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Redistribution of nutritive elements in a 'Gros Michel' banana plant

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Summary

The redistribution of nutritive elements in a vegetative banana plant was studied. For this purpose, silicon was used as an index element, under the presumption that silicon is not redistributed within a plant.

The results indicate that the nutritive elements N, S, P, K and Cu were strongly redistributed from older to younger leaves, in contrast to Mg, Cl, Fe and Zn, which were moderately redistributed. No redistribution could be found for Ca.

Introduction

Distribution and redistribution

Redistribution of nutrients in plants is an important phenomenon in plant growth. Reliable techniques to measure the extent of this phenomenon for various nutrients are urgently needed. In this article such a reliable technique is presented with silicon used as an index element. The fundamental idea behind the use of silicon as an index element is the presumption that within a plant silicon compounds are not redistributed. By comparing the distribution of silicon with that of nutritive elements, some conclusions on the possible redistribution of these nutritive elements can be drawn. In this article the method was applied with the use of a 'Gros Michel' banana plant as a test object.

Before going into details, some basic lines may be drawn. It can be stated that the quantity of a certain element in an organ of a plant is the result of influx and efflux processes. The resulting 'net flux' can be defined as: xylem influx plus phloem influx minus phloem efflux. In the plant, xylem influx is a function of the following factors:

- transpiration
- selective discharge of nutrients into the xylem vessels
- selective uptake of nutrients from the xylem vessels by the organ

– metabolic activity in the organ.

As a first approximation, the net flux into a young growing organ may be described as a resultant of xylem influx, which is increasing in the course of time from nil to a maximum rate, a large phloem influx, and a small phloem efflux. As a contrast, in an old organ the xylem influx is strongly diminished, as is the phloem influx, whereas as a result of a plant trying to re-utilize its nutritive substances, the phloem efflux is rather large.

Methods for measuring redistribution

To obtain an impression of the net flux into a plant organ, one can monitor the growth of plants in the course of time. For that purpose, a number of identical plants must be grown under identical circumstances. The plants can be harvested periodically, and the separate organs can be analysed. With this method, an impression can be obtained of several parameters:
– length of the period of net influx into an organ
– rate of net influx
– time of onset of net efflux.

Information on separate xylem and phloem influxes can, however, not be obtained in this way.

To obtain an impression of the various components of net flux, one may use isotopes. The advantage of this method is that it affords insight in the pathways of the isotope to developing organs, once the isotope is removed from the rooting medium, but the normal supply of the nutrient is continued. A number of difficulties is involved in measuring redistribution in this manner. For instance, to acquire an instantaneous and complete separation of isotope and root system, only nutrient solutions can be used as a rooting medium. Even then, only a qualitative impression, and not a quantitative measurement of redistribution can be obtained.

The idea of measuring redistribution by means of the use of an internal standard was advanced by van Egmond (1975). A prerequisite for the use of an internal standard is that the standard itself is not redistributed. This implies that for the internal standard, phloem fluxes should not exist, whereas xylem influx is to take place in a normal fashion. The use of an internal standard for measuring nutrient redistribution inside plants is explained in the following section.

The use of an internal standard

The use of an internal standard allows a comparison to be made between distribution of a nutrient via the xylem and integrated distribution of that nutrient via both xylem and phloem. The distribution via the xylem is estimated from information obtained on the distribution of silicon, which element is considered to move inside plants only by way of xylem flow. For comparison of the flow of a nutritive element with that of a reference element, it is mandatory to compare the quantity of that nutritive element in a certain plant organ. Expressed as a fraction of the total quantity of that element in the plant, with the fractional quantity of the reference element in that organ. In other words, an evaluation is made of A-organ/A-plant relative to R-organ/R-plant, in which A-organ and R-organ represent the quantities of the nutritive element A and the reference element R in a certain plant organ, and A-plant and R-plant represent the total quantities of these elements in the plant. The accumulation of a nutritive element in an organ by way of xylem flow is then calculated from A-organ = A-plant × R-organ/R-plant. An observed discrepancy between the actual quantity of the nutritive element in the organ and the quantity thus calculated can be considered as indicating the occurrence of redistribution of the nutritive element by way of phloem flow. The larger the discrepancy observed, the stronger is the redistribution.

