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Primary Productivity and Matter Economy of a Maize Plant Population. Ⅲ. Phosphorus Economy in Relation to Dry Matter Production

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옥수수個體群의 一次生産性과 物質經濟. 3. 乾物生産과 燐經濟

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ABSTRACT

Phosphorus dynamics in terms of specific absorption rate, inflow and outflow rates, turnover rate, demand and supply, and utility index of a high yield *Zea mays* L. cv. Bokgyo field were evaluated using an analysis of successive production structures. The analysis was adopted for measuring quantitative changes in the population by stratified clip technique on every two weeks during the growing season. The seasonal trends of specific absorption rate (2.4 mg P/g/day in maximum) and specific absorption efficiency (0.03) closely correlated with that of relative growth rate of the population. The overall inflow and outflow of phosphorus was 3.41 g P/m^2/yr showing the maximum inflow of 2.99 g P/m^2/month in July. While the maximum phosphorus standing crop was 1.4 g P/m^2 showing the maximum turnover rate of 178% in late June. The accumulation of phosphorus along plant height declined monotonically in stems and roots but increased in foliage after heading. The proportions of the total annual demand of phosphorus were 24.4% for leaves, 22.5% for stems, 49.6% for fruits and 3.5% for roots. These demands were met with internal (18.2%) and external (81.8%) supplies. The seasonal highest phosphorus utility index was 1,091 in early June, while the average value was 655.

INTRODUCTION

Biologists and ecologists have devoted much effort to elucidate the development and ability of ecosystem (Macfadeyen, 1948; Margalef, 1963; Odum, 1962). Although the research on metabolism including the study of energy flow of the population is a principal means of the functional analysis of ecosystem, or a measure of the total activity of the population (Teal, 1962), the ecosystem is not necessarily regulated only by energy. Kuenzler(1961 a, b), studying the role of a mussel population in phosphorus cycling and energy flow of a salt

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marsh ecosystem, reported that the population has a much more important effect on the community phosphorus cycle than it has on the community energy flow(Odum, 1962).

As a constituent of nucleic acids, phospholipids, and numerous phosphorylated compounds, phosphorus is one of the nutrients of major importance to biological systems. Further because the ratio of phosphorus to other elements in organisms tends to be considerably greater than the ratio of phosphorus in the available and primary sources, phosphorus becomes ecologically significant as the most likely limiting or regulating element in productivity. So it is very essential to understand its behaviour pattern quantitatively.

Although there are lot of reports on retention, absorption, and return of phosphorus by plant populations or communities in natural ecosystems, there is little information on the changes of behaviour patterns of phosphorus through growth processes of plant populations. By studying these relations, the life of plants would be better understood, particularly in relation to their life habits. Mutoh(1968) maintained the importance of the characteristic movement of phosphorus in the living plant for plant life, though her study was on the individual level of the plants.

Comparison of nitrogen and phosphorus budgets revealed that larger recycling of an element results in a smaller turnover rate of the element in the population(Hirose, 1974). Hirose(1975) also reported that phosphorus was not so 'structuralized' in the population as nitrogen. Generally 'structure' of a system is not merely an aggregation of components, but means the "net" of connections between components. Therefore, the stronger the connections between components, the more structuralized is the system.

Although there are several reports on phosphorus budget in terrestrial ecosystems(Hirose, 1974) there is scarcity of information about the phosphorus economy of crop populations, especially of maize plant population. So the present study was an attempt to specify the seasonal changes of phosphorus assimilation of a *Zea mays* L. cv. Bokgyo population, thus to clarify the relation of phosphorus assimilation to the growth in dry matter as well as nitrogen assimilation, in consideration of the phosphorus budget as a whole and its recycling in the plant body of the population.

