

## ECOPHYSIOLOGY OF THE SAND SEDGE, *CAREX ARENARIA* L. I. GROWTH AND DRY MATTER DISTRIBUTION

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### SUMMARY

The growth and the dry matter distribution of sand sedge plants were followed in time by means of an indirect estimation method. This method enabled us to calculate the time courses of both the growth of the whole plant, and the growth of the individual shoots from measurements of the shoot length, the number of leaves and the length and width of the leaf laminae only.

The growth rate of each individual shoot decreases with time. In the primary shoots 1–7 the amounts of dry weight added during the experiment were equal to each other, indicating a higher growth rate for the younger shoots. A comparison of dry weight production and increase in dry weight of shoots gave the amount of dry matter import or export by those shoots. The dry matter production in the tip part of the rhizome (two shoots, a shoot bud, the rhizome parts and the roots attached to them) proved to be far too small to maintain the growth of the non-assimilating tissue in this part. There must be a considerable export from the older plant part towards the rhizome tip region. It should be mentioned that the results presented here are similar to those obtained from  $^{14}\text{C}$  studies. Because of its simplicity the method we used would be very suitable for use in field studies.

### 1. INTRODUCTION

This study on growth and dry matter distribution in sand sedge plants forms part of an investigation on the physiological properties that permit the far creeping growth of these rhizomatous plants. In studies on plants that grow with rhizomes or stolons it is important to find out to what extent the shoots are dependent on each other (TIDMARSH 1939, GINZO & LOVELL 1973, ALLESSIO & TIESZEN 1975).

There are two main methods of studying dry matter distribution patterns in such a complicated plant system. The most usual approach is to investigate the  $^{14}\text{C}$  distribution pattern after administration of  $^{14}\text{CO}_2$  to a shoot or leaf (FORDE 1966a & b, GINZO & LOVELL 1973, NYAHOZA et al. 1973, ALLESSIO & TIESZEN 1975).

The other method one can apply is to estimate the dry matter distribution indirectly by making use of the correlation between measurable features and the dry weight of plant parts as determined by parallel destructive sampling of comparable plants (DYKYJOVÁ et al. 1970, EVANS et al. 1961, ONDOK 1971).  $^{14}\text{C}$  assimilate distribution patterns have the disadvantage that they show the

situation at a certain moment only. Indirect estimation of the dry matter distribution, on the other hand, allows one to follow changes in dry matter distribution in time without harvesting or damaging the plant under observation. Indirect estimation studies have not yet been used to follow dry matter movements from one part of a plant to another quantitatively, as has been possible in  $^{14}\text{C}$  experiments. Whereas  $^{14}\text{C}$  is useful for short term experiments only, the present study shows that the indirect method can be used successfully to study dry matter distribution patterns in middle term and long term experiments.

## 2. MATERIALS AND METHODS

### 2.1. Plants and plant culture

Sand sedge plants (*fig. 1*) were obtained by vegetative multiplication from a single plant originating from a small sand-drift near Blaricum, province of Noord-Holland, the Netherlands.

Standard plant material for the present experiments was obtained by cutting a young piece of rhizome from an older plant. A standard plant consisted of a rhizome with roots, two green shoots, a shoot bud of 1 to 4 cm length and a rhizome tip.

The plants were grown in containers on coarse sand. Once a week they were supplied with nutrient solution (STEINER 1972), and were watered, when necessary, to keep the sand at field capacity. The plants were grown in a

