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LIFE FORMS OF THREE SENECIO SPECIES IN RELATION TO ACCUMULATION AND UTILIZATION OF NON-STRUCTRAL CARBOHYDRATES

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SUMMARY

Within the section *Jacobaei* (Thunb.) Dumort. of the genus *Senecio* L. the species *S. aquaticus* L. is a monocarp while *S erucifolius* L. is a perennial. The life form of *S. jacobaea* L. is somewhat intermediate, tending more to monocarpism than to perenniality. As a result of flowering, the carbohydrate reserves in all structures of *S. aquaticus* gradually fall to very low values when the seed is maturing. Following a slight decline in summer, the carbohydrate reserves of *S. erucifolius* increase from the onset of flowering until the aerial parts die off in autumn. At this time the highest concentrations are found in the rhizomes and the roots.

Though decreasing significantly during the generative phase of development, and even when this stage has passed, the carbohydrate reserves of *S. jacobaea* remain at a relatively high level.

Neither *S. aquaticus* nor *S. jacobaea* develop specific structures for the storage of carbohydrates, like the rhizomes of *S. erucifolius*, which facilitate vegetative reproduction. Still, (adventitious) shoots at the roots and stembases may be formed. The carbohydrate reserves of *S. aquaticus* are insufficient for these shoots to develop into new individuals.

Differences between the three species in the changing patterns of soluble carbohydrate reserves reflect the interspecific diversities of life form.

1. INTRODUCTION

The significance for the development of plants of their nonstructural organic compounds has been widely investigated. The majority of such studies dealt with agricultural crops and perennial weeds. In most cases, attention focussed on productivity and regrowth, following defoliation. Relatively little attention has been paid to the interrelation between non-structural organic compounds and such phenomena as longevity, life form and reproduction strategy.

Molisch (1928) was one of the first to note the connection between monocarpism and carbohydrate metabolism. He postulated that senescence and death were caused by exhaustion of organic reserves, resulting from their translocation to developing seeds and fruits. This proposition proved to be false. For instance, Archbold & Mukerjee (1942) demonstrated that carbohydrates stored in barley grains originate primarily from photosynthates of the ear.

Still, the conception of Molisch that senescence and death of monocarps are closely associated with flowering and fructification, is generally accepted. This conclusion may be derived from a review, presented recently by WOOLHOUSE (1974). In addition, MOONEY (1972) stressed the prominent role played by carbohydrate reserves with regard to longevity and reproduction strategy.

Of late, much attention has been drawn to the net allocation of energy during the life cycles of organisms. Concepts like r- and k-selection (MACARTHUR, 1961), reproductive strategy (HARPER, 1967) and reproductive effort (OGDEN, 1968) were developed to solve problems in the fields of evolution- and population-ecology. Questions on how the limited energy is employed play a leading part. Mathematical models, such as discussed by LEON (1976), have contributed to realize the significance of life histories for the maintenance and expansion of populations in different habitats. However, these studies are almost exclusively based on estimates of dry matter and their derived caloric values without cognizance of the carbohydrate reserves.

The question of how monocarpic and perennial herbs differ physiologically is beyond the scope of the above-mentioned studies. No resort needs to be taken to parameters like "reproductive effort" to explain why certain plants are capable of vegetative reproduction, failing in others.

It has been presumed that, following fructification and withering of aerial parts, perennial herbs are capable of regeneration from buds, when adequately supplied with previously stored carbohydrates. Three *Senecio* species, all belonging to the section *Jacobaei* (Thunb.) Dumort., were employed to test the hypothesis. As reported by CLAPHAM et al. (1962) and also found by the author, the species have an equal number of chromosomes ($2\ n = 40$). Interfertility is illustrated by the frequent occurrence of fertile offsprings with intermediate morphological characteristics that were found when the three species were cultivated in close proximity. Life forms, described by BAKKER (1966), CLAPHAM et al. (1962), HARPER & WOOD (1957), HEGI (1929), HEUKELS & VAN OOSTSTROOM (1973), and ROTHMALER (1958) are as follows:

S. aquaticus L.: winter annual to biannual*)
S. jacobaea L.: biannual to perennial
S. erucifolius L.: perennial

Vegetative propagation is possible for each of the three species:

a. by means of adventitious sprouts on the roots,
b. from buds at the stem basis,
c. from short rhizomes at the underground part of the stem basis.

a. CAIRNS (1938) described in detail how the propagation from adventitious sprouts of *S. jacobaea* takes place.

