

Phosphorus Cycle in Three Herb Plant Populations in the Basin of Mt. Geumoh

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金烏山 盆地의 三種 草本植物 個體群의 磷의 循環

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ABSTRACT

The seasonal pattern and the annual magnitude of the internal (or biochemical) and plant-soil cycles of phosphorus in adjacent three different herb plant populations—*Helianthus tuberosus* L., *Artemisia princeps* Pampan and *Phalaris arundinacea* L.—in an old field of the basin in the Mt. Geumoh were investigated. A lot of the phosphorus demand for the three populations was supplied by the withdrawal from below-ground organ in early growing period, by the absorption from soil in mid-growing period and by the withdrawal from stem in later growing period. But in the *A. princeps* and *P. arundinacea* populations, a great deal of phosphorus seemed to be absorbed prior to the first withdrawal. The annual amount of the phosphorus flowing through the internal cycle was about 59% of the total phosphorus flow on the organ level in the *H. tuberosus* population, 41% in the *A. princeps* population and 32% in the *P. arundinacea* population, indicating that the tuber plant had the most developed internal cycle system. The annual amount of phosphorus which took part in the plant-soil cycle in the stand of the three populations was in the range of 4.49–5.65 gP m⁻², corresponding to only 3–8% of the extractable phosphorus contained in the soil of 0–20 cm depth. The fact that the *H. tuberosus* population is higher in the extent of internal cycle but smaller in the magnitude of plant-soil cycle and lower in the turnover rate of phosphorus than the other two populations suggests that the growth of *H. tuberosus* population may be less dependent on soil phosphorus availability than those of the other two populations.

INTRODUCTION

Since the Switzer and Nelson's proposal (1972) of three cycles, such as biochemical cycle including nutrient redistribution within a stand, biogeochemical cycle between soil, standing crop and litter subsystems, and geochemical cycle incorporating the relation between input to and output from an ecosystem, much attention has been paid to the scale and significance of the biochemical cycle in the nutrition of plant communities. In the case of phosphorus cycle, Hirose (1972) found that 39% of annual demand was supplied by biochemical cycle in a

Solidago altissima population and Attiwill (1980) confirmed that 46% of it was supplied by the biochemical cycle in a mature *Eucalyptus obliqua* population. Moreover, it has been suggested that the biochemical cycle acts as an important strategy of increasing the utilization efficiency of a limiting resource (Westman, 1978; Luxmoore et al., 1981) and an important factor in the formation of a conservative, efficient and comparatively self-regulated nutrient cycle (Gray, 1983).

We reported that the annual phosphorus inflows, i.e., annual phosphorus demands, in the populations of *Helianthus tuberosus* L., *Artemisia princeps* Pampan and *Phalaris arundinacea* L. in an old field at the basin of the Mt. Geumoh were 1.35, 9.63 and 7.60 gP m⁻² respectively and that the *H. tuberosus* population with the smallest relative growth rate (RGR) among the three populations was largest in efficiency of phosphorus utility (EPU) among them (Lyu and Song, 1986). In this study, the attention was on seasonal patterns of the phosphorus withdrawal and annual scales of the biochemical cycles, i.e., internal cycles, and plant-soil cycles of phosphorus in the three populations.

MATERIALS AND METHODS

Flow of biomass and phosphorus. The data on biomass and phosphorus quantities in the previous paper (Lyu and Song, 1986) were used for the analysis and determination of the withdrawal, flow rate and allocation of the matters in the three herb plant populations. When a standing crop of matter in a whole plant population or an organ is regarded as a matter pool on the level of the population or organ, the increase or decrease of the pool will be brought about by the balance between the inflow and the outflow of the matter. The inflow and outflow on the organ level represent the sum of the inflow to and outflow from each organ, respectively.