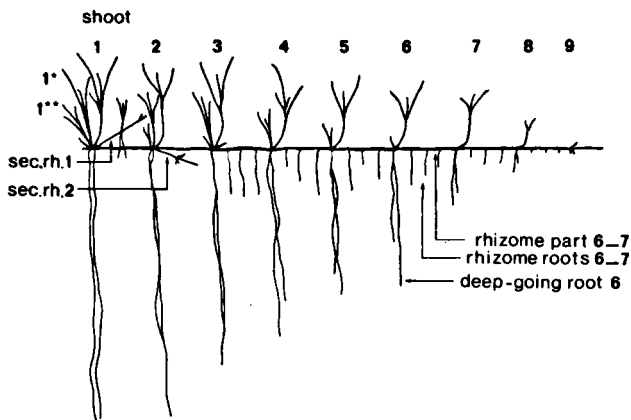


Fig. 1. Sketch of the sand sedge plant system. Indicated are primary shoots, numbered from old to young. Secondary shoots, which received the same number as the primary shoot at whose base they appear, are marked with one asterisk only. Tertiary shoots have two asterisks. Secondary rhizomes are also numbered according to the primary shoot at whose base they emerged, as were the deep-going roots. Rhizome parts are referred to by the numbers of the shoots they connect. Rhizome roots are numbered according to the rhizome part on which they are growing.

For the sake of clarity, no rhizome roots are drawn on the two oldest rhizome parts.

climate room at 20°C, at a light intensity of about 75 W/m<sup>2</sup> (Philips HPI) for 16 hours a day.

Two series of plants were grown. One consisted of plants whose various visible growth values were measured once or twice a week, so that the growth could be followed in an indirect way. The second series was a reference series, from which plants were harvested at regular intervals.

## 2.2. Measurements on the plants used for indirect growth estimation

On the plants used for indirect growth estimation the following values were measured once or twice a week: 1. For all leaf laminae the length, and the width at the base. 2. For each individual shoot, the number of leaves and the shoot length, measured from the rhizome to the tip of the longest leaf. At the end of the experiment the plants were harvested and treated in the way described in 2.3.

## 2.3. Measurements on the harvested plants

At harvest all growth values measured on the first group of plants (2.2.) were also measured on the harvested plants to obtain calibration lines. Thereafter a separation was made of all individual shoots, shoot buds, deep-going roots, rhizome parts between the primary shoots, rhizome roots on these rhizome parts and the rhizome tip. All these plant parts were dried in an oven at 90°C for 24 hours and were all weighed separately afterwards.

# 3. RESULTS

## 3.1. Indirect estimation of the leaf area

From precise measurements of leaf area according to the trapezium method (ONDOK 1968) and measurements of length (*l*) and width (*w*) at the base of leaf laminae the following relation could be calculated:

$$\text{Lamina area} = 0.75 \times l \times w \quad (1)$$

(cf. ONDOK 1968 and KVĚT & MARSHALL 1971).

The leaf area of a shoot is the sum of all lamina areas on that shoot.

## 3.2. Indirect estimation of individual shoot dry weight

The relation between shoot dry weight and the product of shoot length and number of leaves is given by the calibration curve shown in *fig. 2*. By means of this relation and by measuring the shoot length and counting the number of leaves only (*fig. 5*) we were able to follow the development of the dry weight of each individual shoot in the course of time.

## 3.3. Calculation of the amount of dry matter imported or exported by the shoots

An overall picture of the calculation which led to the determination of the import or export of dry matter by individual shoots of a plant is given in *fig. 3*.

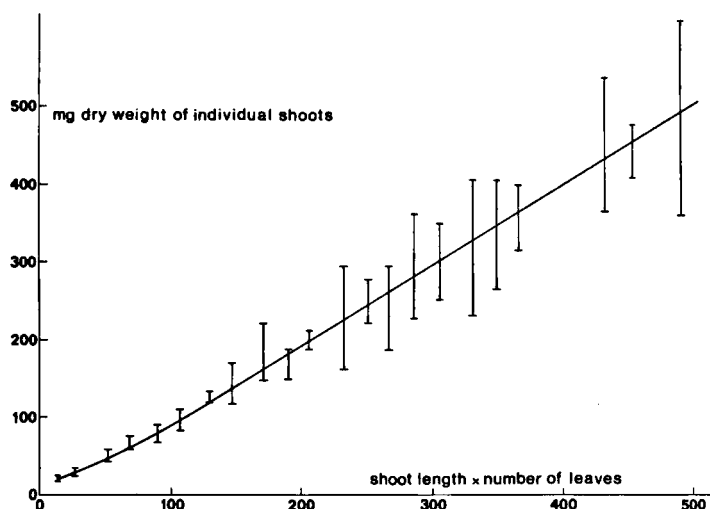


Fig. 2. The relation between individual shoot dry weight and the product of shoot length (cm) and number of leaves. The vertical bars indicate the 95% confidence interval.