MATERIALS AND METHODS

The plant and soil materials obtained from the growth analytical and primary productivity study of the maize population(Huque and Song, 1980), were used in this study. A suitable amount of each of oven-dried powdered samples were carefully measured into porcelain crucible and burnt in muffle furnace at 550 C for 6 hours to obtain ash weight and so the organic matter content. The ash samples were digested with conc. HCl for 1 hour at 110 C to make silicate insoluble and thus to prepare ash solution. After removing silicate by filtration, phosphorus content was determined spectrophotometrically by the ammonium-vanadate-molybdate method at 440 nm. Oven-dried soil samples were burnt for 12 hours and the ash was used for determining phosphorus like plant materials. Meteorological

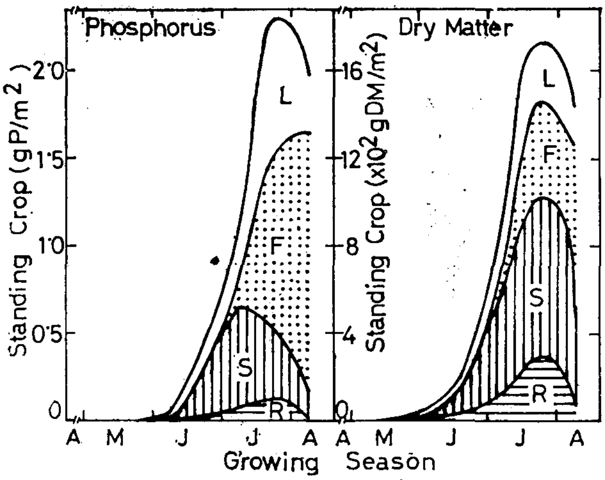


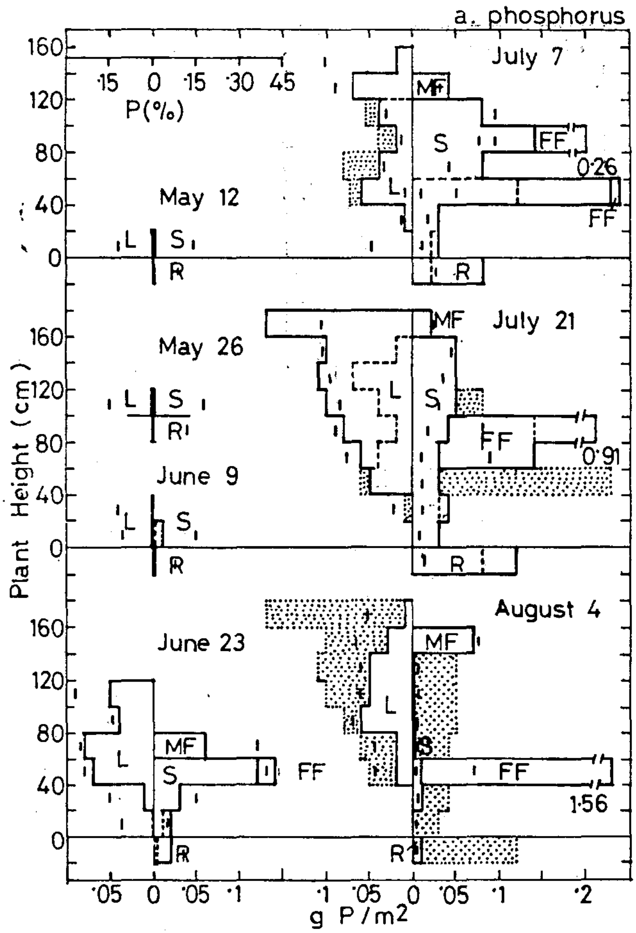
Fig. 1. Changes in standing crops of phosphorus and dry matter in different organs of *Zea mays* population: leaves, L: stems, S: flowers and fruts, F: and roots, R.

data during the population growing season and the seasonal changes in the maize field soil during the population development have been presented in the first report of this series(Huque and Song, 1980). Vertical distribution of phosphorus and dry matter have been diagrammed by applying the stratified clip technique(Monsi and Saeki, 1953). The specific absorption rates of phosphorus were determined after Welbank (1962) and Williams (1948). Net assimilation, turnover rates of inflow and outflow of phosphorus, and the annual phosphorus budgets were analysed by the methods of Hirose (1971) and Song and Monsi(1974).

RESULTS AND DISCUSSION

Standing crop of phosphorus in the population. Seasonal changes in the total phosphorus standing quantity of the maize population are shown in Fig. 1. The phosphorus quantity of each organ at every stratum was calculated by multiplying the respective phosphorus percentage with the respective biomass. The basic growth pattern in terms of phosphorus was similar to that in terms of dry matter till the onset of heading in late June, after which it differed widely. In this respect, it also differed from the late growth pattern in terms of nitrogen of this population(Huque and Song, 1981).

