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Life histories of two clonal populations of Stratiotes aloides L.

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Abstract

Life-history characteristics of two north Swedish populations of *Stratiotes aloides* L. are compared. One population consists of an emergent phenotype, living in a nutrient-rich lake. The other population is entirely formed by submersed plants, living in a nutrient-poor, riverside lagoon. Plants from each population transplanted to the other habitat showed that the emergent form was able to develop a submersed habit, whereas no significant change was observed in the submerged form.

The life cycle of the species is characterized by a winter-green period, during which the emergent form retained 36% and the submerged form 63% of its maximum biomass, respectively. Leaf turnover of both forms followed the same pattern, with successively increasing losses of old leaves during the growing season, resulting in an overwintering rosette made up of freshly-produced leaves. The number of turions and offsets produced by the emergent form is somewhat higher than those of the submerged form but the latter is suggested to allocate a greater proportion of energy to forming well-developed offsets. Under *in situ* experimental conditions during the growing season, the number of plants in both populations increased by 70% and no mortality was observed.

Concentration of potassium in the plant tissues of both forms increased throughout the growing season, that of calcium increased up to the time of peak biomass in August. The contents of phosphorus of the emergent plants transplanted to the lagoon decreased and the nitrogen content increased in relation to the mineral contents of the emergent plants in the lake. The opposite pattern in the contents of phosphorus and nitrogen was found for the submerged plants transplanted.

Introduction

Many different methods of vegetative propagation are found among aquatic macrophytes, e.g. stolons, rhizomes, tubers and turions (Schulthorpe, 1967). Fragmentation of vegetative units can often take over the propagation and dispersal function of seeds (Abrahamson, 1980). A species which relies heavily on vegetative propagation is *Stratiotes aloides,* producing offsets and turions. This dioecious macrophyte is usually gregarious, often occurring in enormous numbers and often in monospecific stands (de Geus-Kruyt & Segal, 1973). Only female plants occur in Great Britain, Scotland and the Nordic countries (Cook & Urmi-König, 1983). *Stratiotes* appear in submerged and emergent forms, often together within the same lake but with the former in deep water and the latter in shallow water (Kornatowski, 1976).

Clones enlarge by a process of growth, not reproduction (Cook, 1983). In *Stratiotes* the clone fragments into unconnected ramets, a process that leads to lateral spread of a genet. Such clonal fragmentation in the aquatic environment may facilitate dispersal and successful colonisation of new areas (cf. Salzman, 1985; Hutchings & Bradbury, 1986). Plant clones can be very large and therefore probably very old (see Cook, 1983). A population of *Stratiotes* in a lake in northern Finland, became established during the early post-glacial period (about 9000 B.P.), according to finds of subfossil leaf spines in the lake sediments (Tolonen, 1981). There are four known populations in Swedish Lapland, all of which are considered to be as old as the above-mentioned Finnish population. One of these populations has been described previously by the author (under former surname of Erixon, 1979a, 1979b).

The aim of this study is to compare the structure and clonal growth of two populations of *Stratiotes aloides* in northern Sweden. The first population is characterized by the presence of only submerged plants. The second consists of emergent plants that flower regularly. To determine whether this indicated an environmentally-determined plasticity or not, transplantations were made of submersed plants to the habitat of the emergent population and vice-versa.

Study sites

The two localities studied are situated in Lapland, in northern Sweden (Fig. 1). They lie 50 km apart and they are situated in different catchment areas.

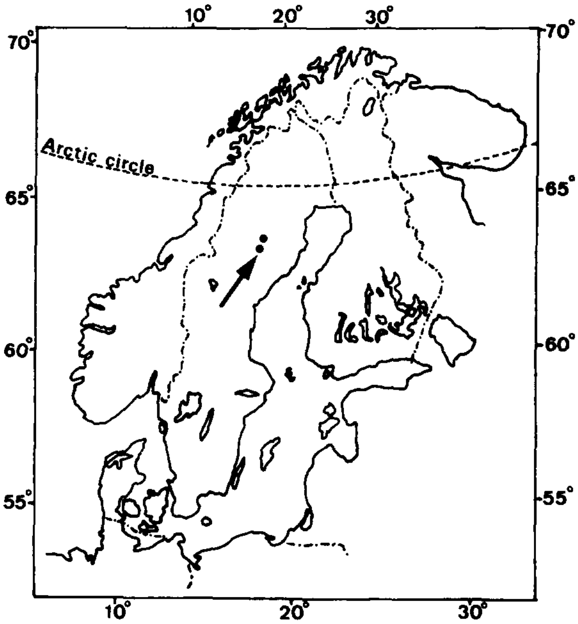

Fig. 1. The location of the populations of *Stratiotes aloides* studied.