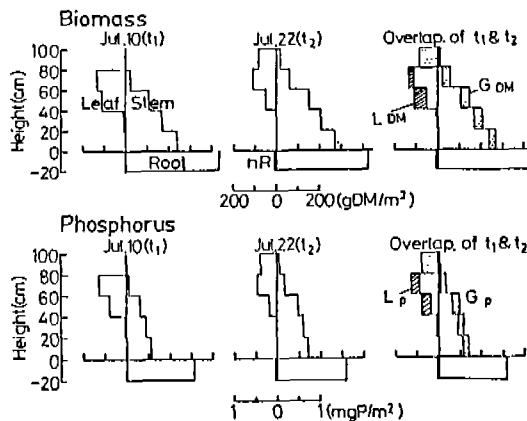


Fig. 1. Model explanations of two successive vertical distributions of biomass and phosphorus in a plant population. L and G represent outflow and inflow of matters on the organ level respectively in a time interval, t1 and t2.

These were determined by overlapping two successive vertical distribution diagrams(Hirose, 1971)(Fig. 1). The inflow on the population level represents the net production in biomass and absorption in phosphorus. The outflow on the population level means the loss of matters by death or shedding. These values were obtained by subtracting the withdrawal from the flow on the organ level.

Biomass withdrawal. The amount of biomass withdrawn from dying leaf in a time interval(W_{DM}) was determined by following equation (Hirose, 1974);

$$W_{DM} = L_{DM} \frac{lw - dw}{lw}$$

where L_{DM} represents the outflow of biomass on the organ level (Fig. 1), lw and dw indicate the dry weight of live and dead leaves respectively on the basis of the same leaf area. The ratio of biomass withdrawal to the standing crop in stem was assumed to be equal to that of leaf. The decrease in the biomass of below-ground organ during the first half of the growing period was assumed to occur mostly by translocation.

Phosphorus withdrawal. The amount of phosphorus withdrawal (W_p) in an organ during a time interval was determined by following equations;

$$D_p = L_{DM} \times C \times T$$

$$W_p = L_p - D_p$$

where D_p represents the loss of phosphorus by death; L_{DM} and L_p , the outflows on the organ level of biomass and phosphorus respectively during a time interval (Fig. 1); C , the mean content of phosphorus in each organ during a time interval; T , the proportion of phosphorus content in dead organ to that in the same live one. The decrease in phosphorus of storage organ was assumed to occur by translocation.

RESULTS

Biomass flow and withdrawal. In the *H. tuberosus* population, the maximum inflow rate on the organ level was $141 \text{ gDM m}^{-2} \text{ wk}^{-1}$ in June (Fig. 2, left). The maximum inflow rate resulted from the vigorous withdrawal from tuber in early growing period. A vigorous withdrawal occurred also in stem in late growing period. The maximum inflow rates on the organ level in the *A. princeps* and *P. arundinacea* populations were 154 and $204 \text{ gDM m}^{-2} \text{ wk}^{-1}$ in July, respectively. The withdrawal rates in the two populations were much smaller than that in the *H. tuberosus* population all through the growing period.

Phosphorus flow and withdrawal. In the *H. tuberosus* population, two peaks in the phosphorus inflow rate on the organ level, i.e., $0.71 \text{ gP m}^{-2} \text{ wk}^{-1}$ in June and $0.59 \text{ gP m}^{-2} \text{ wk}^{-1}$ in late growing period, were noticed (Fig. 2, right). The first peak resulted mainly from the vigorous

