Acta Bot. Neerl. 29 (2/3) p. 165–178.

ECOPHYSIOLOGY OF THE SAND SEDGE CAREX ARENARIA L.

II. THE DISTRIBUTION OF ^{14}C ASSIMILATES

T. TIETEMA

Botanisch Laboratorium, Lange Nieuwstraat 106, 3512 PN Utrecht

SUMMARY

^{14}C assimilates produced in a single shoot of a sand sedge plant proved to be translocated in the direction of the rhizome tip only. Labelled assimilates were found in all roots in the part of the plant system between the shoot administered with $^{14}CO_2$ and the rhizome tip, in the youngest shoot and in the rhizome tip itself. The percentage of assimilates exported by the mature shoots proved to be 30–35%. The amount of assimilates exported by the youngest shoot decreased from 22% in a 1-shoot system to zero in the bigger plant systems. In the 5-shoot system also the export of the second youngest shoot started to decrease.

In spite of the relatively great sink strength of the rhizome tip with regard to the assimilates exported by the nearby situated young shoots, the main source of assimilates for the rhizome tip proved to be the older shoots, lying at some distance. The ecological importance of this is that the rhizome tip will be able to cross unfavourable habitats, without the need for assimilates from the newly formed shoots in those habitats.

1. INTRODUCTION

In a previous paper (Tietema & Vroman 1978) the time course of the growth of both the individual shoots and the sand sedge plant as a whole, as measured by an indirect method, has been described. It appeared that all assimilating shoots exported dry matter, with the exception of the youngest. Though it will be clear that the export from the shoots is translocated to the roots and the rhizome, it has nevertheless proved to be impossible to trace the assimilates exported by each separate shoot.

The present paper shows the results of experiments in which $^{14}CO_2$ was used to investigate the distribution of assimilates exported by each separate shoot qualitatively and quantitatively.

2. MATERIALS AND METHODS

2.1. Plants and plant culture

The plant systems used in the experiments (*fig. 1*) consisted of the apical part (1–5 shoots) of a rhizome system. Contrary to the former paper (Tietema & Vroman 1978) now the youngest shoot was given number I, the second youngest shoot number II etc., the highest figure always indicating the oldest shoot of the system. The entire part of the rhizome in front of shoot I is referred to as the rhizome tip. In the results both weight and radioactivity of the rhizome roots are included in those of the rhizome part from which they originated.

The plants were grown on a nutrient solution (Steiner 1972) in a greenhouse.

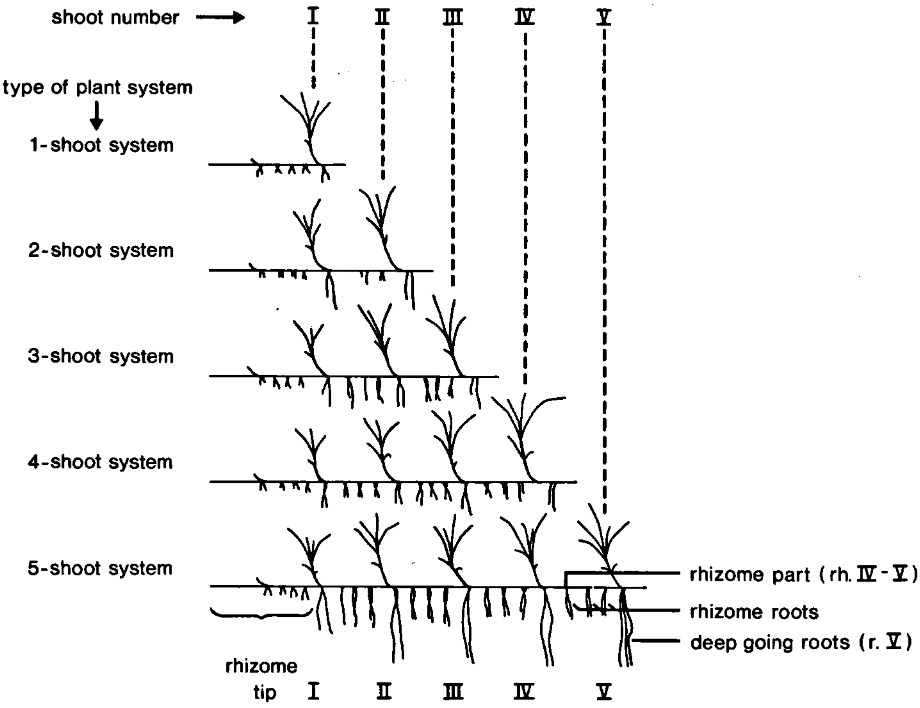

Fig. 1. Survey of the sand sedge plant systems. Indicated are the 1–5 shoot plant systems used in this study. The numbering of the shoots occurred in Roman numerals from young to old; number I being the youngest assimilating shoot. The deep-going roots are numbered according to the shoot at the base of which they emerged. The rhizome parts are referred to by the number of the shoots they connect. The rhizome roots are considered as being a part of the rhizome part on which they emerged. The entire plant part in front of shoot I is called the rhizome tip.

A few days before an experiment the apical part of a rhizome bearing 1–5 shoots was cut off and transferred to the experimental room. There the plants were kept in a 16 hours day at 30 W/m^2 by two 400 W Philips HPI lamps. The nutrient solution was kept at 20 °C, the mean room temperature was 22 °C and the average relative humidity was about 55%.

