semi-natural grasslands (C), (D) and (E). These data were taken at the maximum growth stage of the grasslands; Sown grassland (A) (perennial ryegrass) in May, semi-natural grassland (C) (Japanese lawngrass), (D) (azumanezasa), and (E) (silvergrass) in August. Dry-matter accumulation in aboveground shoots were highest in the semi-natural grassland (D) (azumanezasa-dominant grassland), and semi-natural grassland (E) (silvergrass-dominant grassland) showed the second highest. The shoot phosphorus concentration of semi-natural grassland (D) (azumanezasa- dominant grassland) was as low as 0.5 gPkg^{-1}. Because of the high level of dry-matter accumulation, however, the amount of phosphorus accumulation per square meter was at the same level as that of sown grassland (A) that received fertilizer application. Semi-natural grassland (E) showed considerably low phosphorus concentration at 1 gPkg^{-1} but because the same amount of dry matter was accumulated in aboveground shoots, phosphorus accumulation apparent here was approximately one half of that in sown grassland (A). Semi-natural grassland (C) showed the same tendency, at approximately 1/7 of phosphorus accumulation in aboveground shoots compared with sown grassland (A).

Soil phosphorus fertility (Truog-P) was almost equally low among these semi-natural grasslands at 1 mgPkgsoil^{-1}, while sown grassland (A) was 114 mgPkgsoil^{-1}.

The results suggest that the semi-natural grasses may take up a considerable amount of phosphorus even under very low phosphorus fertility conditions. In particular, azumanezasa- and silvergrass-dominant grassland can maintain high shoot biomass equal to or

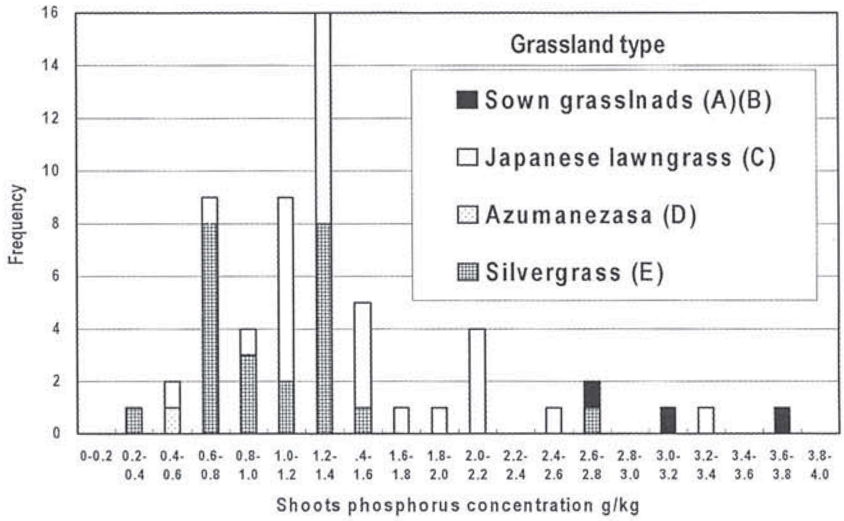

Fig. 1. Frequency distribution of phosphorus concentration of plants collected from each grassland

Table 3. Phosphorus accumulation of the shoots and soil available P at the maximum growth stage (Mean value in 1997 and 1998)

Type of dominant grass	Shoots weight* DM gm^{-2}	P concentration gPkg^{-1} in DM	P accumulation gPm^{-2} shoots	Truog-P mgPkg^{-1}
Perennial ryegrass (A)	667	2.7	1.80	114
Japanese lawngrass (C)	171	1.4	0.24	1>
Azumanezasa (D)	3740	0.5	1.87	1>
Silvergrass (E)	750	1.0	0.75	1>

* upper ground parts including dead shoots

greater than that of fertilized sown grassland. This fact suggests also that the high efficiency of phosphorus utilization in dry-matter production may be a primary factor in their adaptation to low phosphorus fertility.