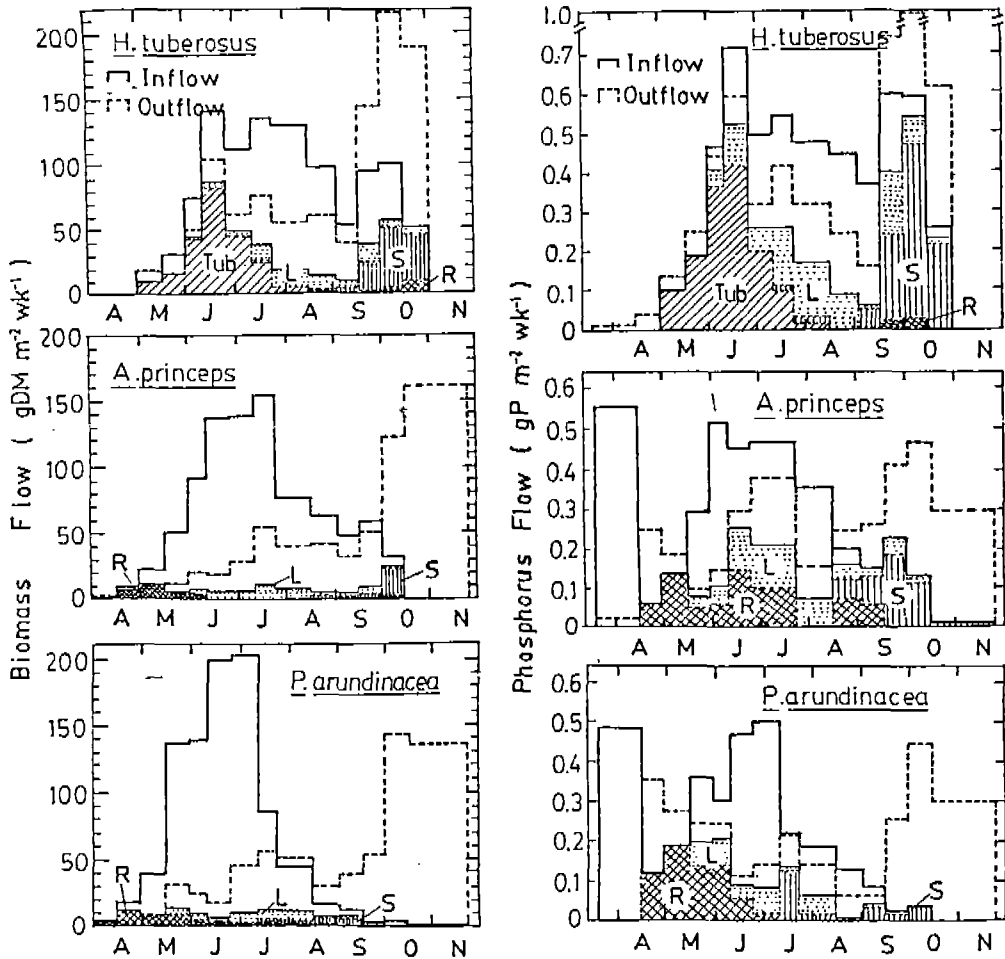


Fig. 2. Seasonal changes of flow rates of biomass(left) and phosphorus(right) in three populations, Mt. Geumoh. Tub, L, S and R represent the matter withdrawals from tuber, leaf, stem and below-ground part, respectively.

phosphorus withdrawal from tuber, while the second peak from the withdrawal from stem. The seasonal pattern of phosphorus inflow rate in the *A. princeps* population also showed two peaks, i.e., $0.55 \text{ gP m}^{-2} \text{ wk}^{-1}$ in early spring and $0.51 \text{ gP m}^{-2} \text{ wk}^{-1}$ in June. The first peak resulted from the abrupt phosphorus absorption from soil just after the soil thaw, and the second peak from the absorption and withdrawal. Most of the phosphorus withdrawn was derived mainly from below-ground part in the first half of the growing period, from leaf in mid-growing period and from stem in the late growing period. The seasonal patterns of phosphorus inflow and withdrawal rates in the *P. arundinacea* population were similar to those of the *A. princeps* population, showing two peaks in inflow rate, i.e., $0.48 \text{ gP m}^{-2} \text{ wk}^{-1}$ in early spring and $0.50 \text{ gP m}^{-2} \text{ wk}^{-1}$ in early July.

Allocation of biomass and phosphorus. The three populations were different in seasonal biomass allocation patterns. That is, the *H. tuberosus* population allocated much portion of biomass to below-ground part at the initial growing time, to above-ground part next and to tuber finally, while the other two populations showed the typical allocation pattern of perennial herb plants, allocating much portion of biomass to leaf at the first, to stem next and to below-ground part finally through the growing period (Fig. 3, left). The seasonal pattern of phosphorus allocation was similar to that of biomass allocation in three populations except for the allocation of most of the phosphorus to below-ground part just after the soil thaw in the *A. princeps* and *P. arundinacea* populations (Fig. 3, right).