The formation of adventitious sprouts on the cut surface of excised roots of both *S. jacobaea* and *S. aquaticus* was observed repeatedly by the author. In the case of *S. jacobaea*, these sprouts may develop into mature plants. The ones of *S. aquaticus* soon withered to death.

b. muds on the rosette crowns of *S. aquaticus* and *S. jacobaea* produce multiple rosettes. Those on the stem basis of mature individuals may develop into

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*) nomenclature after HEUKELS & VAN OOSTSTROOM (1973).

flower bearing short stems. In the case of *S. jacobaea*, buds on the stem basis may also develop into rosettes with adventitious roots. Given favourable weather conditions, the small autumn rosettes thus formed may grow out in the following season and, after following a second wintering, develop into mature plants. The partially delayed flowering of multiple rosettes until the succeeding season exhibited by both *S. aquaticus* and *S. jacobaea*, should not be mistaken for the mode of vegetative propagation, as outlined above.

c. Propagation by means of rhizomes is typical for *S. erucifolius*. The rhizomes are formed in the late summer, soon after the onset of flowering. In the autumn, new sprouts that emerge from these develop into overwintering rosettes.

Although each of the three species appear capable of vegetative propagation, our observations showed that, in effect, such takes place only in *S. erucifolius* and to a limited extent in *S. jacobaea*. The question arises whether actual differences in reproductive behaviour can be related to the preceding accumulation of non-structural carbohydrates and their subsequent utilization as a source of matter and energy.

To this purpose the sole estimation of dry matter allocation falls short. The same can be remarked about the distribution of free energy in plants. The latter approach, widely followed after the publication of LONG (1934), provides values that show a narrow correlation with dry matter-minus-ash data. Concurrently HICKMAN & PITELKA (1975) question the value of calorimetric methods for the purpose of establishing energy allocation patterns in plants with primarily carbohydrate seed reserves. Dry matter and calory data only provide information about the energy allocated to different organs. They reveal little about the potential availability of this energy (VERDUIN 1972), particularly with regard to vegetative reproduction. With this object in mind, mobilizable energy reserves must be distinguished. In many instances separation of these from the bulk of dry matter can be realized with sufficient accuracy by estimating the readily hydrolizable carbohydrates.

2. METHODS AND MATERIALS

In 1972 achenes of the three species were collected at the following sites, all in the Netherlands at a latitude of 53°N:

S. aquaticus: a pasture on peat in the valley of the Hunze stream, N.E. from Gieten in the province of Drenthe.

S. jacobaea: the inner dunes on the West-Frisian island of Schiermonnikoog.

S. erucifolius: a road side on clay in the NW of the province Friesland.

Germination was effected in March 1973 by incubating the achenes in petridishes on moist filter paper at a temperature of 25°C. Seedlings were raised in a heated greenhouse. The minimum temperature was 18°C and supplementary light from fluorescent lamps was supplied to a daylength of 16 hours. The potting medium consisted of a 1 : 1 mixture of fertilized peat and coarse quartz sand.

In May 1973 *S. erucifolius* seedlings were transplanted to the experimental garden at Haren in the province of Groningen, the Netherlands, at a latitude of 53 °N. In order to prevent possible vernalization by cold spells in May and June, the transplanting of *S. aquaticus* and *S. jacobaea* seedlings to the same out-of-door locality did not take place until July. The loamy sand of the experimental garden had been left unfertilized for the past 10 years. The soil organic matter content measured 3.5 % and the pH, determined in a 0.1 n KCl suspension, was 4.5. The seedlings received neither manure nor fertilizers.

As anticipated, all the plants of *S. erucifolius* flowered in August and produced daughter rosettes in the autumn of 1973. On the other hand, the transplants of *S. aquaticus* and *S. jacobaea* remained in the rosette stage until the summer of 1974.

From May until September 1974, on seven dates (viz. 28 May, 17 June, 1 and 15 July, 5 and 19 August and 11 September), samples were drawn from each of the three species. The eighth and final sampling took place on 13 January 1975. On each occasion, 5 plants per species were dug up. In the case of *S. erucifolius*, the offsprings which originated vegetatively from a seedling, were treated as belonging to one and the same individual. The last samples drawn from *S. erucifolius* were limited to rhizomes and young rosettes with their adhering roots. Of the two other species, only the stem basis and the roots were sampled as still living structures.

The plants were rinsed with tap water and subdivided into the following parts:

1. *Roots*. As described by HARPER & WOOD (1967) the primary root of *S. jacobaea* cannot be distinguished from the numerous adventitious roots. The same applies to the other species.

Some differentiation in thickness takes place. This is most pronounced with the roots of *S. erucifolius* and least with those of *S. aquaticus*.

2. *Stem basis*. It entails both crowns of rosettes as well as the swollen subterraneal parts of stems.
3. *Stems*.
4. *Leaves*. All leaves are lumped together.
5. *Capitula*. Not all the achenes of *S. erucifolius* had matured fully.
6. *Rhizomes*. Only *S. erucifolius* had developed rhizomes and young sprouts that were included in this subsample.