2.2. Administration of $^{14}CO_2$

$^{14}CO_2$ was administered from 10–11 a.m. starting 4 hours after the beginning of the light period. First, the shoot to be treated was enclosed in a glass bulb. This glass bulb stood in a series connection with two small washing bottles and a Wisa membrane pump. The first washing bottle contained 25 μ Ci $Na_2\,^{14}CO_3$ from which $^{14}CO_2$ was released by injecting 1 ml 1 N H_2SO_4. After 1 hour the remaining $^{14}CO_2$ was trapped in 2 ml 1 N KOH, injected in the second washing bottle. Shortly after this the glass bulb was removed and the plant was allowed to translocate the labelled assimilates for 24 hours.

2.3. Autoradiography

24 Hours after the end of the $^{14}CO_2$ administration the plant systems were harvested, mounted on Circulon board as fast as possible and freeze-dried at -20 °C. Subsequently they were covered with X-ray film (Kodak No Screen Medical X-ray film NS2T). The exposure time was 1 day. The X-ray film was completely developed.

2.4. Quantitative assessments

The various parts of the plant system, shoots, rhizome parts (including their own rhizome roots) and deep-going root systems were separated and freeze-dried at -20 °C. The dry weight of the separate plant parts was determined and they were all ground to powder in a Retsch Ultra Zentrifugal Mill Z.M.1 with graterholes of 0.5 mm.

At least three samples with an average weight of 4 mg were taken from the powder of each plant part. The samples were solubilized in Soluene 100 (Packard) for 48 hours at 60°C. Plant parts with a weight lower than 15 mg were solubilized without previous grinding. The radioactivity of the samples was counted in a toluene scintillation mixture in the ^{14}C standard channel of a Packard Tri Carb Liquid Scintillation Spectrometer. The amount of ^{14}C present in each sample was calculated in d.p.m./mg. The total amount of ^{14}C present in each separate plant part was calculated from the average values of the various samples taken from that plant part. All experiments were repeated at least three times.

3. RESULTS

3.1. Autoradiographs

Plates 1–3 show the distribution of ^{14}C assimilates after administration of $^{14}CO_2$ to the various shoots of plants with three shoots. In all cases a considerable amount of radiocarbon was retained by the shoot treated with $^{14}CO_2$. All shoots showed an export of radiocarbon in the direction of the rhizome tip. Radiocarbon was found in the roots of the treated shoot and in those of the shoots closer to the rhizome tip; in the youngest shoot, especially in its meristematic tissues and in the rhizome tip. In plants with four shoots (*plate 4–7*) the pattern of radiocarbon distribution proved to be basically the same as that in 3-shoot plants. The only important difference between 3- and 4-shoot plants proved to be the absolute lack of export of radiocarbon by the youngest shoot of the latter (*plate 7*).

The minor importance of radiocarbon translocation through the rhizome in basal direction is conspicious in both plant types (*plate 2, 3, 5* and *6*).

The faint labelling of the mature shoots, situated between the treated shoot and the rhizome tip (*plate 1*, shoot nr. II, *plate 4*, shoots nr. II and III and *plate 5*, shoot nr. II) is assumed to be caused by redistribution of radiocarbon via the xylem and is quantitatively of no importance (*fig. 2*).