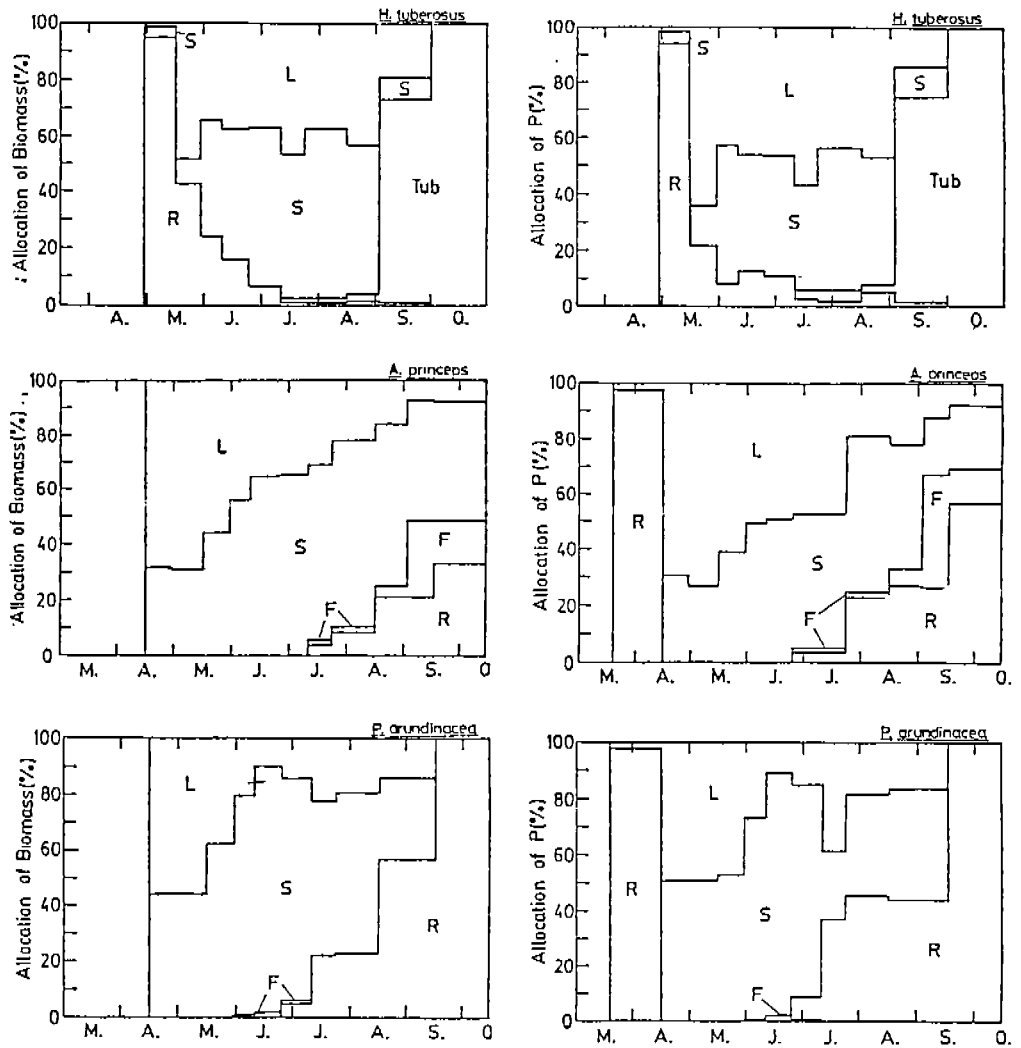


Fig. 3. Seasonal changes of biomass and phosphorus allocations to each organ in three populations, Mt. Geumoh. L, S, R, Tub and F represent leaf, stem, below-ground part, tuber and reproductive organ, respectively.