3. Characteristics in the phosphorus dynamics in semi-natural grassland

In semi-natural grasslands (C) and (E), phosphorus accumulation in the aboveground shoots and underground parts was analyzed from the viewpoint of their seasonal changes (Fig. 2). The aboveground shoots included live shoots, dead shoots, seeds, and other shoots including dead stands. The underground part included roots and subterranean stems. The phosphorus accumulation of shoots increased from spring through summer in both grasslands, and decreased until fall in (E) but did not decrease in (C). This decrease may be partly due to seed scattering, but considering the seed weight, it cannot be explained by that alone, even though the phosphorus concentration of the seed was high. Phosphorus accumulation of dead shoots in (C) changed slightly during the season, but semi-natural grassland (E) showed a considerable decrease from March to July, and a slight increase from July to September. Phosphorus accumulation in the underground parts indicated a difference between the two semi-natural grasslands. That of (C) increased slightly from March to November; as much as 0.13 gm^{-2}, while a major decrease from March to July, as much as 0.81 gm^{-2}, and recovery in November were observed in (E).

Table 4 shows the seasonal changes of soil phosphorus between the semi-natural grasslands, (C) and (E). Truog-P and Olsen-P were analyzed as available P since they were considered to be good indexes for the amounts of phosphorus uptake by plants (Kondo *et al.*[8]), Olsen *et al.*[10]). In the silvergrass grassland (E), total-P, inorganic-P, Truog-P and Olsen-P showed no significant seasonal change. A significant seasonal change in available P was observed in the Japanese lawngrass grassland (C), where it was low in April and increased after July. The reason total-P and inorganic-P were high only in April in Japanese lawngrass (C) is not known. Figure 3 shows the amount of phosphorus accumulation of the shoots and available phosphorus (Olsen-P) in the soil, expressed as mg/m^2, for both grasslands. In Japanese lawngrass-dominant grassland (C), both the seasonal change in shoots and in available P showed a strong correlation, particularly in the increase from March to June, while no such relationship was found in grassland (E): silvergrass-dominant grassland.

4. Model calculation of phosphorus dynamics in semi-natural grasslands

A phosphorus dynamics model between plant and soil was constructed through the following procedures (Fig. 4). Assuming that the amount of phosphorus at i-th sampling time, with P_i representing shoots, and D_i representing dead shoots and litter parts, phosphorus amounts at i+1th sampling time can be expressed as

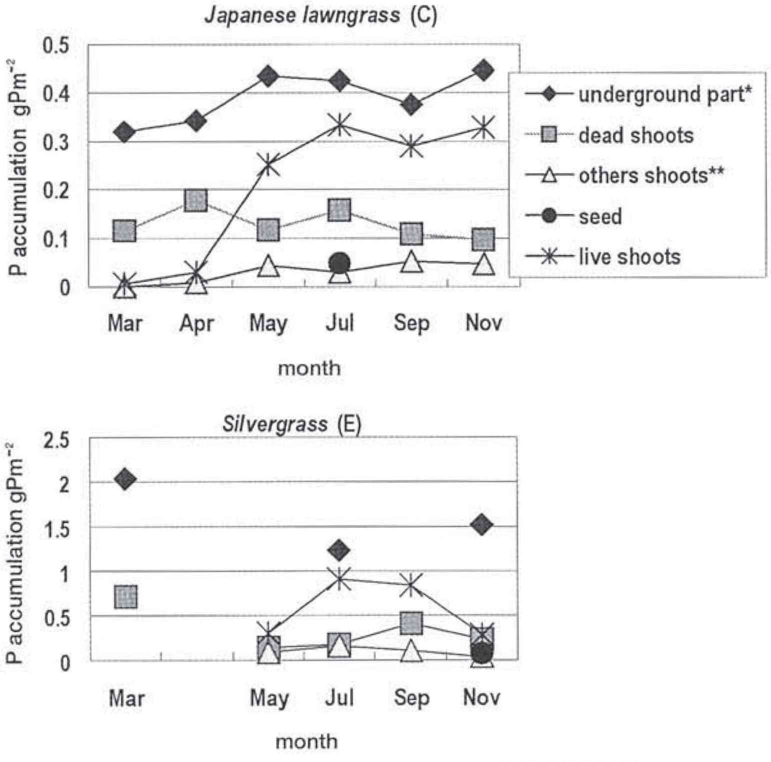

Fig. 2. Seasonal changes in P accumulation in semi-natural grasslands.
(*: Roots and subterranean stem, **: Live shoots except the dominant grass)

Table 4. Seasonal changes in soil P of semi-natural grasslands (1998) ($mgPkg^{-1}$dry soil)