Requirements to be met by a reference element

To be able to function as a reference element, an element must meet certain requirements. These requirements are:

a) a continuous accumulation of the reference element in the organ under study
b) a partitioning of the reference element over the various organs of a plant in accordance with the partitioning of water in the transpirational flow
c) absence of any redistribution of the reference element by means of phloem flow
d) absence of any toxic effect exerted by the reference element
e) presence of a good analytical method to measure the reference element.

In the current study, the element silicon was chosen as a reference element for the following reasons:

ad a) Mengel & Kirkby (1978) noticed that, in general, older plants contain more silicon than younger plants do. Takahashi and Miyake (1977) distinguished three plant families as being silicon accumulators, namely the Gramineae, Cyperaceae and Musaceae (to which latter family the banana plant belongs). These plants accumulate much silicon in their tissues.

ad b) Both Jones & Handreck (1965) and Wynn Parry & Winslow (1977) observed a partitioning of silicon in the plant according to the transpirational flow. Mengel & Kirkby (1978) noticed that silicon in the accumulators is found mainly in the aboveground parts, and only to a small extent in the roots.

ad c) Yoshida et al. (1962) concluded that silicon in rice tissue is not redistributed. They based their conclusion on the finding that in rice plants, originally grown on a Si-containing nutrient solution and subsequently transferred to a Si-free solution, no Si was transferred from the older leaves to the leaves that had developed after the transfer. (This redistribution test method bears strong resemblance with the above-mentioned isotope method, with this difference that in the case of Yoshida Si supply was discontinued at the moment of the transfer). In the Si treated plants, the silicon was detected under the cuticle and at the membranes of epidermis cells. Mengel & Kirkby (1978) noticed that in monocots silicon is deposited mainly in the cell walls of the epidermis. The form in which silicon is deposited is primarily as hydrated amorphous $SiO_2 \cdot nH_2O$.

ad d) It is well known that silicon is a non-toxic element. Because of its restricted solubility, no excessive concentrations can be detected in soil solutions.

ad e) Accurate methods to measure silicon do exist. For reliable sampling, contamination of the above-ground parts of the plant with soil must be avoided.

As a final remark, it may be mentioned, that large variations in the Si-supplying capacity of a soil are buffered by a selective uptake pattern, consisting of a plant's ability to exclude Si at higher concentrations, and to absorb it preferentially at lower concentrations, as was shown by van der Vorm (1980).

Redistribution and the mineral nutrition of the banana plant

In the following, use of the reference-element method, as applied to a vegetative 'Gros Michel' banana plant, will be discussed. In the past decades, several studies on the mineral nutrition of banana plants were carried out. Freiberg (1964) reviewed the results of these studies. De Geus (1967) listed optimum contents of nutritive elements in the leaves of banana. In a more detailed study, Twyford & Walmsley (1973, 1974, 1976) gave detailed information on concentration patterns of nutrients in the 'Robusta' banana plant. Jauhari et al. (1974) included silicon in their study of 'Dwarf Cavendish' banana plants.

To obtain reliable information on patterns of redistribution of elements within a plant, it is necessary to make use of samples reflecting the flow pattern of moisture inside the plant. This means that separate samples must be obtained of blade, midrib, sheath and petiole.

Materials and methods

In this study, an approximately 12-month old vegetative 'Gros Michel' banana plant was used. The plant was raised in a heated greenhouse on a sandy soil, supplied with organic and inorganic fertilizers. Leaves older than the No 15 leaf had already been shed. Each leaf was subdivided into blade, midrib, petiole plus sheath. The leaves 1 (youngest), 3, 6, 9, 12 and 15 (oldest) were used for chemical analysis. After thorough washing with water, the rhizome and the roots were also sampled.

To prepare them for chemical analysis, the samples were cut, dried at 70 °C, and milled. To determine N, P, K, Ca, Mg and Na, the dried material was digested according to the method of Lindner & Harley (1942), some salicylic acid being added to prevent NO_3^- from being lost during the digestion. NO_3^-, Cl^- and SO_4^{2-} were determined in a water extract. Organic S was calculated from total S minus SO_4^{2-}-S. Total S was determined after a digestion procedure as described by van Eck & Novozamsky (1977). Fe, Mn, Cu and Zn were determined in a digest obtained according to the Schaumlöffel (1960) procedure. Si was determined gravimetrically in the classical procedure of chloration, filtration, dry-ashing in a Pt-crucible, and treatment with HF.