The Leaf Area Ratio (LAR), i.e. the ratio between leaf area and plant dry weight ( $\text{cm}^2 \cdot \text{mg}^{-1}$ ), plays a central part in this calculation.

At first the LAR was determined in the series of plants harvested at different ages. The result (fig. 4) was used as a calibration line. The LAR was found to increase slightly in time. The explanation for this is that the rhizome part is relatively large in a young growth stage; in older stages, however, the contribution of the rhizome to the total weight is somewhat lower due to an initially higher growth rate of the shoots.

A similar tendency was found after a harvested plant had been cut into parts that corresponded in size with the plant at different times during its growth.

The time course of the LAR calculated for a single plant from these plant parts was found to run parallel with the time course of the LAR calculated from the harvested plant series (fig. 4).

We decided to use the LAR at the time of harvest as a base for the dry matter balance calculations. From this point the development of the LAR in time could be read from a line parallel to the calibration line. When the time courses of the leaf area and the LAR were known, the total dry weight of a plant could be computed at any moment, without destruction of the plant (fig. 7). From the increase in dry weight in time the Relative Growth Rate (RGR;  $\text{mg} \cdot \text{mg}^{-1} \cdot \text{day}^{-1}$ ) could be calculated. The Net Assimilation Rate (NAR;  $\text{mg} \cdot \text{cm}^{-2} \cdot \text{day}^{-1}$ ) could be obtained from:

$$\text{NAR} = \text{RGR} \times \text{LAR}^{-1} \quad (2)$$

From the measurements of the leaf area of each shoot at time intervals of 2–8 days, the time course of the growth in leaf area of the individual shoot was obtained (fig. 6). Then leaf area and NAR were used to calculate the amount of

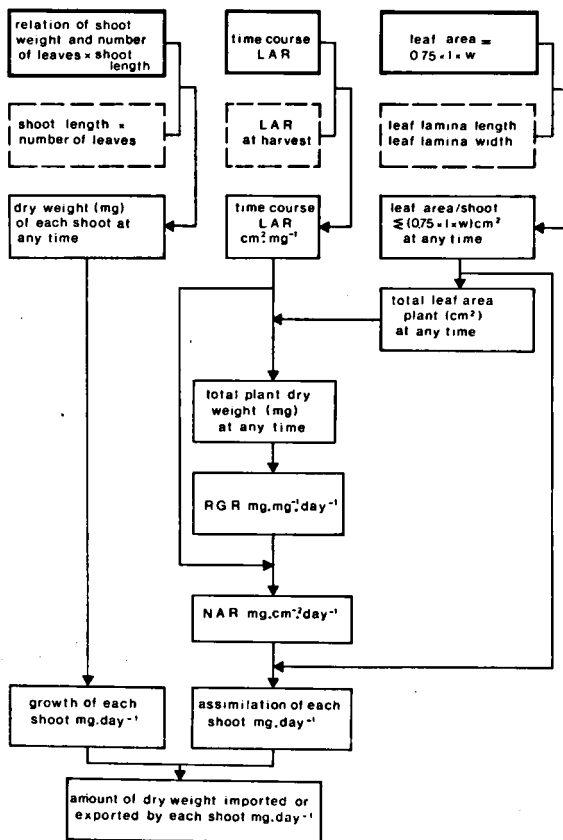


Fig. 3. The scheme of calculations that leads to the determination of the amount of assimilate import or export of a shoot. The thickly lined compartments contain calibration lines or relations which were determined from a series of reference plants.

The compartments in the dotted lines show the real measurements on the plant followed. All other compartments were calculated with the information obtained from the first two types of compartments.

dry matter produced by each shoot every two days. The amount of dry matter that was built into each shoot in the course of every two days could be read from fig. 5.

Subtraction of the dry matter increase of a shoot during two days from the production of the same shoot during the same interval gave the surplus or shortage on the assimilate balance of that shoot. If there is a shortage of assimilates, this will be compensated by import from the shoots that produce a surplus.