Locality 1

Locality 1 was the lagoon Abborravan, adjacent to the river Vindelälven (218 m a.s.l.). Under mean water-level conditions, Abborravan covered an area of 3.5 ha. The water-level amplitude usually reached 3 m during the vegetation period, i.e. the maximum water depth varied from about 1 to 4 m during the course of a growing season.

The magnitude of the water-level fluctuations in Abborravan do not permit the development of a marginal, floating mat of sedges and mosses, as was found in locality 2. Instead, the littoral zone, composed of fine-grained sediments, was covered by isoetid type of vegetation. The submersed community was completely dominated by *Stratiotes*, from the shallows into the deeper water. The floating-leaved aquatic vegetation comprised *Nymphaea candida, Nuphar lutea and Polygonum amphibium.* For a more detailed description of the macrophytic vegetation in the Abborravan lagoon, see Erixon (1979a, 1979b).

The physical and chemical conditions of the water are shown in Table 1. The bottom sediment was a deposit of gyttja. Its contents of nitrogen and phosphorus were 2.2 and 0.64 mg g^{-1} dry weight, respectively.

Locality 2

Locality 2 was the lake Sör-Tuvträsk (276 m a.s.l.) which covered an area of 3 ha. The fluc-

Table 1. Physical and chemical conditions of the water in the lagoon Abborravan (1) and in the lake Sör-Tuvträsk (2).

Loca-lity	Date	Temp. °C	Colour Pt units l^{-1}	pH	Conductivity $\mu S\ cm^{-1}$ (25 °C)	Total-N $\mu g\ l^{-1}$	Total-P $\mu g\ l^{-1}$	Na^+ $mg\ l^{-1}$	K^+ $mg\ l^{-1}$	Ca^{++} $mg\ l^{-1}$	Mg^{++} $mg\ l^{-1}$
1	820606	9.4	30	6.90	28.6	235	11.5	1.64	1.13	4.80	0.71
	0630	17.4	20	6.93	33.1	210	9.4	1.10	0.42	3.78	0.62
	0724	15.6	20	7.40	33.0	225	7.4	0.97	0.45	4.74	0.68
	0810	16.3	20	7.50	37.0	260	5.8	1.10	0.55	4.83	0.76
	0827	15.3	25	7.20	33.0	267	7.5	1.16	0.81	4.39	0.70
	1005	7.9	20	6.55	31.5	290	4.0	1.69	1.06	4.46	0.84
	1026	0.9	20	6.54	35.7	240	3.8	1.61	1.10	3.97	0.77
	1108	0.5	20	6.20	48.8	255	12.9	1.88	1.53	5.48	0.92
	830225	–	150	6.20	88.0	–	–	–	–	–	–
2	820606	11.5	120	6.85	54.2	595	120.0	2.17	1.12	6.93	1.35
	0630	18.0	115	7.10	50.9	530	101.0	2.02	1.10	6.52	1.21
	0722	16.4	115	7.50	50.0	475	48.5	2.15	1.09	5.72	1.23
	0810	19.0	100	7.50	46.0	510	48.0	1.89	0.95	7.14	1.25
	0827	15.0	105	7.20	54.0	507	37.0	2.21	1.19	7.42	1.33
	1005	7.8	100	6.57	49.2	430	59.0	2.25	1.16	9.06	1.40
	1107	0.6	125	6.15	65.4	485	18.8	2.10	1.13	7.91	1.40
	830225	–	150	5.64	75.0	–	–	–	–	–	–

tuation in water level is minimal, only 0.3 m and maximum depth is 2.5 m. In Sör-Tuvträsk, the hydrosere development, beyond the shore and floating mat communities, is a fringe of emergent *Stratiotes*, growing in a depth-range of 1 to 1.3 m. No submersed community was present. Floating-leaved species were represented by *Potamogeton natans* and *Nymphaea candida*.