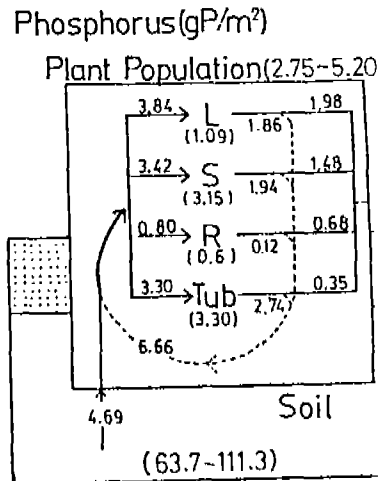
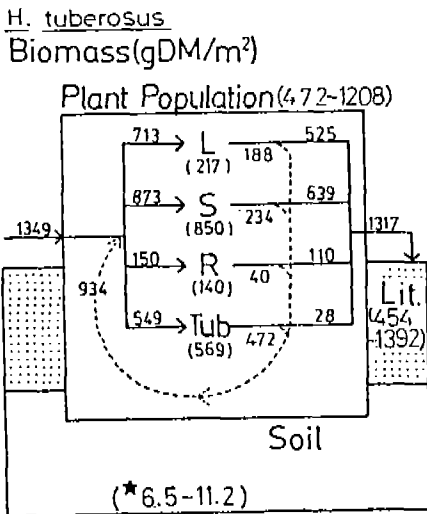
On the other hand, the annual phosphorus allocation to below-ground part was 32.5 and 35.8% of the annual phosphorus inflow respectively in the *A. princeps* and *P. arundinacea* populations, while the value was only 7.6 and 7.5% respectively in the annual biomass

Table 1. Percentages of annual allocation of biomass and phosphorus(P) to each organ in three populations, Mt. Geumoh

	<i>H. tuberosus</i>		<i>A. princeps</i>		<i>P. arundinacea</i>	
	Biomass	P	Biomass	P	Biomass	P
Leaf	31.1	33.8	30.4	30.6	21.2	20.0
Stem	38.2	30.1	58.2	33.9	70.7	43.8
Root & Rhizome	6.6	7.0	7.6	32.5	7.5	35.8
Tuber	24.1	29.1				
Reproductive organ			3.8	3.0	0.6	0.4
Total	100	100	100	100	100	100

allocation (Table 1). The difference between biomass and phosphorus in annual allocation to below-ground part in the *H. tuberosus* population was not so much large as that in the *A. princeps* and *P. arundinacea* populations.

Plant-soil cycle and internal cycle. The amount of annual inflow, outflow, allocation and withdrawal of biomass and phosphorus to each organ of the three populations were expressed in cycle schema (Fig. 4). The annual biomass flow on the population level, that is, the amount of biomass flowed through the population pool all through the growing period was 1302-1349, 1610-1632 and 1633-1693 gDM m⁻² respectively in the *H. tuberosus*, *A. princeps* and *P.*