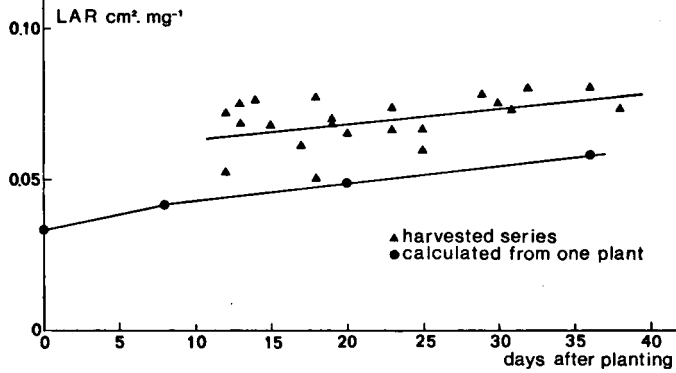


Fig. 4. The time course of the Leaf Area Ratio.

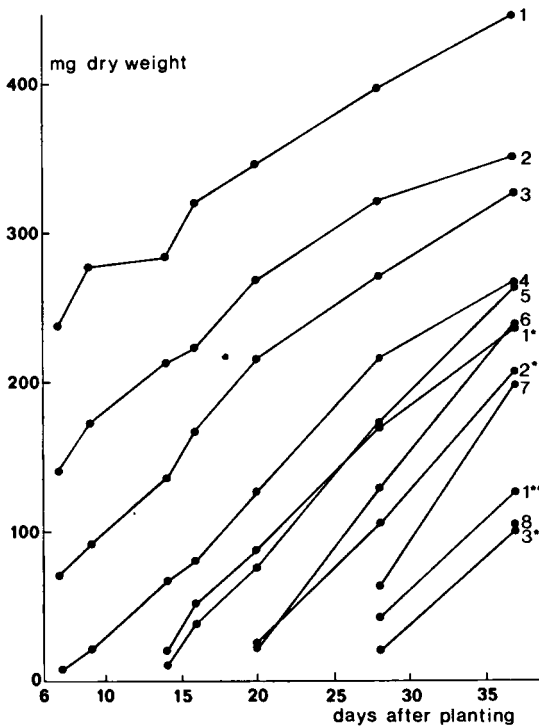


Fig. 5. Increase in dry weight of the individual shoots. Dry weights computed from shoot length  $\times$  number of leaves.

### 3.4. Growth and dry matter balance

The results obtained with the method described above are demonstrated on one plant chosen from a group of seven plants. There were no essential differences between plants, but the fact that the development of new shoots and secondary rhizomes was not completely synchronized made statistical treatment of doubtful benefit.

The dry weight of the shoots increases almost linearly, but tends to decrease with increasing shoot age (*fig. 5*). Young primary shoots have a higher growth rate than older ones. The growth rate of secondary shoots is lower than the growth rate of the primary ones of the same age (*fig. 5*).

Like the growth rate of the dry weight, the growth rate of the leaf area decreased with increasing shoot age (*fig. 6*). The growth rate of the leaf area in secondary and tertiary shoots is conspicuously lower than in primary shoots.