The relevance of this explanation can be seen from the experiment represented

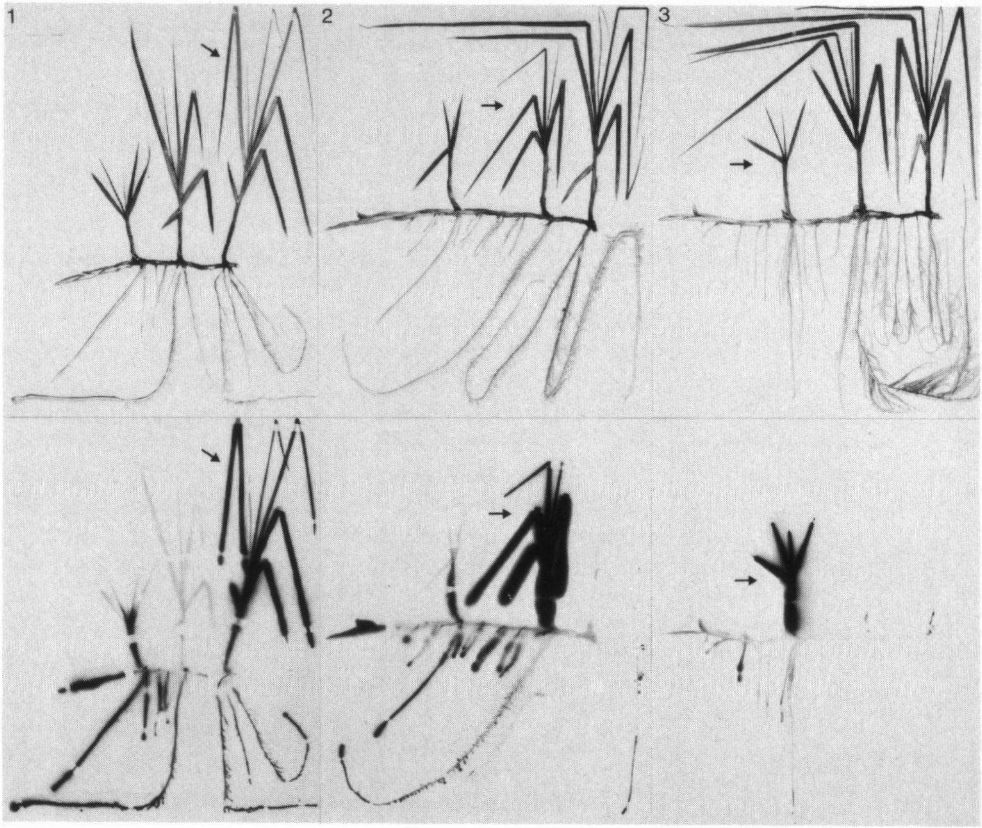

Plate 1–3. Distribution patterns of radiocarbon in 3-shoot plant systems, after administrating the subsequent shoots with $^{14}CO_2$. The arrows indicate the shoot treated with $^{14}CO_2$ (photographs above, autoradiographs below).

in *plate 8*. Here the transpiration of the second youngest shoot (nr. II) was strongly reduced by placing this shoot in a highly humid atmosphere caused by a faint drizzle. The radiocarbon import of the shoot was reduced very much, when compared with its neighbour and with the comparable shoots in *plate 4*. The partial labelling of only one leaflet is probably due to an incomplete reduction of the transpiration. *Plate 9* shows that larger plant systems follow the same distribution pattern as the smaller ones.

3.2. Quantitative assessments

The distribution of the ^{14}C assimilates from each of the shoots of a 4-shoot system has been quantified in *fig. 2*. This quantification confirms the distribution patterns already shown qualitatively in *plate 4–7*. Relative to their weight the younger organs, whether they are shoots, roots or rhizome tip were most success-

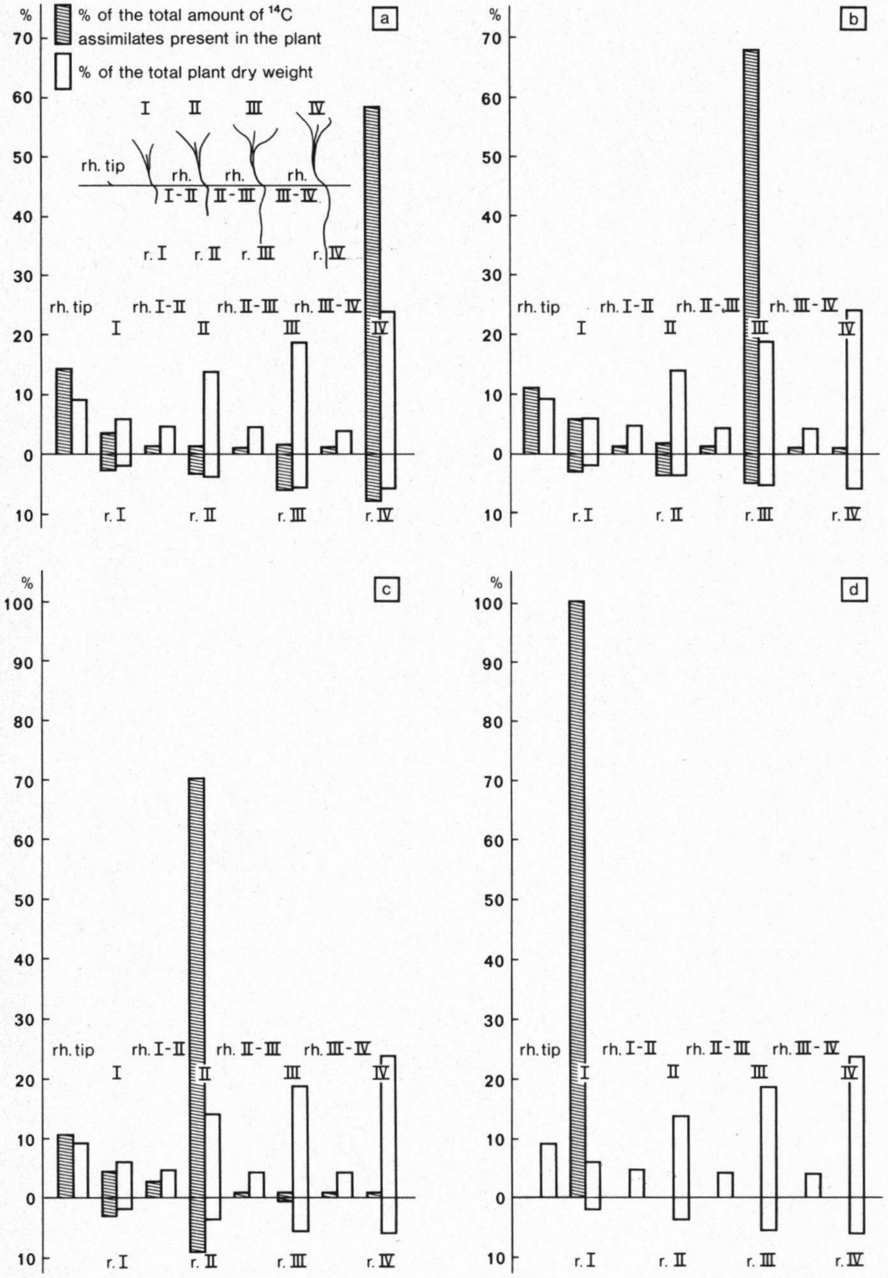

Fig. 2. The quantitative distribution of ^{14}C assimilates, exported by the various shoots in a 4-shoot plant system. $^{14}CO_2$ has respectively been supplied to: IV (a), shoot III (b), shoot II (c) and to shoot I (d).