The maximum attained quantity of phosphorus standing crop in the population was 1.4 g P/m^2 in late July, i.e., the period of peak biomass production(Fig. 1). The amount of phosphorus available for seed production was 0.55 g P/m^2 in August. The ratios of T/R and F/C in terms of phosphorus quantity at the maximum LAI period were 17.8 and 0.45, respectively. The T/R value was much higher than that for nitrogen, while the F/C was almost same to that of nitrogen (Huque and Song, 1981).

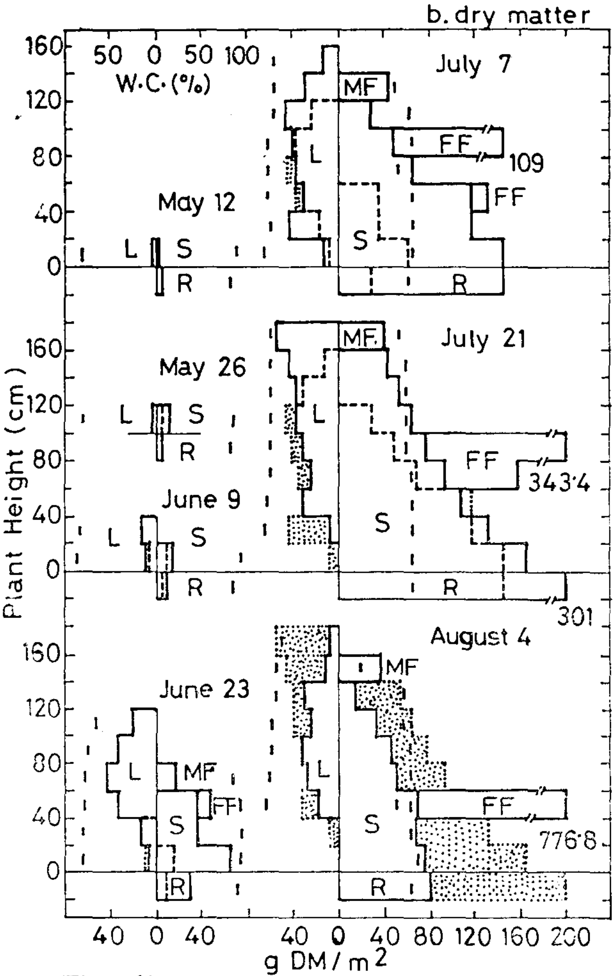


(Fig. 2-a)

Fig. 2. Seasonal trends in vertical distribution of phosphorus (a) and dry matter (b) standing crops in *Zea mays* population: L, S, MF, FF and R, stand for leaves, stems, male flowers, fruits and roots, respectively. P, Phosphorus content; W. C., water content (For detail see text).

Vertical distribution of phosphorus. The vertical distribution of phosphorus and dry matter and their changes in the maize population have been demonstrated in Fig. 2 a and b (Monsi and Saeki, 1953). The phosphorus contents and dry matter in the photosynthetic and non-photosynthetic organs have been included on each date in the second and first quadrants, respectively, while those of root were included in the fourth quadrant.

The phosphorus content(%) in each organ at every stratum has been shown by limiting with short vertical lines against respective phosphorus quantities in the profile diagrams. The vertical distribution of phosphorus was generally more in the upper regions than in the lower ones, both in stems and leaves, specially during vigorous growth period. But at the end of the growing season, the distributions were almost uniform althrough, lowest being



(Fig. 2-b)

in stems. The average phosphorus content ranged from 0.083% in early May to 0.26% in late May in foliage; 0.16 and 0.09% in late May to 0.017 and 0.016% in August in stems and roots, respectively. Thus the phosphorus content steadily increased in the photosynthetic organs with the advances in growth, while reverse was the case with nonphotosynthetic organs, i.e., it declined monotonically both in stems and roots as the population drew closer to the end. Such a declining tendency has also been reported in the stems of *Solidago altissima* (Hirose, 1974).

The vertical distribution diagrams represent the seasonal changes in the patterns of spatial accumulation of phosphorus and dry matter in the population. The dry matter was distributed more in the nonphotosynthetic organs than in the photosynthetic system, whereas phosphorus distribution showed marked differences after the onset of flowering, especially in stem the phosphorus quantity monotonically declined at the end of the population growth. Flowers and fruits shared the highest amounts of all the parts.