The growth of the plant as a whole (*fig. 7*) calculated from the LAR and the

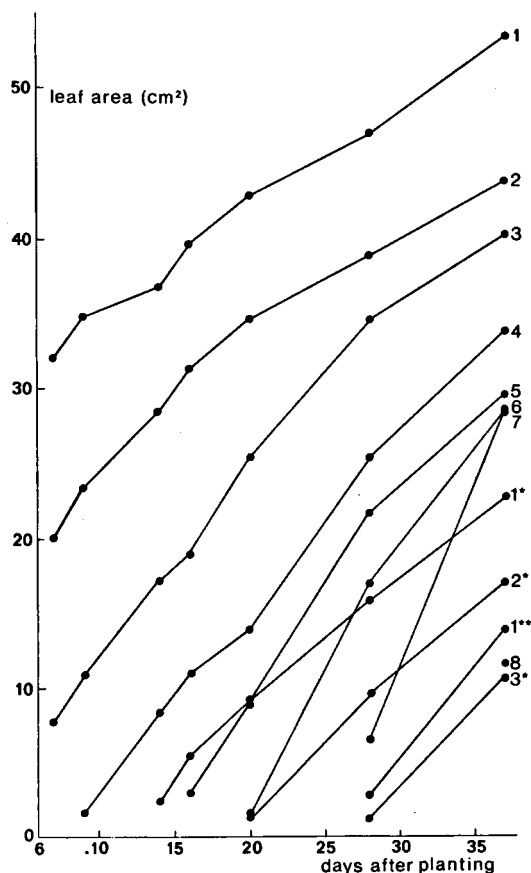


Fig. 6. Increase of leaf area of individual shoots. Leaf area computed by  $\Sigma(0.75 \times \text{lamina length} \times \text{lamina base width})$ .

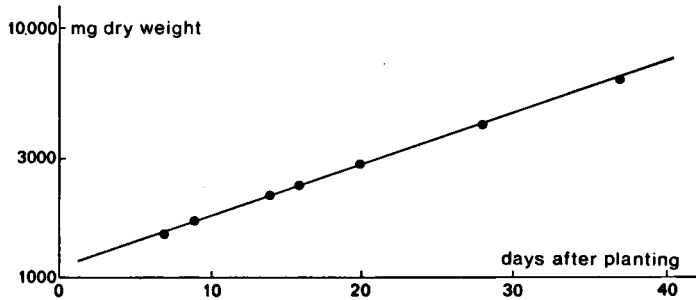


Fig. 7. Dry matter increase of the whole plant.

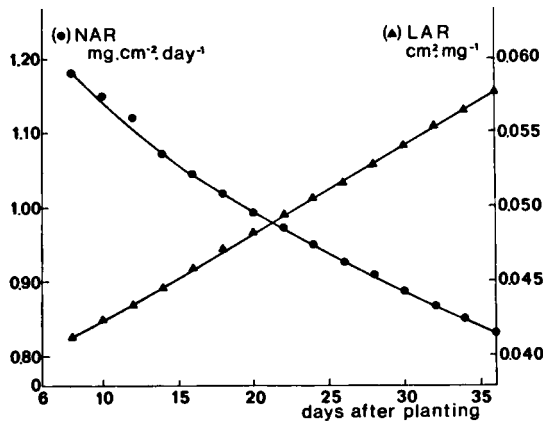


Fig. 8. Time course of the Net Assimilation Rate and the Leaf Area Ratio.

total leaf area of the plant shows that the total dry weight of the plant increases exponentially, with a RGR of  $0.048 \text{ mg.mg}^{-1}.\text{day}^{-1}$ . The NAR calculated according to equation (2) decreases in time (*fig. 8*). This is the consequence of its relationship with a constant RGR and an increasing LAR.

There is a great similarity between the changes that occur in the dry matter balance of the shoots in the course of time (*fig. 9*). The final percentage of assimilates retained by the shoots is 10–20% of their own net assimilation. This results in an export of 80–90% of their assimilate production.

Absolute amounts of import or export are shown in *fig. 10*. The oldest shoots show an initially high export followed by a temporary decrease. In younger shoots this feature becomes less important.

### 3.5. Dry matter distribution at harvest

At the end of the experiment the dry matter distribution in the plant (*fig. 11*) shows that the weights of the three oldest primary shoots deviate from those of the other primary shoots (*fig. 11a*). *Fig. 5* shows that shoots 1 to 7 increase in weight with equal amounts of dry matter during the experiment. These amounts