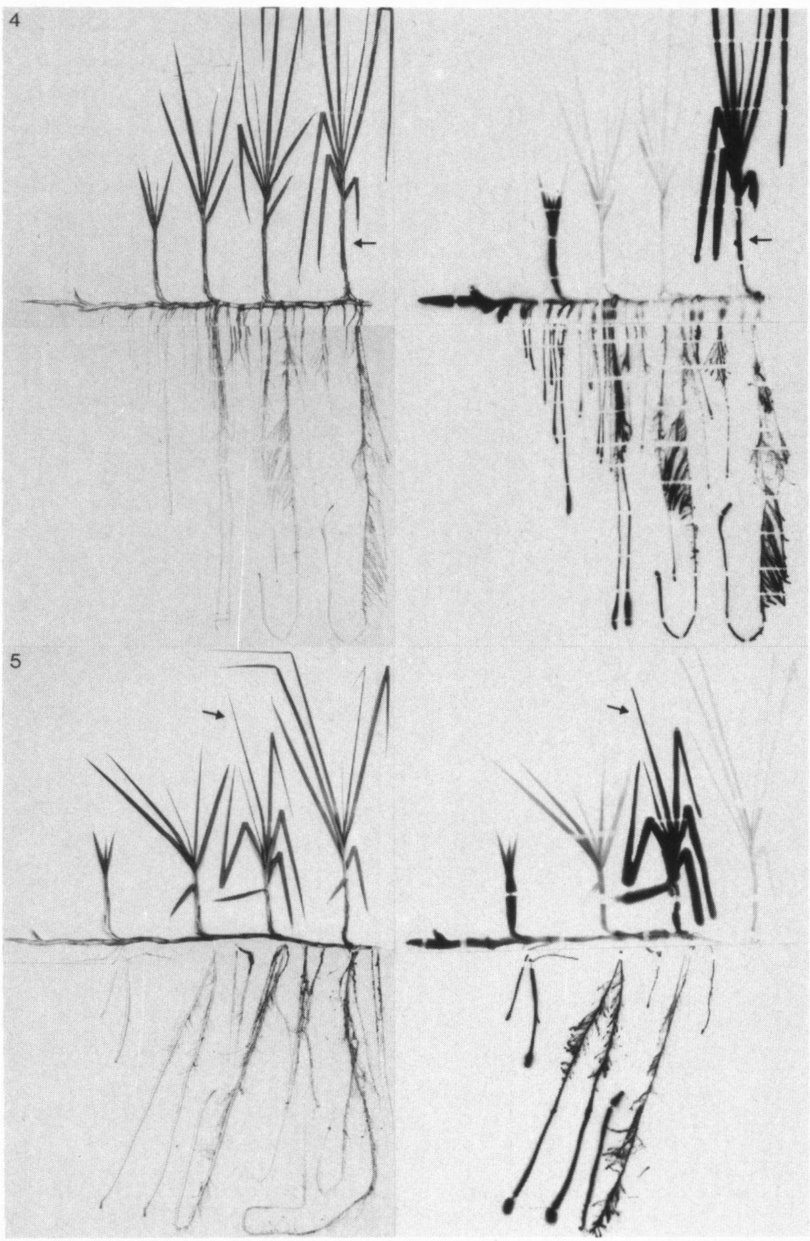

Plate 4–7. Distribution patterns of radiocarbon in 4-shoot plant systems, after administrating the various shoots with $^{14}CO_2$. The arrows indicate the shoot treated with $^{14}CO_2$ (photographs left, autoradiographs right).

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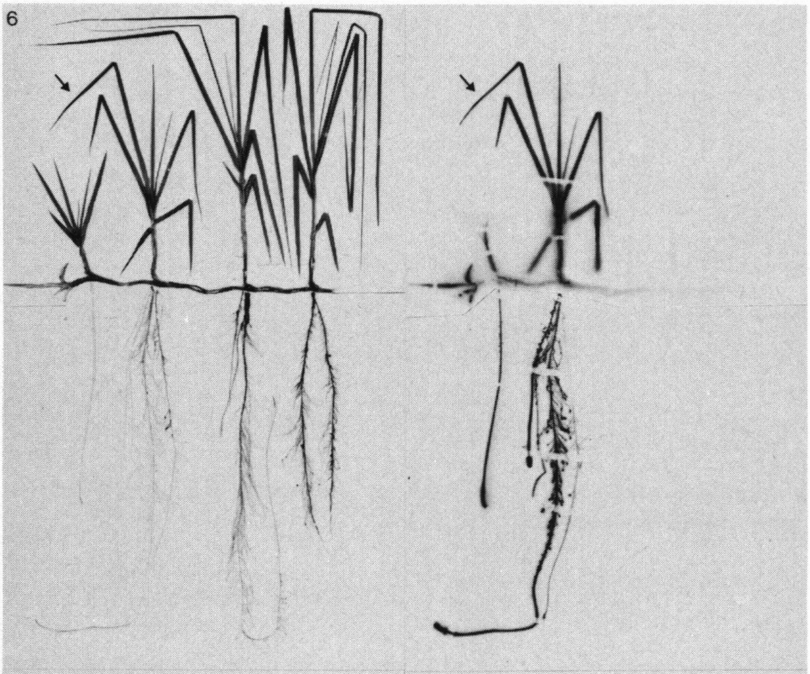