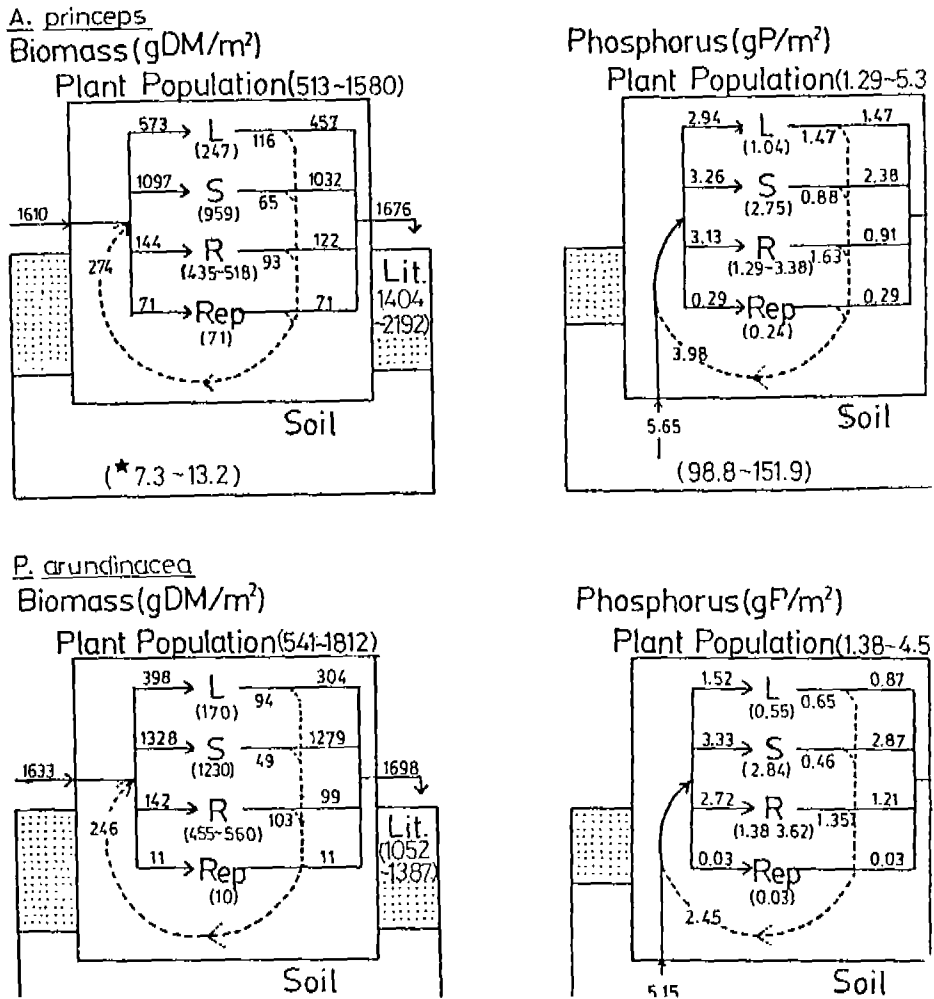


Fig. 4. Annual allocations to each organ, plant-soil cycles and internal cycles of biomass and phosphorus in the stand of three populations, Mt. Geumoh. The numerals in parentheses and on arrows represent the pool size and annual matter flows, respectively. The numerals with * represent the pool size of organic matter in kgC m⁻² in the 20cm soil depth. The dotted arrows indicate internal cycles. L, leaf; S, stem; R, root and rhizome; Tub, tuber; Rep, reproductive organ; Lit, litter.

arundinacea populations. And the fact that the differences between the inflow and outflow of biomass were not large indicates that the three populations were in quite stable state in terms of yearly variation of population pool size. The amount of annual biomass internal cycles in the *H. tuberosus*, *A. princeps* and *P. arundinacea* populations was 934, 274 and 246 gDM m⁻², accounting for 41, 15 and 14% of annual biomass demands, respectively.

On the other hand, the amount of annual phosphorus plant-soil cycles in the *H. tuberosus*, *A. princeps* and *P. arundinacea* populations was 4.49-4.69, 5.05-5.65 and 4.98-5.15 gP m⁻², respec-

tively, which corresponded to only 3-8% of the extractable phosphorus contained in 0-20 cm soil depth. The amount of annual phosphorus internal cycles in the *H. tuberosus*, *A. princeps* and *P. arundinacea* populations was 6.63, 3.98 and 2.45 gP m⁻², accounting for 59, 41 and 32% of annual phosphorus demands, respectively.

DISCUSSION

The turnover rate of biomass and phosphorus illustrated in Fig. 5 represents the ratio of the matter flow rate to the standing crop on the population level. In biomass, the three populations