The physical and chemical conditions of the water are shown in Table 1. The bottom sediment was a deposit of gyttja. Nitrogen and phosphorus were 3.4 and 1.4 mg g^{-1} dry weight, respectively.

A stable winter ice-cover forms at both sites at the beginning of November; break-up of the ice starts at the beginning of May. The thickness of the ice-cover is about 0.7 m.

Methods

Field observations and sampling

The localities were regularly studied during 1982 and 1983, at the times of year shown in Table 1, and additionally on a number of occasions both before and after the main investigation period. Field observations included measurements of the vertical positions of the plants i.e. the positions in the water column, the flowering times and the occurrence of any floating dispersal units. Sampling was carried out by raking, in order not to damage the plants. This proved satisfactory, since even when the roots had penetrated the sediment, they were easily uprooted. The sampled plants were put into plastic bags and stored in a cold-storage room for up to 48 hours, before being analyzed.

Phenological and morphological data, plant age and biomass determinations

A picture of a *Stratiotes* plant is shown in Fig. 2, with indication of the modules used in the descriptions and plant measurements. The age of a *Stratiotes* plant is not easily determined in the field. However, newly-produced daughter plants can be recognized by the fresh-appearance of the cicatrices of their former attachment to the parent stolons. On a basis of the condition of the cicatrices at least one year old plants can be confidently recognized.

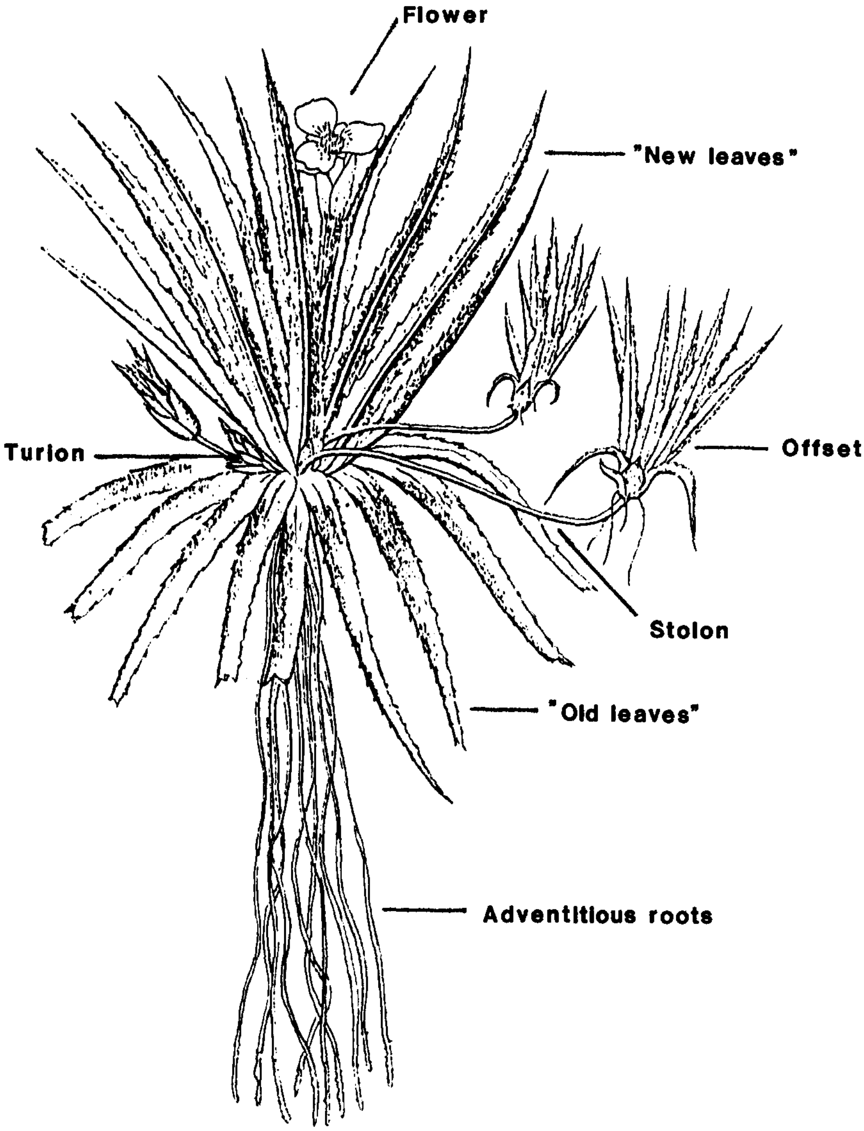

Fig. 2. The habit of the emergent form of *Stratiotes aloides*. Turions and well-developed offsets are rarely found at the same time on the plants growing in the localities studied. (Picture redrawn after Nolte, 1825). Terminologi, see Kornatowski (1979).