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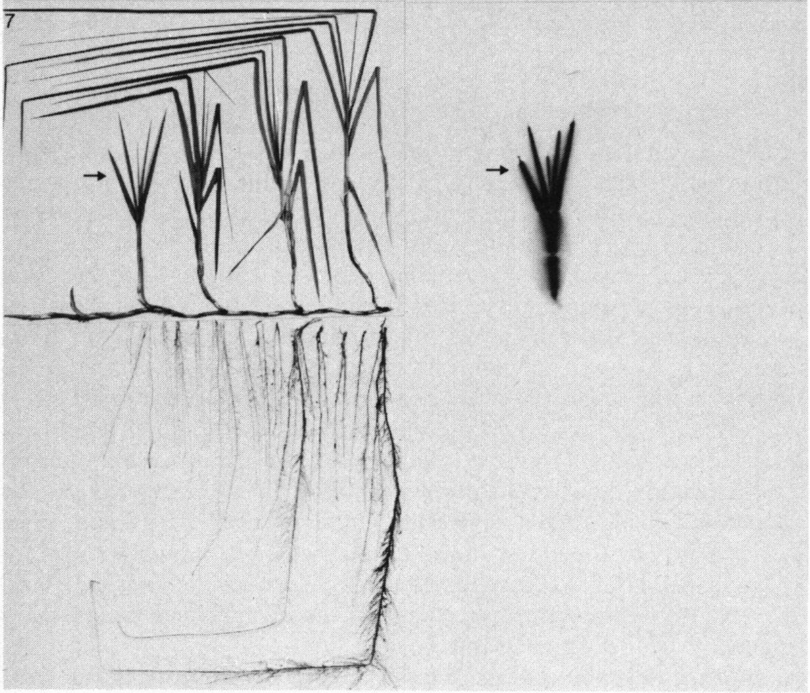

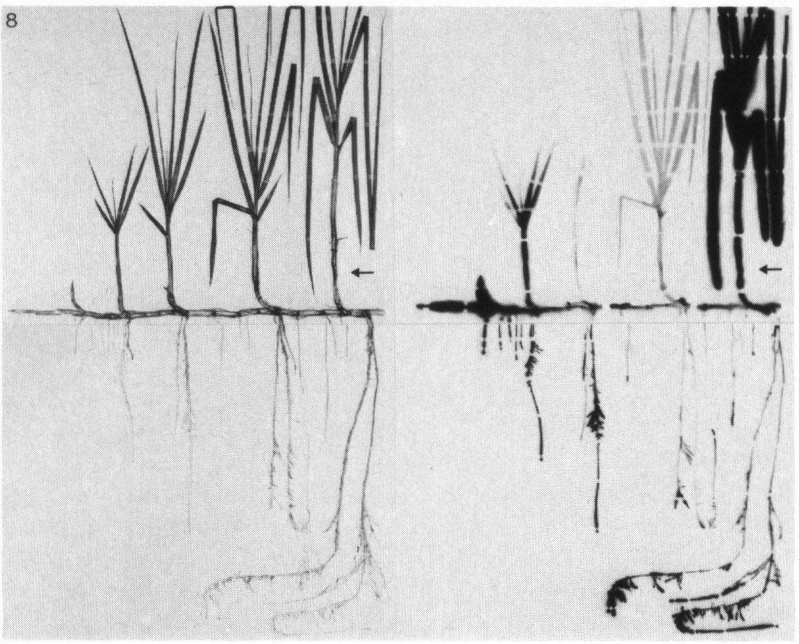

Plate 8. Distribution pattern of radiocarbon in a 4-shoot system, in which the transpiration of shoot II was prevented. Shoot IV was treated with $^{14}CO_2$ (see arrow) (photograph left, autoradiograph right).

ful in attracting assimilates. The import of radiocarbon by mature shoots, by redistribution via the xylem, proved to be of minor quantitative importance.

The percentage radiocarbon exported by a shoot treated with $^{14}CO_2$ proved to change strongly with differing shoot age. The younger the shoots, the smaller is the export percentage of their ^{14}C assimilates. Shoot IV, for instance, exported a little over 40% of the amount assimilated, whereas shoot I did not show any export at all. Shoot II and III showed intermediate values. The export of radiocarbon from the shoots of 1–5 shoot systems is compared in *fig. 3*. Shoot I of a 1-shoot system becomes shoot II when the system has developed into a 2-shoot system and so on. In *fig. 3* the export percentages of the oldest shoot (shoot I, II, II, IV and V respectively) of 1–5 shoot systems are shown. The connecting line (a) represents the relation between the percentage of assimilates exported and the age of the shoot. In fact line a shows the time course of the percentage of assimilates exported by the oldest shoot during the period in which the plant system grows from a 1-shoot system to a 5-shoot system. Similar lines have been obtained by connecting the export percentages of the second oldest shoots of 2–5 shoot systems, etc. (*fig. 3*, line b, c and d).

The export percentage values of the oldest shoot of the plant systems examined (*fig. 3*, line a) showed considerable variation as indicated by the standard errors.