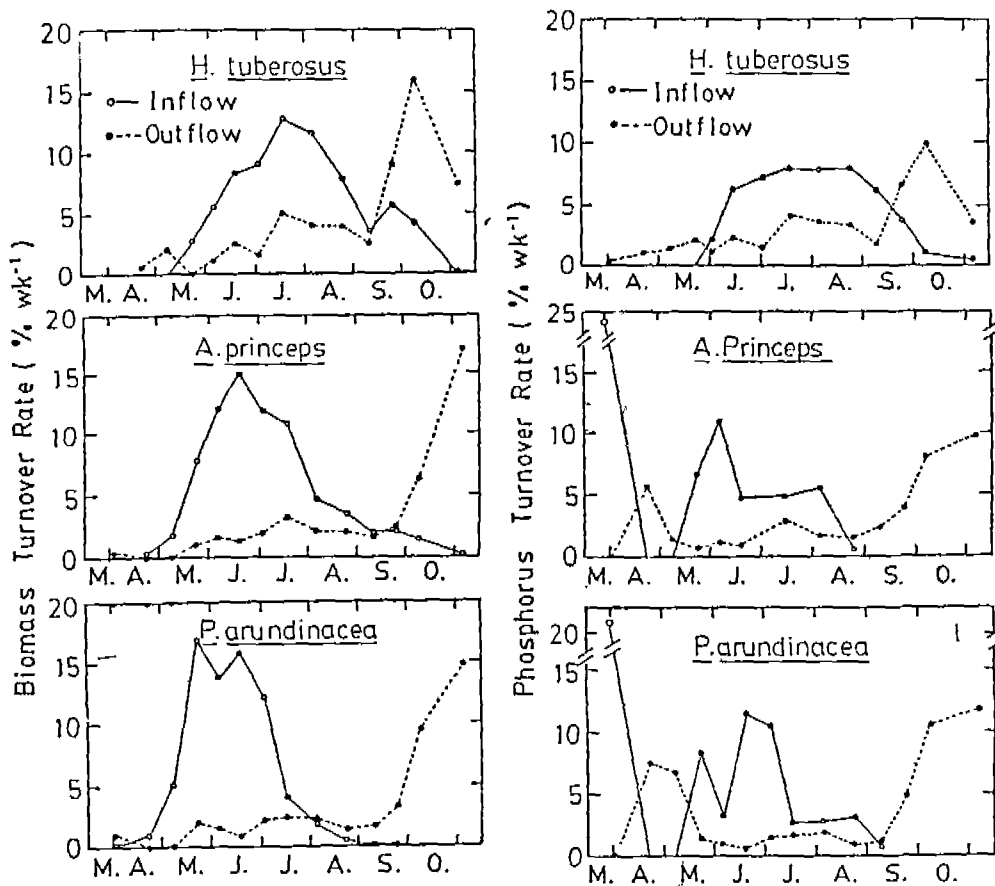


Fig. 5. Seasonal changes of turnover rate of biomass and phosphorus in three populations, Mt. Geumoh.

were similar to each other in the seasonal pattern of turnover rate, but different in the maximum turnover rate of inflow, showing 12.8, 15.2 and 17.0% wk⁻¹ in the populations of *H. tuberosus*, *A. princeps* and *P. arundinacea*, respectively.

In contrast to the case of biomass, the three populations were different in the seasonal pattern

of turnover rate of phosphorus, showing a bell shape in the turnover rate of inflow in the *H. tuberosus* population and large turnover rates of both inflow and outflow in early spring in the other two populations. The maximum turnover rate of inflow in the *H. tuberosus* population was $8.0\% \text{ wk}^{-1}$ in August, much smaller than those in the *A. princeps* ($23.1\% \text{ wk}^{-1}$) and *P. arundinacea* ($20.7\% \text{ wk}^{-1}$) populations.

On the other hand, the turnover rate of phosphorus inflow was smaller than that of biomass inflow during the mid-growing period in the three populations. But the turnover rates of phosphorus in- and outflows in early growing period were much larger than those of biomass in the *A. princeps* and *P. arundinacea* populations. Therefore, we could assume that the phosphorus activity of the three populations was lower than the biomass activity in the population metabolism during the mid-growing period, but the reverse was true in early spring in the *A. princeps* and *P. arundinacea* populations.

Several researchers have suggested that allocation strategies are species-specific (Katherine et al. 1979) and the plant with the greatest growth rate allocates the largest proportion of photosynthetically fixed carbon to additional photosynthetic tissues (Mooney, 1972; Johnson and Tieszen, 1976; Tieszen and Detling, 1983). But contrary to these suggestions, the *P. arundinacea* population with the largest RGR among the three populations allocated only 21.2% of the biomass inflow to photosynthetic organ all through the growing period, while the *H. tuberosus* population with the smallest RGR allocated 31% of biomass inflow to the organ (Lyu and Song, 1986) (Table 1). Therefore, it is assumed that the difference in growth rate is dependent on the photosynthetic capacity of leaf rather than on the allocation strategy.

The significance of the internal cycle, i.e., withdrawal, in the aspect of adaptation to nutrient stress is not clear yet. Several researchers have suggested that plants use nutrients more effectively by developing their nutrient internal cycle systems (Luxmoore et al., 1981), and that the nutrient withdrawal from leaf decreased with increase of soil nutrient availability (Stachurski and Zimka, 1975; Turner, 1977; Shaver and Melillo, 1984). But the views of the others were contrary to the suggestions (Ostman and Weaver, 1982). Moreover, Chapin and Kedrowski (1983) found that the extent of phosphorus recovery from leaves was not significantly correlated with phosphorus status, suggesting a high extent of recovery was not an important adaptation to nutrient stress. However, the extent of internal cycle of phosphorus in the three populations tended to increase as the phosphorus absorption was inhibited (Lyu, 1985). In addition to this, the three populations developed in the stand of similar soil phosphorus availability were considerably different in the extent of internal cycle of phosphorus (Fig. 4). These results suggest that the internal cycle contributes to the adaptation of plant having nutrient stress by reinforcing the cycle to some extent, though the cycle may be practically species- or life form specific.