To determine the newly assimilated phosphorus and biomass by the net production (including translocation from other parts) and the old-lost biomass and phosphorus by shedding (including translocation to other parts), the growth of respective organs in the plant population was analysed by comparisons of the two successive profile diagrams (Midorikawa, 1959; Hirose, 1971). Remarkable increases in fruit materials at the end of the population growth attributed to the largest allotment of net production as a characteristic of this economic crop plant as has also been reported in the case of nitrogen in other crop species (Song, 1978).

Matter flow through the population. A. Phosphorus absorption rate and absorption efficiency. 'Specific absorption rate' *Ap* and 'specific absorption efficiency' *AEp* of phosphorus as calculated during the maize population development are shown in Fig. 3. The average mineral absorption rate, subsquently termed specific absorption rate, here of phosphorus(*Ap*), was calculated after Welbank(1962) and Williams(1948) by adopting the formula: $Ap=\frac{(P_2-P_1)(\ln W_{R2}-\ln W_{R1})}{(t_2-t_1)(W_{R2}-W_{R1})}$. The *Ap* rapidly increased from the early phase and reached the maximum of 2.4 mg P/gDM/day in late June, followed by steady decrease to 0.1 mg P/gDM/day by the end of the population growth. Thus the peak of *Ap* appeared later to that of specific absorption of nitrogen, *An* of this population (Huque and Song, 1981). The *Ap*, like *An*, did not show any definite correlation with the availability of phosphorus in the maize field. However, the declining trend of *Ap* positively correlated with the lower availability of phosphorus. The highest *Ap* preceeded the maximum growth taking place in July. The slow *Ap* at the latter half of the growing season might also owe to

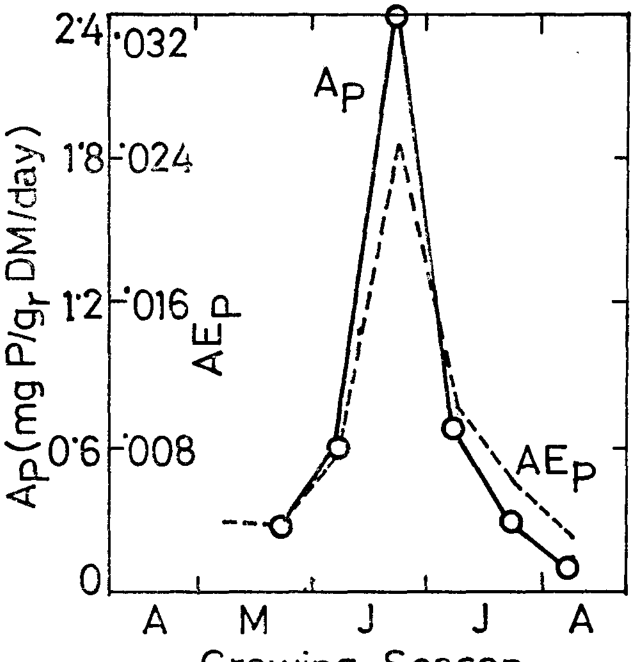


Fig. 3. Specific absorption rates (*Ap*) and specitic absorption efficiencies (*AEp*) of phosphorus of *Zea mays* population.

the development of efficient phosphorus recycling system in the plant population.

The specific absorption efficiency of phosphorus i.e., the ratio of net assimilation to mean root biomass between two periods, sharply rose to the maximum of 0.029 in late June and then gradually decreased to the lowest value at the end of the population growth due to the decrease in the root absorption activity. On the other hand, *Ap* and *AEp* appeared to be directly correlated with the seasonal trends of *RGR* of this population (Huque and Song, 1980).

In consideration of the extreme intricate nature of mineral absorption by root system in the natural field, these measures have the merit of practicability, and their use can lead to interesting and useful conclusions. In spite of the idea of relating mineral uptake to total root dry weight, as yet comparatively little work has been done on these lines. It would be valuable to have comparative figures for a range of plants differing in life from and in ecological preferences.

B. Phosphorus assimilation and distribution pattern. The changes n the phosphorus and biomass contents indicate the dynamics of the population growth. The changes in the phosphorus standing quantity, like biomass, is the resultant of gain (net production) and loss (defoliation) of the matter during a growth period, and the successive changes of the respective organs reveal the real feature of the plant population growth (Hirose, 1971). The rates of withdrawal of phosphorus and dry matter were assumed to be 50 and 10%, respectively (Iwaki, et al., 1969; Oland, 1963).