Results and discussion

Silicon distribution

As mentioned earlier, sampling was arranged in accordance with the 'transpirational sinks'. That means that the leaves had to be severed at the base of the plant, that is near the corm. Because of the complexity of its structure, the corm itself was sampled as a whole organ.

In Fig. 1, the relationship is presented between silicon accumulation in the various leaves and a parameter of transpirational flow. As can be seen, the two variables are closely correlated, but their relationship depends on leaf age. This dependency may be ascribed to a diminished metabolic activity in the older leaves, and a correspondingly lower rate of transpiration in those leaves. The presented correlation confirms the postulate of Jones & Handreck (1965) and of Wynn Parry & Winslow (1977) that silicon in the plant is distributed according to the transpirational sinks.

In the introduction it was indicated that in the procedure aimed at using an internal standard to supply information on the degree of redistribution of nutrients, relative amounts of the elements are taken into account. These relative amounts can be expressed as percentages. In Table 1 an impression is given of the distribution of Si over the various plant parts. The silicon contents are expressed as content (%) of Si in an organ, relative to the total amount of Si in the whole plant. An example may be given: The third leaf had a dry weight of 70.9 g. The Si content in the dry matter of the leaf was 0.75 %. Hence, the amount of Si in the third leaf was $70.9 \times 0.75 / 100 = 0.53$ g. By means of graphical interpolation for the unanalysed leaves, the total amount of Si in the whole plant was estimated at 15 g. Thus, the third leaf of the plant contained $(0.53/15) \times 100 = 3.55$ % of the total amount of Si in the plant. In this way in Table 1, estimates of relative distribution of silicon in the plant are presented.

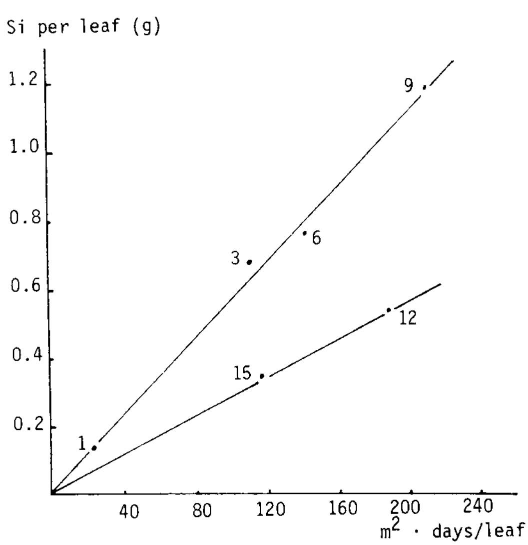


Fig. 1. Accumulation of Si per leaf as plotted against the product of leaf surface area, in m^2, and leaf age, in days, as a measure of the total transpiration per leaf. Numbers indicate ranking order of age of leaf (1 is youngest, 15 is oldest).

Table 1. Distribution of Si in a 'Gros Michel' banana plant.

Organ	Percentages of total plant Si* (%) in			
	blade	midrib	sheath + petiole	whole organ
Leaf 1	0.24	0.15	0.56	0.95
Leaf 3	3.55	0.40	0.59	4.54
Leaf 6	3.77	0.61	0.82	5.20
Leaf 9	6.40	0.69	0.90	7.99
Leaf 12	2.48	0.37	0.76	3.61
Leaf 15	1.44	0.23	0.73	2.40
Rhizome				5.9
Roots				15.7

* By graphical interpolation, the total amount of Si in the whole plant was estimated to be 15 g.