The three populations were much different in the seasonal pattern of the ratio of withdrawal to inflow of phosphorus (Fig. 6). A great portion of phosphorus supplied for the initial growth of each organ was derived from tuber in the *H. tuberosus* population, while a great portion of it

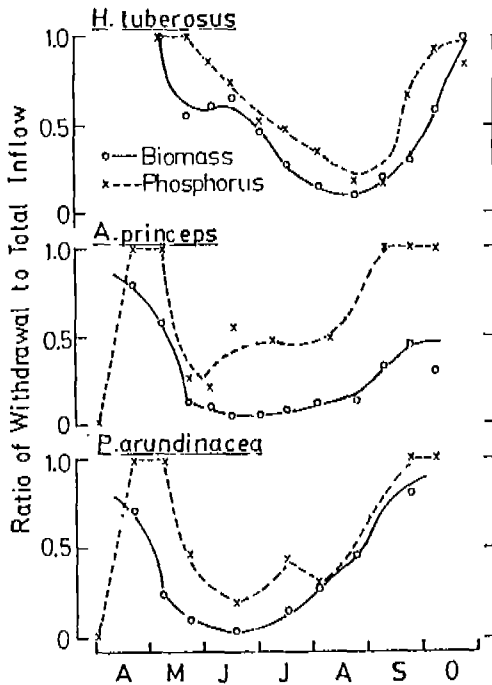


Fig. 6. Seasonal changes of withdrawal proportions to total inflow of biomass and phosphorus in three populations, Mt. Geumoh.

was derived from soil in early spring, prior to the withdrawal from below-ground part, in the other two populations. Therefore, according to the major way of supplying the phosphorus demand, we may divide into three stages through the growing period in the *H. tuberosus* population; withdrawal-absorption-withdrawal; and into four stages in the other two populations; absorption-withdrawal-absorption-withdrawal.

On the other hand, the fact that the *H. tuberosus* population is larger in the scale of the internal cycle and smaller in the scale of the plant-soil cycle and turnover rate of phosphorus as compared with the *A. princeps* and *P. arundinacea* populations suggests that the growth of *H. tuberosus* population may be less dependent on soil phosphorus availability than those of the other two populations.

摘 要

金鳥山盆地에 서로 인접하여 발달한 뚱단지(*Helianthus tuberosus* L.), 쑥(*Artemisia princeps* Pampan) 및 갈풀(*Phalaris arundinacea* L.) 個體群을 대상으로 磷의 内部轉流量的 계절변화와 植物-土壤間의 年間 磷의 循環량을 考察하였다.

三個體群의 生長初期에는 生長에 필요한 磷의 대부분이 地下部로부터의 流轉에 의해서, 中期에는 많은 量이 土壤으로부터의 흡수에 의해서 그리고 末期에는 대부분이 줄기로부터의 流轉에 의해서 供給되었다. 그러나 쑥과 갈풀個體群에서는 生長初期의 流轉에 앞서 많은 量의 磷이 土壤으로부터 供給되는 것으로 보였다. 뚱단지個體群에서 年間 磷의 内部流轉量은 器官水準의 磷流入量의 59%인데 비해 쑥과 갈풀個體群에서는 각각 41% 및 32%였다. 三種植物의 年間 植物-土壤間 磷循環量은 4.49-5.65gPm⁻²로서 土壤깊이 20cm 內의 可用性 磷含量의 3-8%였다. 뚱단지個體群이 다른 두 個體群에 비해 磷供給에 있어서 内部流轉에 대한 의존도가 큰 반면 植物-土壤間의 磷循環의 규모가 작고 磷流轉換率(turnover rate of P)이 낮은 것으로 보아 뚱단지 個體群의 生長이 可用性 土壤磷의 결핍에 따른 영향을 보다 적게 받는 것으로 추측 되었다.

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