To study the phenological and morphological development, 30–40 plants were sampled at random, on the dates shown in Table 1. The number of offsets, turions, leaves, roots and flowers were counted on each individual plant. The average and the maximum lengths of leaves, stolons, roots and peduncles were also measured. The development of offsets still attached to the mother plant was followed by measuring the maximum leaf length. Fresh weight was determined after washing each plant free from any foreign material (snails, mud etc.), whereafter the plants were left in perforated plastic bags for two hours to drain off any water surplus. Dry weight was determined after drying at 50 °C in an oven fitted with a fan for forced circulation of air.

Chemical analyses of plant tissue

Dried plant material was digested in a mixture of perchloric-hydrochloric acid. Ca, Mg, K and Na contents were determined by atomic absorption spectrophotometry. P (total-phosphorus) was determined spectrophotometrically, by the molybdenum blue method (Murphy & Riley, 1962) and N (total-nitrogen) by the Kjeldahl method.

Transplantation experiment

Seventy *Stratiotes* plants were transplanted from the lagoon to the lake and 60 from the lake to the lagoon. They were grown in side wire cages (each 1 × 1 × 1.2 m; 20 mm mesh). Two cages were placed out in each water body. The experiment was started in May, before the roots had started to develop and when the plants were still resting on the bottom. Before transplantation, phenological and morphological data, plant ages and live biomass were noted for each plant. One cage in each lake was left intact until November. The other was used for sampling, following the time schedule shown in Table 1. About 5 plants were removed each time. Because of the ice conditions, no cages containing plants were left out over the winter. Two more cages of smaller dimensions (0.5 × 0.5 × 1 m) were also placed out but without transplantation between the populations. These cages each contained 10 emergent plants and 15 submerged plants and were left undisturbed throughout the growing season.

Results

Seasonal distribution in the water column and phenology

The difference in the seasonal vertical positions of plants at the two study sites are shown in Figs. 3 and 4. About 90% of the plants in the lake were floating at the end of May, whereas the plants in the lagoon remained on the bottom throughout June. Most of the lake plants formed their roots from the floating position. The opposite behaviour pattern was found in this lagoon. Each independent plant in both the lake and the lagoon had become anchored by roots to the bottom substratum in July.

Flowering started in late July in the lake and culminated in early August. By the middle of August flowers were no longer visible. The submerged population in Abborravan had been kept under observation throughout the period 1975 to 1983, but only two flower-buds were ever found (1982). Daughter-plants (offsets) were produced in the late spring, or continued their development if they had been produced the preceding year.