The monthly changes of net production of the population are shown in Fig. 4. The annual inflow rates (*Rin*) and outflow rates (*Rout*) of phosphorus and dry matter were 3.41 g P/m^2/year and 2,233 g DM/m^2/year, respectively. The total annual *Rin* is equal to total annual *Rout*. The seasonal trends of *Rin* showed almost a bell-shaped pattern with a peak of 2.99 g P/m^2/month against 1,638 g DM/m^2/month, both also appearing in July.

The distribution ratios of net phosphorus assimilation were, 24.4% to leaves, 22.5% to stems, 3.5% to roots and 49.6% to flowers and fruits (Fig. 5). The highest share was in flowers and fruits in July. While the annual distribution ratios of dry matter were, 15.5% to leaves, 33.9% to stems, 13.5% to roots, and 37.1% to flowers and fruits. The differences in the allotment and distribution ratios are considered to bring about large differences not only in total dry weight of the plants, but also in their constitution, i.e., the structure of the plant as productive system (Monsi, 1960; Kuroiwa, 1960).

C. Turnover rate of phosphorus. Seasonal trends of monthly turnover rates of inflow (*rin*) and outflow (*rout*) of phosphorus and dry matter in the maize population are shown in Fig. 6. The term 'turnover rate' was calculated as the rate of inflow or outflow of matter to the mean standing crop at a month interval during the population growing season (Odum, 1960; Reiner, 1953). The inflows of phosphorus and dry matter attained the maximum turnover rates of 178% and 163% per month in late June, respectively. The *rout* of phosphorus also first appeared late in June like that of nitrogen of this population

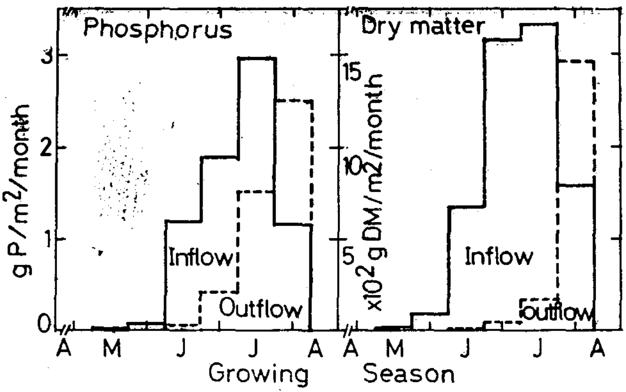


Fig. 4. Changes in monthly net assimilation (inflow) and accumulation in litter (outflow) of phosphorus and dry matter of *Zea mays* population.

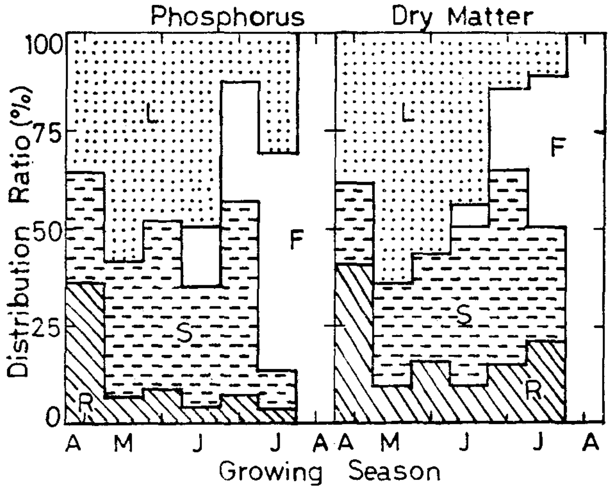


Fig. 5. Distribution ratios of net phosphorus assimilation and dry matter to different organs of *Zea mays* population: leaves, L: stems, S: fruits, F: and roots, R.

(Huque and Song, 1981). After which both *rin* and *rout* of phosphorus and dry matter were almost similar from late June to the end of the population growth, though *rin* of phosphorus showed a slight increasing trend in late July. This slight increase might be attributed to the requirement of fruit development and maturity, supplied through enhanced absorption from soil. However, it differs from that of phosphorus in *Solidago altissima* (Hirose, 1975), especially in respect of delayed appearence of *rout*, which might be owing to the absence of mutual shading effect during the initial period of development. Interestingly, the seasonal trend of *rin* of phosphorus very closely correlated with the trends of *Ap*, *AEp* and *RGR* of this population. These characteristics suggest the presence of balanced economic utility among phosphorus, nitrogen and dry matter of this population.