Dominant species	Month	Soil depth cm	Total-P	Inorganic-P	Truog-P	Olsen-P
Japanese lawngrass (C)	April	0-2.5	2176	1714	4	7.4
		2.5-5.0	1645	1407	3	4.9
		5.0-10.0	1389	1218	3	3.9
	July	0-2.5	1034	743	9	17.2
		2.5-5.0	700	456	7	12.3
		5.0-10.0	521	306	5	7.9
	September	0-2.5	-*	-*	22	14.7
		2.5-5.0	-*	-*	18	10.4
		5.0-10.0	-*	-*	10	7.5
	November	0-2.5	1023	737	23	21.5
		2.5-5.0	757	501	16	15.1
		5.0-10.0	497	291	7	8.0
Silvergrass (E)	April	0-2.5	566	428	4	9.3
		2.5-5.0	556	418	4	9.0
		5.0-10.0	577	434	4	7.6
	July	0-2.5	567	410	5	7.9
		2.5-5.0	580	448	5	7.8
		5.0-10.0	559	417	5	-*
	November	0-2.5	521	371	5	8.0
		2.5-5.0	533	391	4	6.7
		5.0-10.0	488	346	4	5.9

* : no data

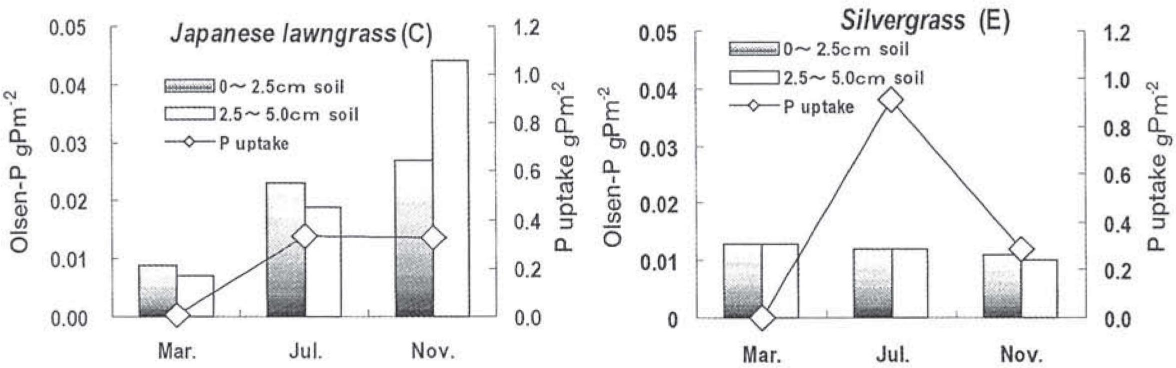

Fig. 3. Seasonal changes in accumulation of P in aboveground part and soil available P

follows;

$$P_{i+1} = P_i + \Delta p_1 - \Delta d - \Delta p_2 \qquad \text{Eq. (1)}$$

$$D_{i+1} = D_i + \Delta d - \Delta x \qquad \text{Eq. (2)}$$

where Δp_1 is the translocation of phosphorus up to plant shoots from the roots, Δp_2 is the phosphorus flow from the shoots down to roots, Δd is that from shoots to dead shoots and litter, and Δx is that from dead shoots or litter to soil. From Eqs. (1) and (2), phosphorus translocation during the period of day i and day i+1 can be expressed as;

$$\Delta p_1 = (P+D)_{i+1} - (P+D)_i + \Delta x + \Delta p_2 \qquad \text{Eq. (3)}$$

Equation (3) shows that Δp_1 and Δd can be calculated by estimating Δx and Δp_2. In this experiment, it is assumed that the value of Δx and Δd is equal.