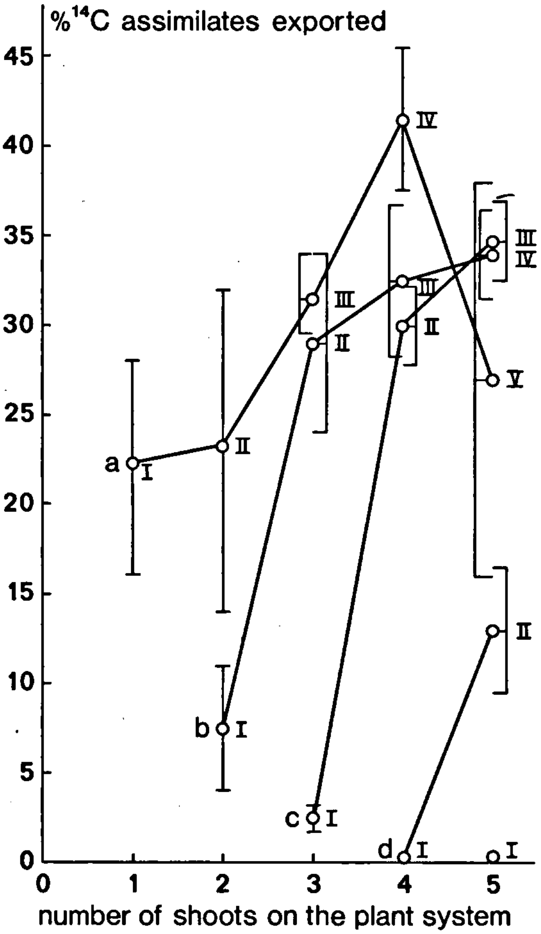

Fig. 3. Export percentages of the subsequent shoots in 1–5 shoot plant systems. The lines (a–d) indicate the changes in the export percentage of a shoot, when a small plant system becomes a bigger one.
The vertical bars indicate the standard errors. For further explanation see text.

Thus the tendency of the change in export percentage with increasing age is less clear here than for the younger shoots (*fig. 3*, line b, c and d). The results obtained for the latter are in good accordance with each other and with those obtained earlier using a different method (Tietema & Vroman 1978). In general we can conclude that under the growth conditions given, a particular shoot starts its export with a low export percentage that will increase during its lifetime and will finally reach an average level of ± 33% of its own assimilation.

The export of radiocarbon from the oldest shoots tends to increase with the size of the plant system (*fig. 3*). However, the youngest shoots show the opposite behaviour (*fig. 4a*). The second youngest shoot behaves in an intermediate way (*fig. 4b*) exporting like an old shoot in 2–4-shoot systems, having an increasing export with increasing plant size, and like a youngest shoot in a 5-shoot system, in which its export decreases drastically. Also the distribution of the exported