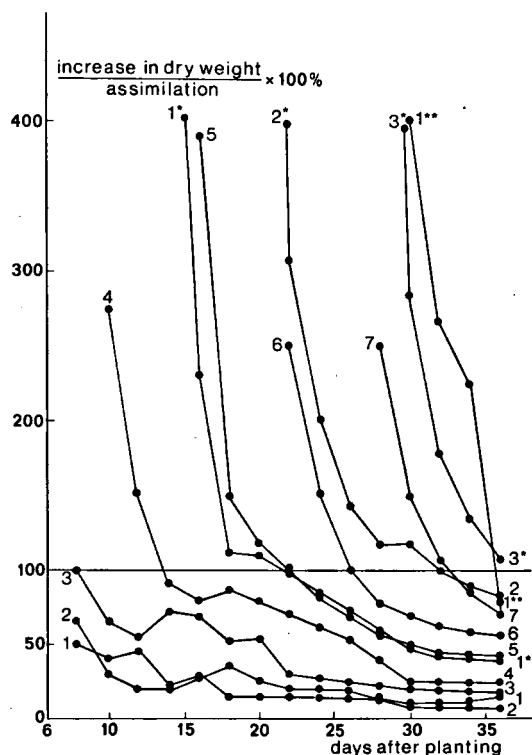


Fig. 9. The growth of each shoot, expressed as a percentage of its own assimilation. Above the 100% line shoots import assimilates, below that line they start to export assimilates.

of dry matter are approximately 250 mg, which is in fact the mean weight of shoots 4 to 7 at the end of the experiment. If this value is subtracted from the weights of the shoots 1 to 3 at harvest time, the dry weights of these shoots at the moment of planting are computed roughly. It seems that the growth of the standard plant is arrested when this plant is cut off from a bigger plant system (see 2.1). When the standard plant starts its visible growth, about a week after planting, the higher growth rate of the youngest shoot is levelled off and all three shoots start growing at approximately the same speed. Each newly formed primary shoot starts growing faster than the previous one, thus achieving the dry matter distribution of *fig. 11a*. Differences in growth rate do not occur among secondary shoots (*fig. 5*). At harvest this results in dry weights that increase proportionally to the age of the secondary shoot (*fig. 11b*). The same holds for the tertiary shoots (*fig. 11c*) and the secondary rhizomes (*fig. 11e*).

In the dry weight distribution over the subsequent parts of the main rhizome (*fig. 11f*) and the deep-going roots (*fig. 11g*) the parts of the plant present at planting are recognized again as exceptional in the whole sequence. The dry weights of the rhizome roots (*fig. 11h*) do not show a regular pattern.

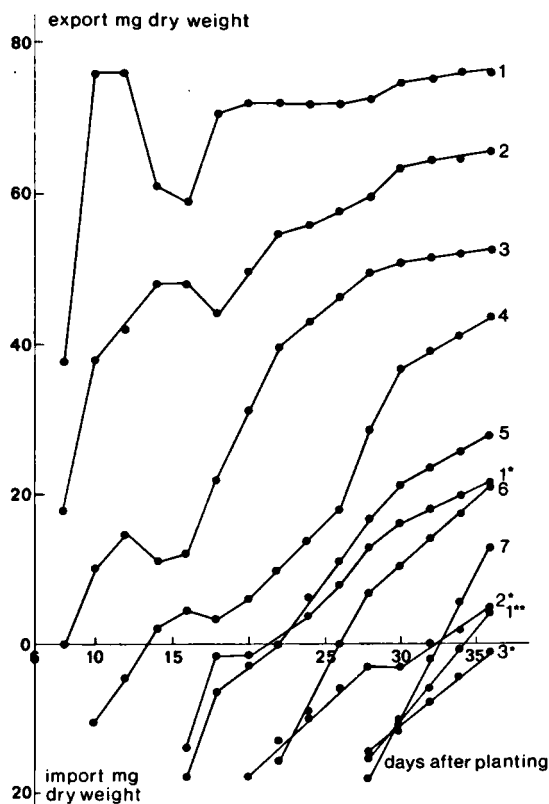


Fig. 10. Time course of absolute import or export per shoot.

#### 4. DISCUSSION

The indirect estimation method presented here enabled us to determine the increase in dry matter of individual shoots in the course of time. At the time of harvest these predicted shoot weights proved to be in good accordance with the real shoot dry weights (*fig. 11a, b and c*). The difference between our method and that of EVANS *et al.* (1961) is that we were able to follow the growth of individual shoots, whereas they could follow the growth of whole grass tussocks only.

Shoots 1 to 7 showed the same net increase of dry matter during the experiment. Since these shoots differ in age, this feature must have been caused by a higher growth rate of the younger shoots.