Demand and supply of phosphorus. Seasonal trends in the requirements of phosphorus for the growth of organs and their supplies in the maize population are illustrated in Fig. 7.

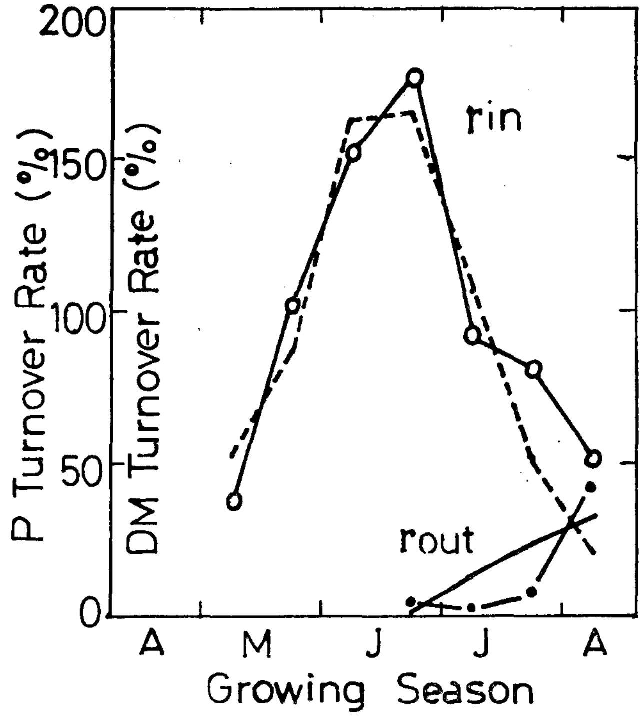


Fig. 6. Monthly turnover rates of inflow and outflow of phosphorus and dry matter (P:rin, ○—○; rout, —, and DM: rin, - - -; rout, ·—·) of *Zea mays* population.

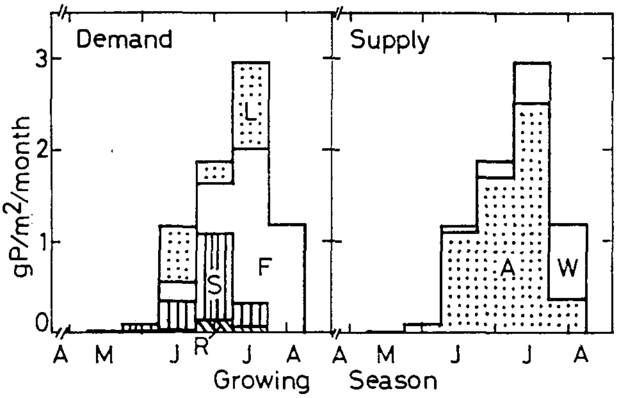


Fig. 7. Changes in demand and supply of phosphorus in *Zea mays* population: L, leaves; S, stems; F, fruts; R, roots; A, absorption from soil; and W, withdrawal from senescing organs.

In the early stages of growth, most of the phosphorus was consumed in the growth of leaves and stems, whereas in the later stages it was consumed mostly for the growth of reproductive organs.

Out of the total annual phosphorus demand (3.41 g P/m²/year), the proportions of allotment in terms of gram per square meter of ground area were, 0.83(24.4%) to the

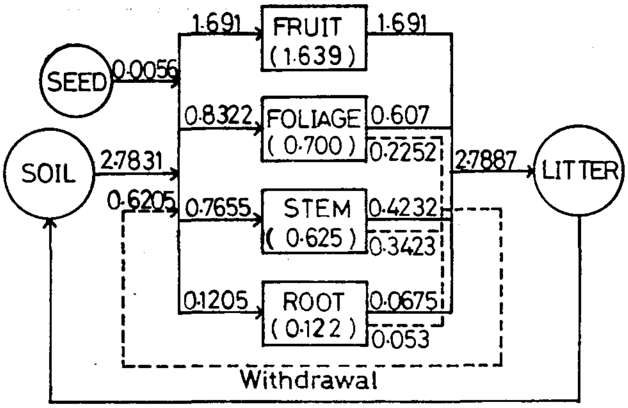


Fig. 8. Annual phosphorus budget of *Zea mays* population. Amounts on arrows indicate flux rates in g P/m^2/year, and those in parentheses, the maximum standing quantities in g P/m^2. The maxima of standing crops were attained at different growing stages.