The distribution of nutrients, as compared with that of silicon

Just as for silicon, for all nutrients estimates of relative distribution in the plant can be calculated. By comparing the distribution pattern of silicon with that of a nutrient, an impression can be obtained of the discrepancy in the distribution of the two elements. The degree of discrepancy is indicated with the use of the following formula:

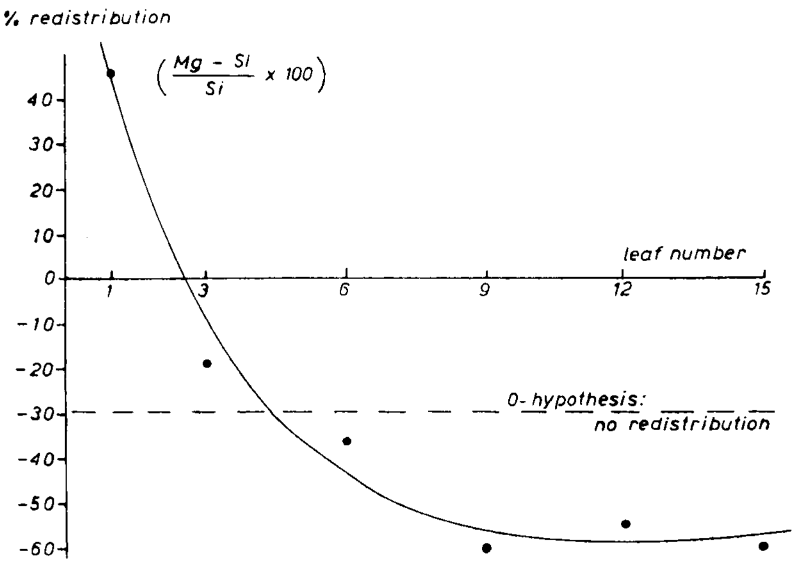
$$100(Rn - Rs)/Rs$$

in which Rn is the relative nutrient content, and Rs is the relative Si content. If the quotient shows a positive value, it can be said that phloem flow is making a contribution to the influx of that particular nutrient into the organ under consideration. When the quotient shows a negative value, this can be interpreted as an indication that there is an efflux of the nutrient from the organ by way of phloem flow.

The first example applies to organic N in leaf 3. The relative content of organic N (that is total N minus NO_3^--N) in leaf 3 was 8.73 % (i.e. 6.99 % in the blade + 0.58 % in the midrib + 1.14 % in the petiole plus the sheath). According to the above-mentioned formula, the relative distribution is then (8.73 - 4.54)/4.54 = 0.92. This indicates that next to organic N entering via xylem flow, an additional quantity of organic N amounting to 92 % of the quantity entering by xylem flow, is entering the leaf 3 as a result of phloem flow.

The second example deals with P in leaf 9. The relative content of P in leaf 9 was 6.03 % (i.e. the summation of the content in blade, midrib and petiole plus sheath). The relative Si content in leaf 9 was 7.99 % (i.e. the summation of the contents in blade, midrib and petiole plus sheath). The relative distribution is (6.03 - 7.99)/7.99 = -0.24, which indicates that of the P originally entering leaf 9 by xylem flow 24 % has subsequently left the leaf due to redistribution by means of phloem flow.

In Table 2, such results of calculations on influx or efflux by way of phloem



source of variation	degrees of freedom	sum of squares	mean square
deviations from 0-hypothesis	5	8356	
deviations from curved regression	4	114	29
reduction in sum of squares	1	8242	

$$F = \frac{8242}{29} = 284 \rightarrow p < 0{,}5\,\%$$

Fig. 2. Test of significance of departure from 0-hypothesis of no redistribution against curved regression according to redistribution. (For magnesium, see Table 2.)

flow are presented for a number of nutrients and a number of leaves. The use of a statistical method to test the level of significance of redistribution, as presented in Table 2, is explained for magnesium in Fig. 2.

The null-hypothesis line (no significant redistribution taking place) is drawn at the level of the mean relative percentage of redistribution of Mg in the leaves. In the same figure, a regression curve is drawn through the points for Mg, as they were obtained from Table 2, according to a probable redistribution pattern. The deviation of the calculated points from the regression curve and the null-hypothesis line form the basis of the statistical test. Analogous tests were conducted for a number of other nutrients listed in Table 2, except for NO_3^- and SO_4^{2-},

Table 2. Gains or losses of nutrients for the various leaves of the banana plant, as a result of redistribution. Values expressed as percentages of the initial quantities in the leaves accumulated through xylem influx.