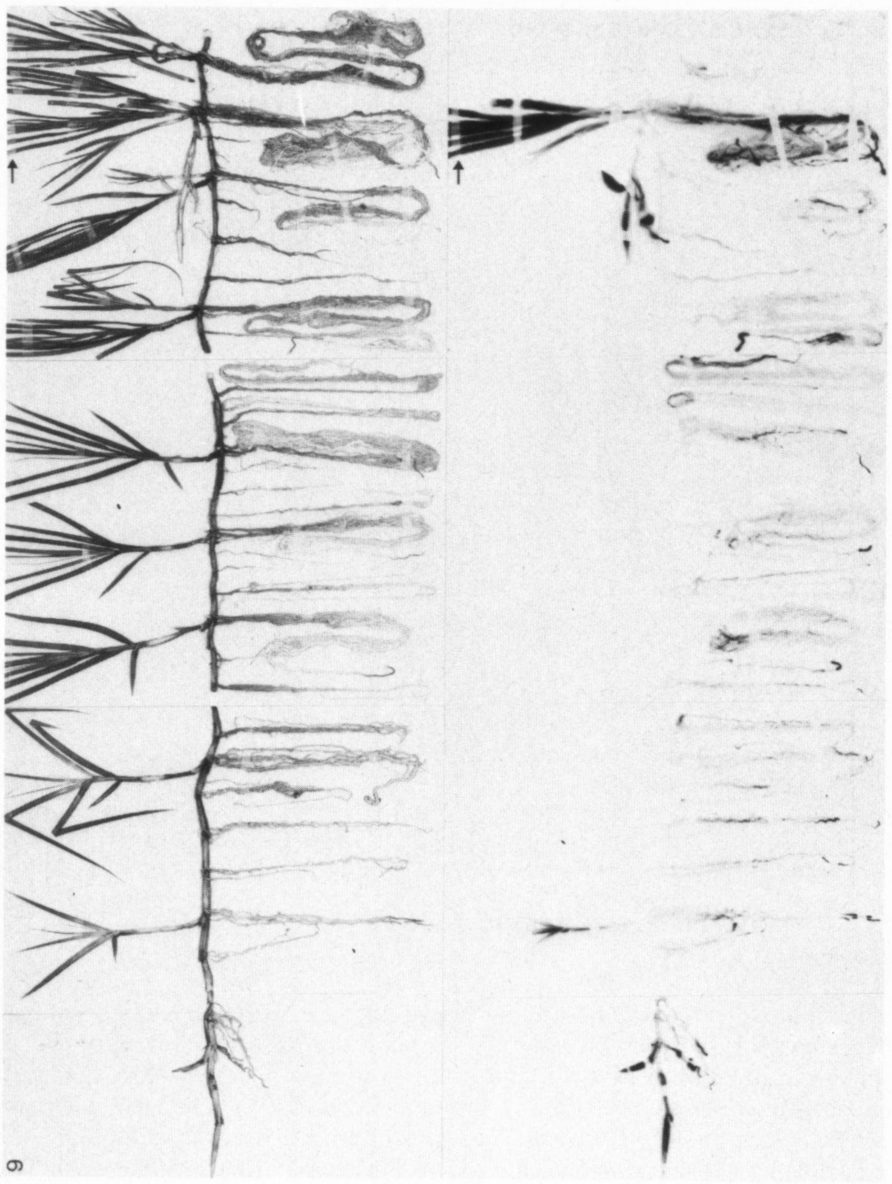

Plate 9. Distribution pattern of radiocarbon in a 9-shoot plant system, in which shoot VIII has been treated with $^{14}CO_2$ (see arrow) (photograph above, autoradiograph below).

Table 1. The amount of ^{14}C assimilates imported by the rhizome tip as a percentage of the total amount ^{14}C recovered from the plant system (± standard error).

Number of shoots on the plant system	$^{14}CO_2$ administered to shoot nr.				
	I	II	III	IV	V
1	18.4 ±6.0				
2	5.4 ±2.7	8.5 ±2.7			
3	1.3 ±0.2	13.8 ±3.3	10.5 ±0.8		
4	0.0 ±0.0	10.3 ±3.1	10.8 ±2.4	14.2 ±3.2	
5	0.0 ±0.0	4.7 ±2.1	7.2 ±2.1	12.4 ±2.5	4.9 ±1.8

Table 2. The amount of ^{14}C assimilates imported by the rhizome tip as a percentage of the amount exported by the respective shoots.

Number of shoots on the plant system	$^{14}CO_2$ administered to shoot nr.				
	I	II	III	IV	V
1	83				
2	72	36			
3	52	47	33		
4	0	34	33	34	
5	0	37	21	36	18

Table 3. The amount of ^{14}C assimilates imported by the roots as percentage of the total amount ^{14}C recovered from the plant system (± standard error).

Number of shoots on the plant system	$^{14}CO_2$ administered to shoot nr				
	I	II	III	IV	V
1	4.5 ±0.9				
2	1.0 ±0.5	6.3 ±3.2			
3	0.5 ±0.1	7.6 ±3.1	12.0 ±1.2		
4	0.0 ±0.0	12.5 ±1.0	12.8 ±3.9	18.8 ±2.9	
5	0.0 ±0.0	4.4 ±0.9	18.6 ±0.8	14.4 ±3.7	11.0 ±3.7

Table 4. The amount of ^{14}C assimilates imported by the roots as a percentage of the amount exported by the respective shoots.

Number of shoots on the plant system	$^{14}CO_2$ administered to shoot nr.				
	I	II	III	IV	V
1	20				
2	13	27			
3	20	26	38		
4	0	41	40	45	
5	0	37	60	42	40

radiocarbon over the various sinks differs quantitatively from one shoot to another. The rhizome tip imports a relatively high amount of radiocarbon from nearby situated shoots (*table 1* and *2*), whereas the roots (all deep-going roots together) import more radiocarbon from the shoots situated at some distance from the rhizome tip (*table 3* and *4*).

4. DISCUSSION

In a plant system like that of a sand sedge, sources and sinks of carbohydrates are related in a rather complex way. Growth of shoots, rhizome tips and roots continues for a long time. Hence assimilate consumption takes place all over the plant system. The production of carbohydrates by the green shoots has to supply not only their own requirements, but at the same time those of the non assimilating plant parts. In the growth conditions used, the mature shoots export 30–35% of the radiocarbon fixed to the non-assimilating parts of the plant (*fig. 3*). In the youngest shoots much more of the radiocarbon fixated is retained and in the bigger plant systems the amount of radiocarbon retained by these shoots even amounts to 100% (*fig. 4a*). In the rhizome the radiocarbon exported moves unidirectionally towards the growing rhizome tip, which imports considerable quantities of the radiocarbon exported (*table 1* and *2*). The unidirectional transport in the rhizome is fed by the export of assimilates from the subsequent shoots on the rhizome. At the same time the roots growing at the nodes of the rhizome act as attraction centers and import their need of assimilates from the translocation stream towards the rhizome tip (*plate 1–8*, *fig. 2*, *table 3* and *4*). The canalized flow of assimilates to the rhizome tip is not drained by the meristems in shoots along the pathway with the exception of the youngest (*plate 1*, *4*, *8* and *9*, *fig. 2*).

The overall distribution pattern of radiocarbon in a sand sedge plant system as presented here is much like that reported for comparable plants. Unidirectional translocation towards the tip of the rhizome or stolon has been reported for several species, e.g. *Saxifraga sarmentosa* (QURESHI & SPANNER 1971), *Ranunculus repens* (GINZO & LOVELL 1973), *Trifolium repens* (HOSHINO 1972) and *Cynodon dactylon* (FORDE 1966). In field studies unidirectional translocation towards the rhizome tip has also been reported for the sand sedge (NOBLE 1976) and for the younger rhizome parts of *Dupontia fischeri* (ALLESSIO & TIESZEN 1975).