A comparable feature was reported by PIETERS (1974) in a study on the growth of poplar leaves. The higher growth rate of the younger poplar leaves proved to be caused by the initiation of larger leaf primordia than in older leaves. This was due to the initiation of more cells, each of which grows to a size equal

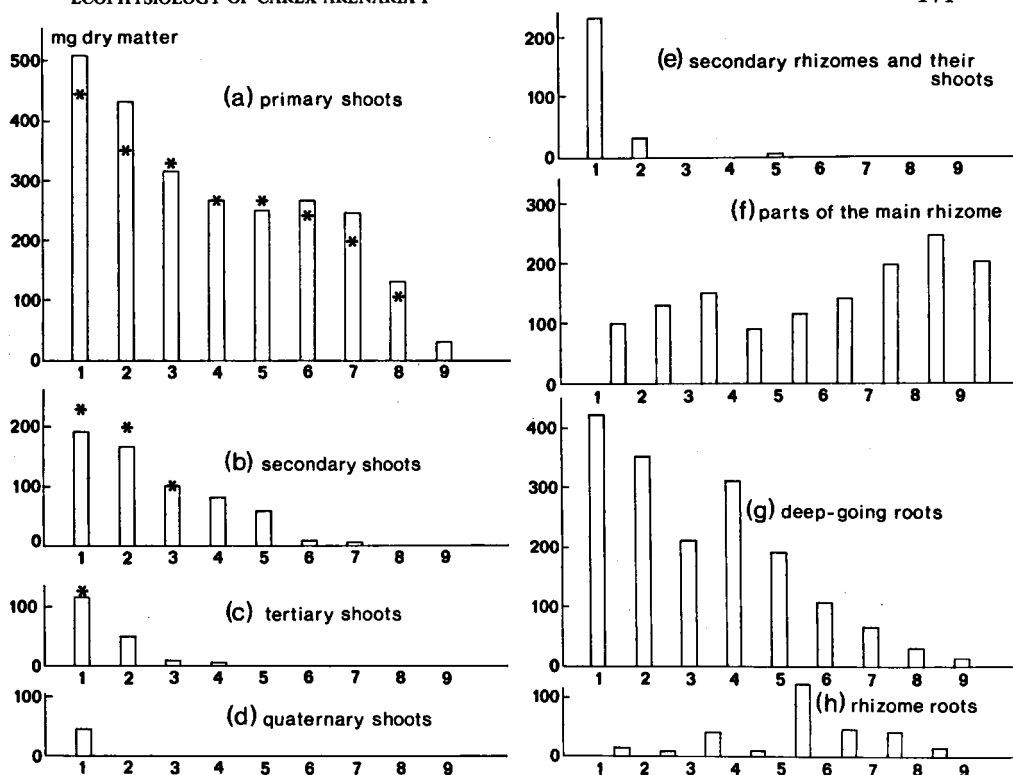


Fig. 11. The distribution of dry matter over the different plant parts actually measured at harvest time. For clarity all different plant constituents are presented separately. The asterisks in the shoot columns in a, b and c indicate the dry weight of the shoot, as predicted by the indirect estimation method (fig. 5). Shoots without an asterisk were still below the soil level at harvest. In the dry weight of the secondary rhizomes the shoots on these rhizomes are included.

to that of the cells in smaller leaves. Transposing these results to our experiments this means that the higher growth rate of younger primary shoots can be explained by an increase in the number of primordium cells initiated. The lower growth rate of secondary and tertiary shoots is probably caused by the initiation of smaller sized shoot primordia. The cause of the initiation of these smaller primordia is probably a difference in the assimilate supply to different parts of the plant. This suggestion could fit in with the observation that increased light intensity causes an increase in primordium size in poplar (PIETERS 1974). If we examine the dry matter balance of the tip part of the plant (shoot 7, 8 and 9, rhizome parts and roots attached to them) it becomes clear that the rhizome of a sand sedge plant is actively involved in dry matter translocation.