Leaf No	N-org.	S-org.	P	K	Ca	Mg	Na
1	+633	+638	+439	+364	−36	+46	+22
3	+92	+105	+44	+30	+12	−19	−67
6	+3	−2	−24	−34	+4	−36	−75
9	−48	−35	−61	−78	−6	−60	−60
12	−42	−54	−54	−78	+19	−55	−44
15	−51	−50	−56	−80	+11	−60	−65
	**[a]	**	**	**	n.s.	**	*

Leaf No	SO_4	NO_3	Cl	Fe	Mn	Cu	Zn
1	+532	+2	+141	+102	+31	+345	+113
3	+73	−22	+17	+27	+54	+50	+1
6	+28	−43	+7	−32	+29	−31	−27
9	−31	−68	−47	−38	−5	−23	−48
12	−26	−60	−31	−41	−2	−7	−18
15	−52	−60	−48	−58	+41	−18	−30
	—	—	**	**	n.s.	**	**

[a] Test of null hypothesis (no redistribution taking place).
* Rejected at $P < 0.05$; ** rejected at $P < 0.005$; n.s. not rejected.

because these nutritive ions are subjected to electrochemical reduction in different parts of the plant. From Table 2 it can be concluded that most nutritive elements are subjected to redistribution. This redistribution manifests itself as an influx into young leaves, and an efflux out of old leaves. The rhizome is considered to function as a 'circulation pump'. Its phloem vessels form the connection between leaves.

Degree of redistribution in the plant

From the data of Tables 1 and 2 and from the total amounts of nutrient in the plant, an impression can be obtained of absolute quantities of nutrients redistributed in the whole plant.

From the data of Tables 1 and 2 and from the total quantities of nutrients in the plant, estimates of absolute quantities of nutrients redistributed in the whole plant can be obtained with the use of the following formula:

$(R_n\text{-}R_s)$ (total quantity of nutrient in the plant)

in which R_n and R_s have the same meaning as stated before. The total quantities of nutrients in the whole plant were calculated to be as follows: Si 15 g, N 60 g, S 5.1 g, P 7.1 g, K 126 g, Ca 22 g, Mg 16 g, Fe 181 mg, Mn 385 mg, Cu 25 mg, Zn 173 mg, Cl 36 g, and Na 2.6 g. With these data, it could be calculated for each leaf whether or not redistribution of nutrients had taken place. This information is presented in the Fig. 3 and 4. Positive values indicate that phloem influx has

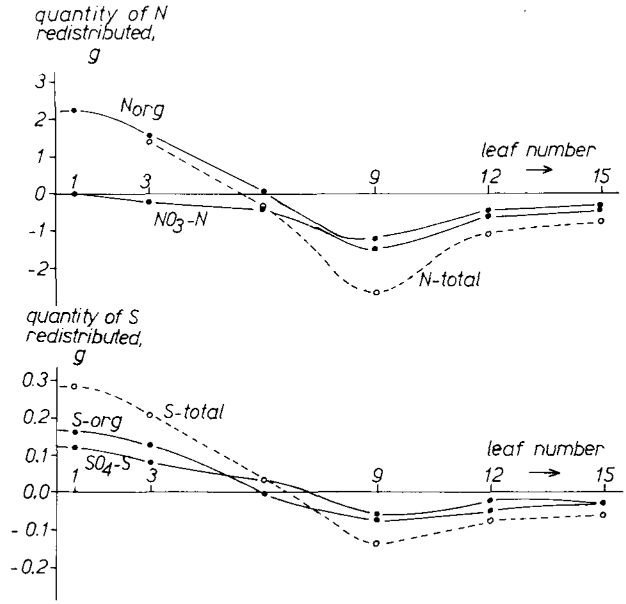


Fig. 3. Quantities of organic and inorganic forms of nitrogen and sulphur redistributed in the various leaves of the banana plant.

made a contribution to the accumulation of the nutrients, whereas negative values point at an efflux of the nutrient through phloem tissue.

In Fig. 3, a distinction is made between organic and inorganic forms of N and S. For the inorganic forms of these nutrients, redistribution proved to be slight. From the graphs of Fig. 4, it can be seen that for many nutrients redistribution is positive in the younger leaves and negative in the leaves of intermediate age. When the surface area below the zero line exceeds that above this line, such a phenomenon can be interpreted as a retention of the nutrient by the roots and the rhizome. The percentages retained are as follows: Si 22, N 18, S 15, P 34, K 45, Ca 18, Mg 37, Fe 33, Mn 5, Cu 25, Zn 30, Cl 31 and Na 69.