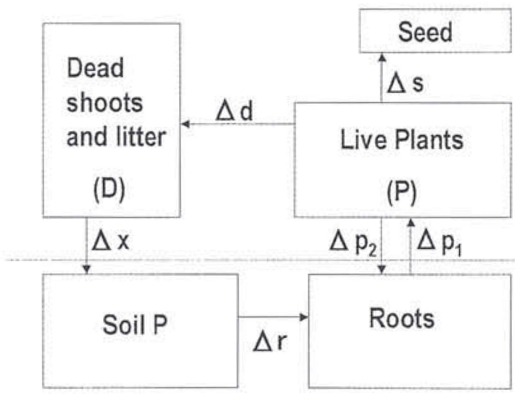

Fig. 4. Model of phosphorus dynamics in semi-native grassland

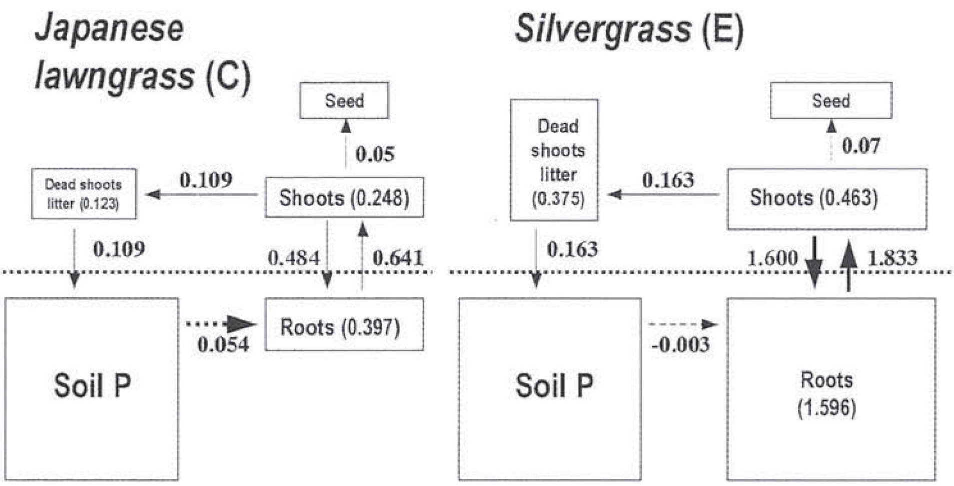

Fig. 5. Phosphorus dynamics in two types of semi-natural grasslands, $gPm^{-2}year^{-1}$ ( ) shows mean annual P accumulation gPm^{-2}

Phosphorus concentrations of living shoots, dead stand and litter parts were extremely different. Due to the insufficient amount of dry matter in dead stand, it is difficult to verify that the phosphorus which translocated to dead stand and litter parts from living shoots Δd was diluted by the lower concentration in dead shoots and litter parts. Sosebee *et al.*[12] showed the translocation route from shoots to roots during dead stand formation through the ^{32}P experiment, where the amount of translocation is proportionate to the difference between the amount of living shoots and dead standing dry matter (Sosebee *et al.*[12], Tanaka[13]).

Considering this information, it is possible to establish the following relationship;

$$\Delta p_2 = (Pc_1 - Pc_2)^* \Delta D \qquad \text{Eq. (4)}$$

where Pc_1 means phosphorus concentration of living shoots, Pc_2 means the concentration of dead shoots, and ΔD means the amount of dry matter translocated during a certain period (Kondo *et al.*[8], Cole *et al.*[1]). That is, the amount of phosphorus translocation from the aboveground part to underground part is assumed to be equal to the amount calculated from the difference in phosphorus concentration among living shoots and dead shoots, and dry matter weight difference in certain period. On the other hand, the amount of P translocated from soil-P to roots can be expressed as

$$\Delta r = (\text{Avail P})_{i+1} - (\text{Avail P})_i \qquad \text{Eq. (5)}$$

where the amount of available soil phosphorus $(\text{Avail P})_i$ at i-th sampling time, available phosphorus amounts at i+1th sampling time can be expressed as $(\text{Avail P})_{i+1}$. However, the amount is just an estimate at present, and requires further precise investigation concerning each component of soil phosphorus in order to clarify the amount of phosphorus translocation between them. In this paper, therefore, the amount is expressed with dotted lines in Fig. 5, which is described here:

Using the model described above, phosphorus dynamics of semi-natural grassland (C) and (E) was estimated (Fig. 5). The amount of phosphorus translocated from roots to shoots was high in silvergrass-dominant grassland (E). But the amount of phosphorus accumulation in dead shoots and seeds was not as much as in Japanese lawngrass-dominant grassland (C). This suggests that a considerable amount of phosphorus is re-translocated to the roots in this grassland. The amount of uptake from the soil to shoots may be negligible if the translocation appears as a change in Olsen-P. In other words, phosphorus in grassland (E) was cycled between living shoots and underground parts. The same tendency can be seen in azumanezasa grassland (D), which can produce high amounts of dry matter even with conditions of very low phosphorus soil fertility and very small amounts of phosphorus provided by the soil. This suggests that these two semi-natural grasses grow depending on the phosphorus cycle between the shoots and underground parts.