The ratio of shoot dry weight to dry weight of the remainder of this plant part is 0.33 (from fig. 11), which means that of all assimilates 75% has been

used for growth of the rhizome and the roots in this plant part. The only shoot that exports assimilates on this plant part is shoot 7. Since the export from this shoot amounts only to 25% (fig. 9) of its own production, this amount will be insufficient to maintain the growth of the tip part. Hence considerable import from the rest of the plant has to be assumed. This implies that the arrested growth of the rhizome that followed the cutting of tip parts from a big plant system as reported by TIDMARSH (1939), was probably caused by an assimilate shortage in the rhizome tip.

Import of assimilates into tip parts of a plant with a growth habit similar to that of the sand sedge is also reported from  $^{14}\text{C}$  distribution studies in *Cynodon dactylon* (FORDE 1966a) and in *Ranunculus repens* (GINZO & LOVELL 1973).

Although the present study does not indicate to what importing part the assimilates exported by one shoot are moving, we were able to determine the total amount of assimilates exported or imported by each shoot. We were also able to make it clear that there has to be a translocation of dry matter along the rhizome towards the rhizome tip. The method used gave detailed results which can be compared with results obtained in studies on  $^{14}\text{C}$  distribution.

An additional advantage of the method we used is that dry matter distribution patterns can be predicted from rather simple measurements, which can easily be performed in the field.

#### ACKNOWLEDGEMENTS

The authors are grateful to Prof. Dr. R. Brouwer for his stimulating comments during the practical work and the writing of the manuscript. They are also indebted to Drs. A. J. E. van Bel, Dr. P. Wolswinkel and Drs. C. Papenhuyzen for their critical reading of the manuscript, to W. van Hiele for the preparation of the figures and to J. J. M. van Doormalen for his technical assistance during the experiments.

#### REFERENCES

- ALLESSIO, M. L. & L. L. TIESZEN (1975): Patterns of carbon allocation in an arctic tundra grass, *Dupontia fischeri* (Gramineae), at Barrow, Alaska. *Amer. J. Bot.* 62: 797–807.
- DYKJOVÁ, D., J. P. ONDOK & K. PRIBÁŇ (1970): Seasonal changes in productivity and vertical structure of reed stands (*Phragmites communis* Trin.). *Photosynthetica* 4: 280–287.
- EVANS, R. A., R. E. ECKERT & F. E. KINSINGER (1961): A technique for estimating grass yields in greenhouse experiments. *J. Range Management* 14: 41–42.
- FORDE, B. J. (1966a): Translocation in grasses. I. Bermuda grass. *New Zeal. J. Bot.* 4: 479–495.
- , (1966b): Translocation in grasses. II. Perennial Ryegrass and Couch grass. *New Zeal. J. Bot.* 4: 496–514.
- GINZO, H. D. & P. H. LOVELL (1973): Aspects of the comparative physiology of *Ranunculus bulbosus* L. and *Ranunculus repens* L. II. Carbon dioxide assimilation and distribution of photosynthates. *Ann. Bot.* 37: 765–776.

- KVĚT, J. & J. K. MARSHALL (1971): Assessment of leaf area and other assimilating plant surfaces. In: *Plant photosynthetic production*. (Z. ŠESTÁK, J. ČATSKÝ & P. G. JARVIS eds.) Junk, The Hague.
- NYAHOZA, F., C. MARSHALL & G. R. SAGAR (1973): The interrelationship between tillers and rhizomes of *Poa pratensis* L. An autoradiographic study. *Weed Res.* 13: 304–309.
- ONDOK, J. P. (1968): Measurement of leaf area in *Phragmites communis* Trin. *Photosynthetica* 2: 25–30.
- , (1971): Indirect estimation of primary values used in growth analysis. In: *Plant photosynthetic production*. (Z. ŠESTÁK, J. ČATSKÝ & P. G. JARVIS eds.) Junk, The Hague.
- PIETERS, G. A. (1974): The growth of sun and shade leaves of *Populus euramericana* “Robusta”, in relation to age, light intensity and temperature. *Meded. Landbouwhogeschool Wageningen* 74: (11).
- STEINER, A. A. (1972): Plantenteelt zonder aarde. *Landbouwk. Tijdschr.* 84: 428–436.
- TIDMARSH, C. E. M. (1939): *The ecology of Carex arenaria* L. Thesis. Cambridge.