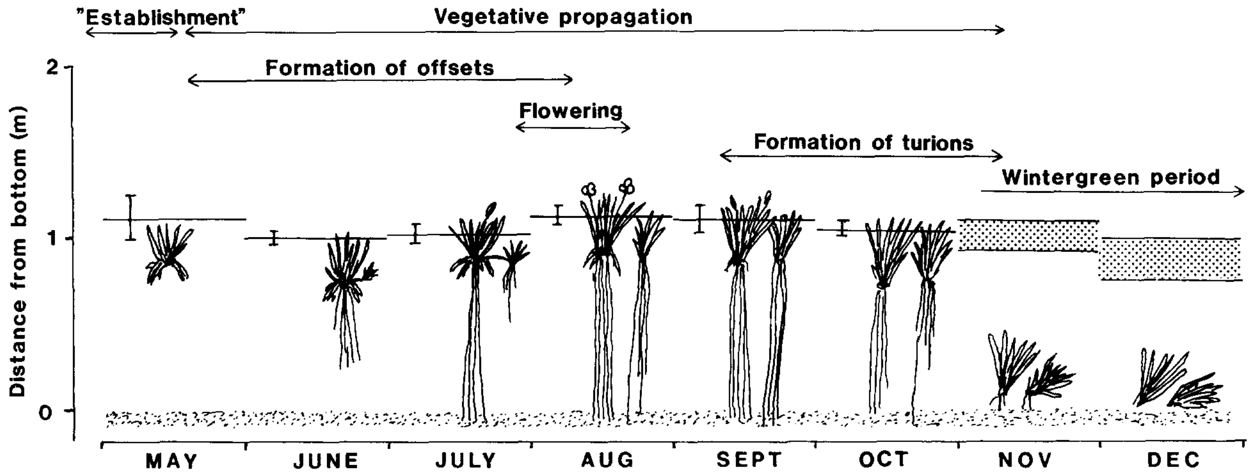

Fig. 3. The life cycle and the vertical movements of *Stratiotes aloides* in the lake Sör-Tuvträsk. The vertical location of the plants are related to the seasonal changes in water level and to the ice cover in winter (1982). The maximum and minimum water levels in each month are indicated by the extents of the vertical bars and the mean values by the horizontal lines. The hatched rectangles indicate the thickness and depth of the ice cover.

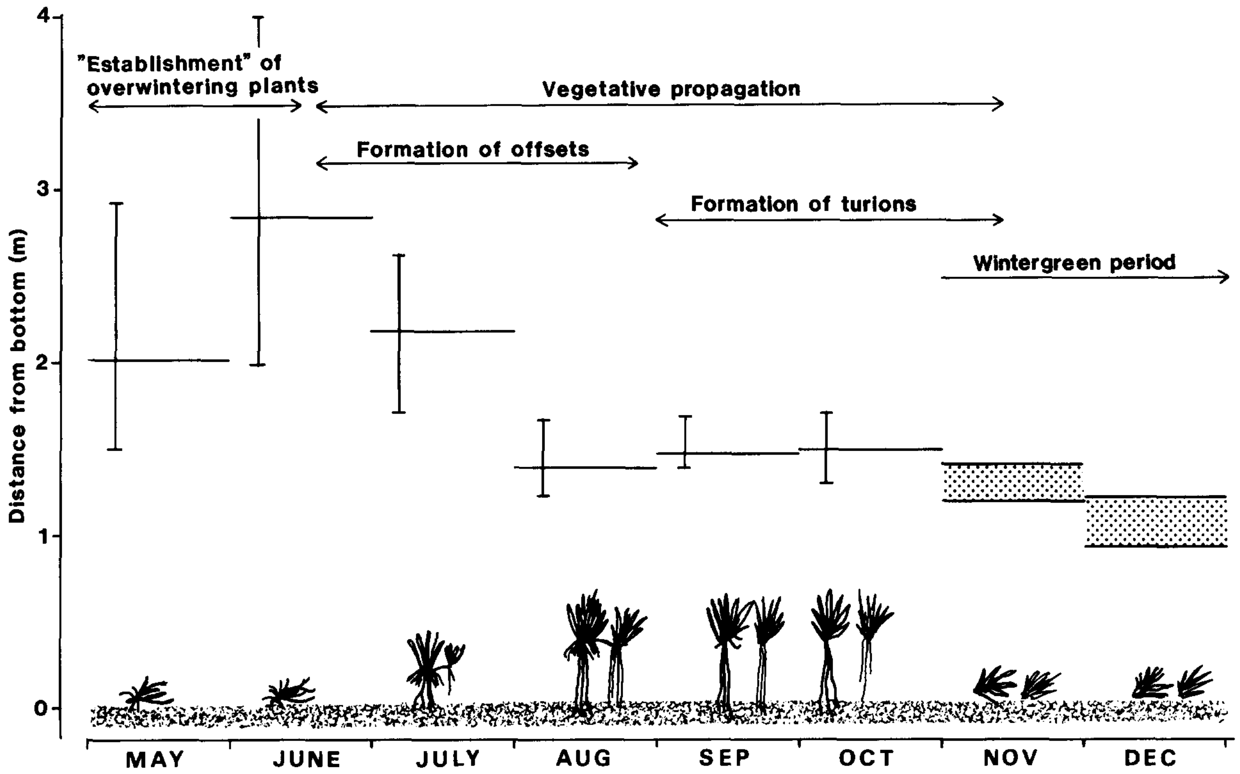

Fig. 4. The life cycle and the vertical movements of *Stratiotes aloides* in the lagoon Abborravan. Symbols as in Fig. 3.