In all the examples mentioned above also the roots were supplied with radiocarbon from the translocation stream to the rhizome tip. The absence of assimilate import into the mature shoots along the rhizome as found in the sand sedge plant apparently is not a universal phenomenon. Mature shoots of *Cynodon dactylon* (FORDE 1966) and of *Dupontia fischeri* (ALESSIO & TIESZEN 1975) both import assimilates from the assimilate stream running through the rhizome to its tip. Simultaneously these shoots load assimilates into the translocation pathway in the rhizome. With regard to this aspect the shoots of the latter two

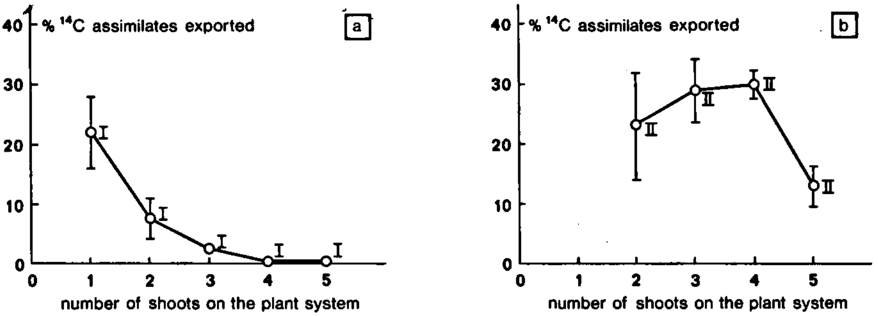

Fig. 4. Changes in the export percentages of the youngest shoot (a) and the second youngest shoot (b) in 1–5 shoot plant systems. The vertical bars indicate the standard errors.

plant species are comparable to the youngest shoot in a 2- or 3-shoot system of the sand sedge plant (*plate 1–3*).

In a sand sedge plant system, the rhizome tip and the roots are more successful in the competition for assimilates to be found in the translocation pathway in the rhizome than the meristematic regions of the subsequent mature shoots on the rhizome. On the other hand the meristematic region of a particular shoot seems to be most successful in claiming assimilates originating from its own leaves. Only the meristematic region of the youngest shoot is able to import assimilates from the translocation stream in the rhizome. Also, this shoot is generally able to retain the complete assimilate production of its own leaves.

However, when the size of a plant system has been reduced very much (e.g. to a 1-, 2- or 3-shoot system) the relationships between sinks and sources change quantitatively. After such a reduction the meristematic region of the youngest shoot no longer succeeds in retaining the whole assimilate production of its own leaves and the youngest shoot starts to export assimilates (*fig. 4a*). In spite of this export the youngest shoots in 2- and 3-shoot systems continue to import assimilates exported by the other shoot(s) (*plate 1* and *2*). When the plant system continues its growth and a new shoot has appeared, the overall assimilate supply of the plant system has been improved so much that the youngest shoot decreases its export, until it reaches zero in a 4-shoot system. In a 5-shoot system the assimilate supply is so abundant that even the second youngest shoot can decrease its export (*fig. 4b*). This decreasing assimilate export by the younger shoots will, at least partly, be accountable for the increasing growth rate reported for those shoots in plant systems of increasing size (Tietema & Vroman 1978).

The ultimate impression obtained from the results discussed above is that intensity of the assimilate export by a shoot is determined by the demand for assimilates in the direct environment of that shoot. The rhizome tip proved to be a very strong sink for assimilates exported by nearby situated shoots (*table 2*). This is seen more often when a strong sink exists close to a source, e.g. the ear and the flag leaf in wheat (Rawson & Hofstra 1969). Although the relative attraction of the rhizome tip for assimilates from nearby shoots is very strong, it should be kept in mind that young shoots do not have a very high production of assimilates and that these shoots tend to decrease their export of assimilates when the plant system becomes bigger. For this reason the major sources for the assimilate supply of the rhizome tip are the shoots situated at some distance from the tip (*table 1*). This is also important from an ecological point of view.

The exploring rhizomatous growth of the sand sedge carries some risk when the rhizome tip enters unfavourable habitats, where new shoots can not grow or produce assimilates. As for its growth the rhizome tip does not depend on assimilates produced by these young shoots, it is possible to cross disadvantageous areas, such as paths or areas in which overblowing with sand occurs. The results presented in *plate 9* and in *table 1*and *2* allow the rhizome tip to cross the situations mentioned above.

In this respect experiments of TIDMARSH (1939) are interesting. He showed that notwithstanding the prevention of the assimilation of the apical shoots, the sand sedge rhizome itself kept growing for at least one metre. Whether this result indicates the maximum length a rhizome can grow under these conditions, is not sure. Preliminary results of our own experiments in the glasshouse have already shown that the physiological capacity is much better.

ACKNOWLEDGEMENTS

The author is grateful to Prof. Dr. R. Brouwer for his stimulating comments during the practical work and the writing of the manuscript. He is also indebted to Dr. O. M. van Andel for her critical reading of the manuscript, to Frouke Gerards-Kuyer for the preparation of the figures and the photographic reproduction of the autoradiographs, to J. J. M. van Doormalen for his assistance during the laborious milling procedure of the plant samples and to Annelies Pons-Bloemen for the correction of the English text.

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