After this separation, the total dry weight of the subsamples was determined after being dried in a ventilator oven at 70 °C. Final grinding to < 0.5 mm took place in a hammer mill. Total water soluble carbohydrates were determined, as described by OTZEN & KORIDON (1970), after accumulation of important contents of starch had been proved to be absent by qualitative investigation.

3. RESULTS

The total dry weight data exhibited in *fig. 1* clearly indicate a most vigorous growth of *S. jacobaea*. In comparison, the dry matter production of *S. aquaticus* was relatively small while the production of *S. erucifolius* was intermediate.

The total amount of water soluble carbohydrates of *S. erucifolius* increased steadily from May to September. In parallel, *S. jacobaea* shows an increase until August, followed by a sharp decline to a level which is still substantially higher than that maintained low and virtually constant throughout the growing season in *S. aquaticus*.

As shown in *fig. 2* the water soluble carbohydrate contents of *S. aquaticus* decreased to very low values in all structures while development from the vegetative rosette stage to the seed bearing generative reproductive stage progressed. *S. jacobaea* showed identical declines in the heads, in the leaves and in the stems. Soluble carbohydrate of the stem bases and roots fell to lower but relatively still high levels in the late summer months. They remained constant until the last sampling date in January. In the aerial parts of *S. erucifolius* the soluble carbohydrate contents stayed on a near even level. But for a temporary decrease in July, during the time of maximum leaf-, stem- and flower expansion, the contents of stem basis and roots increased substantially. Rhizomes, exhibited only by this species, showed high contents of soluble carbohydrates at the end of the summer. A decrease took place during the following autumn and early winter.

In order to express the part of dry matter associated with reproduction, OGDEN (1974) computed the "vegetative reproductive effort" of *Tussilago farfara* L. as the proportional participation of rhizomes in the total increase in dry matter. The validity of such an index holds only in the case of true geophytes that solely employ subterranean parts for storage. The procedure is

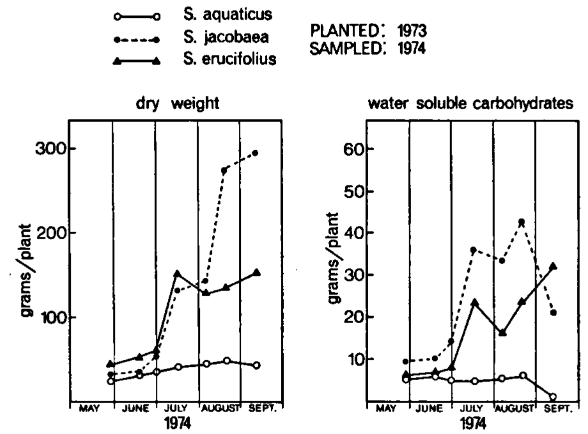

Fig. 1. Time sequence of total dry weight and carbohydrate production.

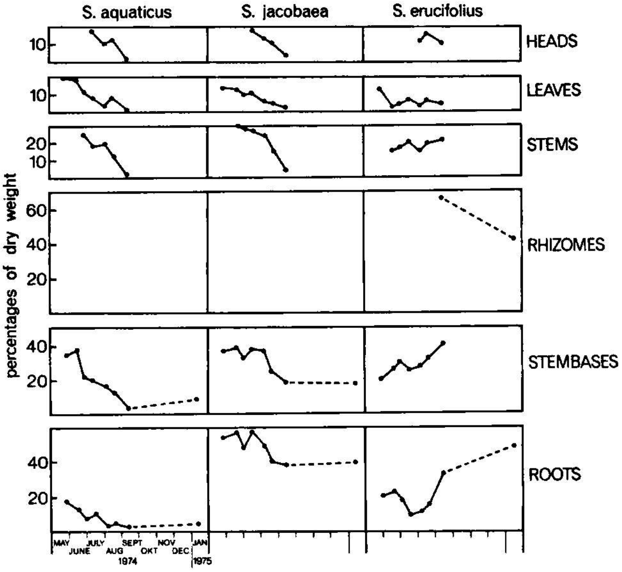

Fig. 2. Time sequence of the contents of water soluble carbohydrates in different structures.

not applicable to the *Senecio* species under experiments; two of them even lack characteristic structures for this purpose. Thus, the dry matter contents of capitula and rhizomes (for *S. erucifolius* only) as well as the contents of water soluble carbohydrates of relevant structures have been plotted in *fig. 3*. In this way, differences between the three species are clearly demonstrated.