In Japanese lawngrass-dominated grassland (C), the amount of phosphorus accumulation of shoots was 54% of that in the silvergrass-dominated grassland (E). The amount of phosphorus translocation to dead shoots and litter from living shoots of this grassland, however, was 67% of that in (E). However, compared with the ratio of phosphorus accumulation in aboveground shoots in these grasslands, the translocation from living tissue to dead in the grassland (C) is fairly large. In the grassland (C), available phosphorus in the surface layer of the soil accumulated during the growing season (Fig. 3), and the phosphorus uptake from the soil to the root was observed (Figs. 3 and 5). This suggests that soil phosphorus significantly contributes to the phosphorus dynamics of the Japanese lawngrass in contrast to the silvergrass grassland. This result is consistent with the report by Kondo *et al.*[7], which showed the high activity of nutrient absorption by the root at the surface layer of the grassland.

In the silvergrass-dominated grassland (E), a large phosphorus accumulation in underground parts was characteristic, and there was little translocation from soil phosphorus to roots. This suggests that the soil phosphorus pool is insignificant in the phosphorus dynamics of the grassland, in contrast to the Japanese lawngrass-dominated grassland (C). That is, the phosphorus cycle of the grassland is considered to be significantly dependant on the phosphorus translocation between the aboveground parts (shoots, dead shoots and litter) and the underground parts (roots) in the silvergrass-dominant grassland (E).

Conclusion

1. Semi-natural grassland such as Japanese lawngrass-dominant grassland (C), azumanezasa-dominant grassland (D) and silvergrass-dominant grassland (E) are able to maintain considerably high grass production even under very low phosphorus fertility conditions.
2. Phosphorus concentrations of 49 species of sown or natural plant species were determined.
3. Two general types of phosphorus dynamics in semi-natural grasslands are recognized; 1) Japanese lawngrass-type grassland, which is significantly assisted by available phosphorus in the surface soil layer and phosphorus accumulated in living shoots, dead shoots, litter and roots, and 2) silvergrass-type grassland, which is significantly dependant on the phosphorus translocation between the aboveground and underground parts of the plants other than soil parts.

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半野草地のリン循環

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摘　要

一般に，土壌中に有効態リンがほとんどない条件においても，野草地は成立し，比較的高い乾物生産を維持していることから，野草は低養分条件において養分を効率よく利用するシステムを持っていると考えられる。本研究では，野草地の低肥沃度条件でも成立する機構を明らかにする目的で，2種類の牧草地および3種類の半自然草地におけるリン循環の特徴を調査した。

1．ペレニアルライブグラスならびにケンタッキーブルーグラス主体の2種類の牧草地，および，シバ，アズマネザサ，ススキ主体の3種類の半自然草地における牧草を含む49種の野草のリン含有率の季節変化を明らかにした。

2．地上部リン吸収量は，施肥条件下にある牧草地と比較して無施肥のアズマネザサ型草地ではほぼ同程度，ススキ型草地では半量，シバ型草地では1/7量であった。

3．土壌中の有効態リンが著しく低い条件においても，野草は相当な乾物量を維持していた。とりわけ，アズマネザサ型草地やススキ型草地では，植物体リン濃度がかなり低いにもかかわらず，施肥を行っている牧草地と同等か，それ以上の乾物量を維持していた。このことから，植物体の乾物生産におけるリン利用性の高さが，野草の持つ低リン酸耐性機構の一つと考えられた。

4．休牧条件におけるシバ型草地とススキ型草地の年間リン循環量は次のような特徴を示した。すなわちシバ草地では土壌から根へのリンの移行が認められ，土壌リンが根を経由して地上部に移行すると解釈でき，リンの循環に土壌リンが強く寄与すると考えられた。これに対しススキ草地（E）では地上部とともに根部にも大きなリン現存量が認められる一方で土壌リンへの依存度はシバほど高くない。すなわち，ススキ草地では地上部（shoots, dead shoots, litter）と根部間におけるリンのやりとりがリン循環の主体を担っていると解釈できる。

5．このように，野草のリン循環にはシバ型草地とススキ型草地のふたつのタイプがあると推定した。前者では根部，枯死茎葉と土壌表層の有効態リンを利用するものであり，後者では地上部と地下部間のリンのやりとりに依存する。

キーワード：野草，リン循環，シバ，ススキ，オルセン-P