Suitability of the Si-index method

In Fig. 5, a simplified schematic picture is presented of the xylem flow and the phloem flow in a banana plant. Sampling must be carried out in such a way that the suborgans which are connected via the xylem vessels are taken together. This is easily done in a banana plant, as it is in many other monocotyledons.

As mentioned earlier, silicon uptake is high in 3 plant families: the Gramineae, Musaceae and Cyperaceae. The high Si levels in these plants facilitate analytical processing. By comparing the translocation of Si with that of other nutrients, one arrives at the conclusion that, at least for banana plants, other elements such as Ca can also serve as reference elements.

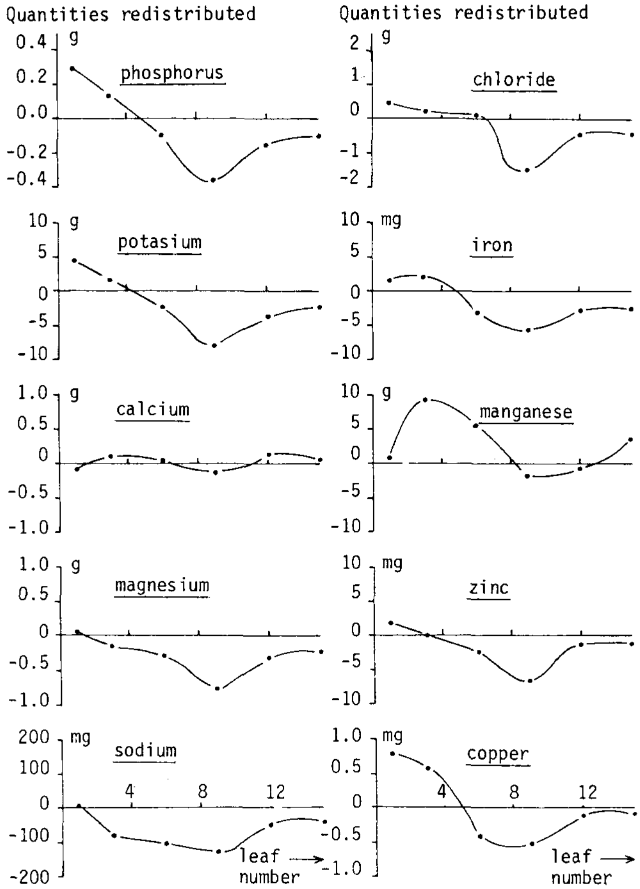


Fig. 4. Quantities of nutrients redistributed in the various leaves of the banana plant.

Conclusions

Re-utilization of nutrients in a plant can be considered as an important phenomenon in plant physiology. Its occurrence may help to explain the diversity of nutrient contents in various organs of a plant, and also to account for the phenomenon of diminishing concentrations of nutrients with increasing plant age. Such knowledge may be useful in that it supplies insight in matters necessitating decisions to be made on timing of fertilizer application and on quantities of fertilizer to be applied as basal dressings and as top dressings. More knowledge on the subject of redistribution is needed for improvement of both the quantity of harvestable material and the quality of the product obtained.

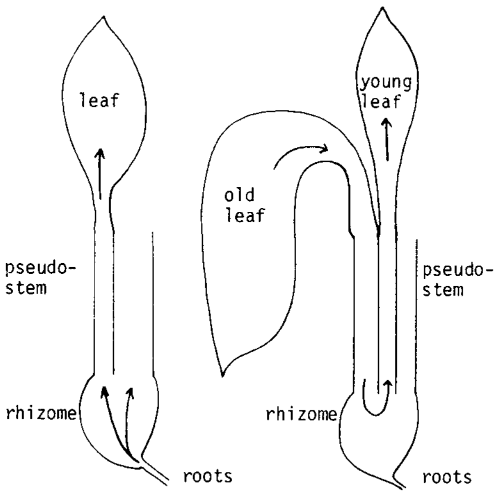


Fig. 5. A schematic presentation of xylem flow and phloem flow in a banana plant.

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