In *S. aquaticus* most of its matter is directed to generative reproduction. Mobilizable reserves are absent by the end of the season. In the case of *S. erucifolius*, the matter employed for generative reproduction accounts only for a relatively small part of the total. However, in this species significant

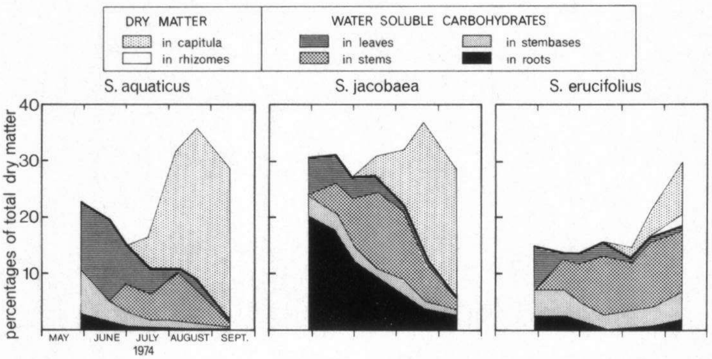

Fig. 3. Time sequence of: a) dry matter in characteristic structures for generative and vegetative reproduction, and b) water soluble carbohydrates in different structures.

quantities of carbohydrates are stored, as reserves of matter and energy for vegetative reproduction, partly in the rhizomes developed only in this species. The physiology of *S. jacobaea* is of a somewhat intermediate nature though tending more towards the extreme exhibited by *S. aquaticus*.

4. DISCUSSION

It may be questioned whether the typical habitat for *S. aquaticus*, as experienced in the experimental garden where the three species were grown side by side, had any effect on its production of water soluble carbohydrates. Though development is usually considered to be affected more strongly by moisture stress than carbohydrate accumulation (Brouwer, 1963, 1967; Davidson, 1969; Russell, 1973), in extreme cases when soil water potentials approach permanent wilting point, decreases in stored carbohydrates appear to occur (Woodhams & Kozlowsky, 1954). Being a species of wet sites, such might have been the case with *S. aquaticus*, grown on a relatively dry site in the experimental garden.

In order to check this remote possibility, samples of *S. aquaticus* were drawn from a naturally occurring stand in the wet valley of the Hunze stream. In *table 1* analytical data extracted from this material are compared with those obtained in samples drawn from the experimental plantings.

Though incomplete, the data in *table 1* show that moisture supplies had no effect on the carbohydrate storage of *S. aquaticus*. Consequently, it may be concluded that differences between the three species in the changing patterns of soluble carbohydrate reserves reflect the interspecific diversities of life forms.

S. aquaticus is a real monocarp. Mobilizable carbohydrates are exhausted when the plant has born seed. The time changing pattern of car-

Table 1. Contents of water soluble carbohydrates in percentages of total dry matter of *S. aquaticus* plants.

Development stage	Rosette		Full bloom		Mature seeds	
Site and date of sampling	Hunze valley 20/9/76	Haren experim. garden 28/5/74	Hunze valley 20/9/76	Haren experim. garden 15/7/75	Hunze valley 20/9/76	Haren experim. garden 11/9/76
Capitula	–	–	13.7	17.0	3.2	2.1
Leaves	13.8	20.4	12.6	8.1	6.1	0.9
Stems	–	–	18.0	18.1	3.5	2.2
Stem bases	20.1	33.8	15.1	19.5	1.9	3.5
Roots	36.5	17.0	12.9	9.8	2.3	2.1

bohydrate reserves is similar to that found by Dina & Klikoff (1974) for the winter-annual *Plantago insularis* Eastw. It also agrees with the conclusion of Struik (1965) that the physiology of biannuals in their second year is the same ar that of annuals.

The restricted vegetative growth in the year of generative reproduction resembles the model of a two-phase plant (Cohen, 1971; Denholm, 1975).

S. erucifolius must be regarded a genuine perennial. Before the onset of winter, carbohydrate reserves are stored in structures characteristic for vegetative reproduction.

S. jacobaea is neither a true monocarp nor a veritable perennial. Carbohydrate reserves decrease in the generative stage. Still, significant quantities remain as a source of matter and energy for vegetative reproduction. These findings are in full accord with the deviating statements concerning the life-form of this species.

The three species differ in reproductive strategy. This is illustrated by disparities in the proportional allocation of dry matter, as presented in *fig. 3*. The balance between generative- and potential vegetative reproduction shifts from the singular monocarp to the distinctly perennial species. A quantitative measure for this shift is the following ratio of weights taken in September, at the end of the growing season.

Dry weights of:

$$\frac{\text{rhizomes} + \text{water soluble carbohydrates in all other parts}}{\text{capitula}}$$

For *S. aquaticus*, *S. jacobaea* and *S. erucifolius* these quotients were computed to be respectively 0.06; 0.26; and 2.28. The closer resemblance of *S. jacobaea* to the monocarpic than to the perennial life form is evident.

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