leaves, 0.77(22.6%) to the stems, 1.69(49.6%) to the reproductive organs, and 0.12 (3.5%) to the roots. These demands were partly, 0.62 g P/m^2/year (18.2%), met with the internal supply, i.e., phosphorus recycled by withdrawing from senescent leaves. The rest of the demand, 2.79g P/m^2/year (81.8%), was met through external supply, i.e., phosphorus absorbed from the soil.

The annual phosphorus budget of the maize population from sowing in April through harvesting in August, is summarized in the Fig. 8. The proportions of annual internal and external suppiles of phosphorus were quite similar to those of nitrogen (19.2% and 80.8%, respectively) of this population. That means, the extent of recycling of stock matters of phosphorus and nitrogen in the maize population and dependence for these on the availability in the habitat were almost similar. From these findings, it becomes clear that there is a very good harmony between the vital elements and biomass of this crop species.

Phosphorus utility. Phosphorus utility(*PU*) is defined as the net dry matter productivity of a unit amount of phosphorus absorbed. The ratio of the amount of dry matter produced to that of phosphorus assimilated during a year, i.e., the phosphorus utility index (*PUI*) as calculated throughout the growing season for this plant to be 655 (Table 1), was implied as an important indicator of the population function in relation to the ecosystem metabolism. However, this value is lower than those reported for perennial plants. It suggests that this plant requires more phosphorus available soil conditions. The reciprocal of *PUI* of 0.15% means the average phosphorus contents of the newly produced matter. The seasonal trend of *PUI* showed a maximum of 1,091 in early June after which it gradually declined with fluctuations but maintained a higher value than the initial even at the end of the growth. The dilution of phosphorus due to the accumulation of dry

Table 1. Seasonal changes of phosphorus utility of the *Zea mays* population. Sown on April 7, 1979

Growing Season							Average
Apr. 7 ~ May 12	May 12 ~ May 26	May 26 ~ June 9	June 9 ~ June 23	June 23 ~ July 7	July 7 ~ July 21	July 21 ~ Aug. 4	
613	731	1,091	574	841	548	682	655

matter might be attributed to the rise in *PUI* with growth. Unlike nitrogen utility index, *NUI*, the *PUI* of the maize population did not show any definite correlation with the availability of phosphorus in the field (Huque and Song, 1980). The highest *PUI* appeared while the soil had a low phosphorus supply. Plant populations of small *PUI* require a relatively large amount of phosphorus for their growth and so they are inefficient in phosphorus utilization, i.e., plant populations of high *PUI* values are efficient in phosphorus utilization for their growth (Hirose, 1974). The *PUI* value of this population could not be compared with other crop plants lack of data. However, this species appeared to be more efficient in *PU* than to its nitrogen utility, *NU* (Huque and Song, 1981).

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摘 要

옥수수個體群의 生長期間中 生產構造의 發達과 乾物生產過程에 따른 燐의 動態, 即 土壤으로부터 吸收率, 同化率, 回轉率, 需要供給의 收支 및 利用効率의 季節的 變化를 分析하였다. 燐의 吸收率 (最大 2.4 mgP g^{-1} day^{-1}) 및 吸收効率(0.03)은 個體群의 相對生長率과 密接한 相關을 보였고, 生育期間中 總 同化率은 3.41 gPm^{-2} 로서 月 最大 同化率은 2.99 gPm^{-2} $month^{-1}$ (7月)였다. 한편 個體群의 燐現存量의 變化는 最大値 1.4 gPm^{-2} 였고, 最大 回轉率은 178% 를 나타내었다. 生育期間中 個體群의 各 器官別 燐의 需要量은 葉 24.4%, 莖 22.5%, 根 3.5% 및 種實 49.6% 였으며, 總 燐要求量의 81.8% 는 土壤으로부터 吸收되였고 나머지 18.2% 는 個體群內의 轉流에 의해 供給되었다. 옥수수個體群의 燐利用指數는 最大値가 6 月에 1,091 이며 平均指數는 655 였다.

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