However, most of the offsets in the lake were already free from the mother-plants by the beginning of August, while offsets in the lagoon were free about 3 weeks later. Turions were produced at both sites in September and became completely detached from the mother-plants in spring. In October the roots started to decay and the plants began to sink. This procedure was complete at beginning of November at both sites.

Seasonal changes in plant weight

The changes in fresh weight and in dry weight of *Stratiotes* plants from the two populations are shown in Figs. 5 and 6. The general pattern was that the weights of individual plants increased up to the beginning of August, thereafter decreased to a mid-winter minimum. The weight difference between the two populations was quite striking, the plants in Sör-Tuvträsk weighting three to four times more than those in Abborravan. The mass of the emergent plants in midwinter represented 36% of the maximum mass, while the submerged plants overwintered with 63% of their midsummer mass.

Development of leaves and roots

The seasonal development of leaves and roots is shown in Tables 2 and 3. Maximum leaf length was recorded in August at both localities. The subsequent decline was due to leaf abortion and decay of the leaf tips. Emergent plants had more than twice the number of roots than submerged plants and they were twice as long. The maximum numbers of new leaves recorded were fairly similar in both cases. The seasonal changes in leaf formation and leaf senescence are shown in Fig. 7 for both sites. Old, senescent leaves predominated on the plants in early summer, but were successively aborted later on. In autumn only new leaves were present on the plants.

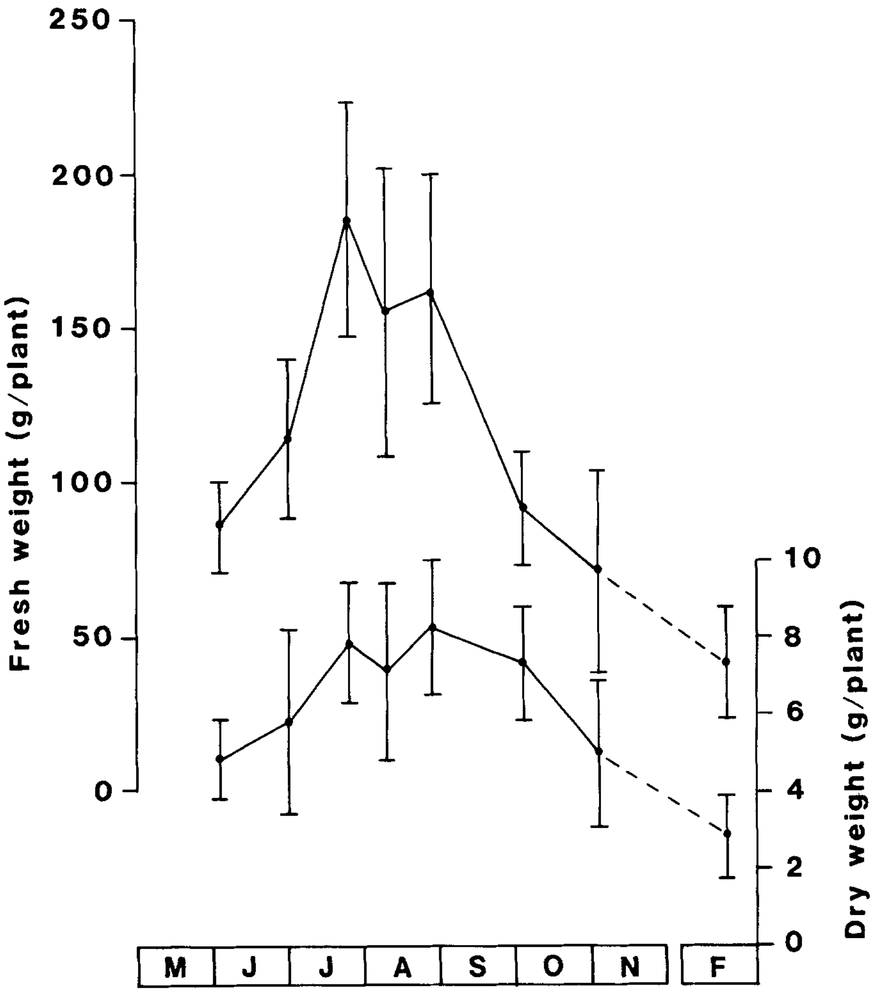

Fig. 5. Seasonal changes in fresh weight (upper line) and in dry weight biomass (lower line) of *Stratiotes* plants in the lake Sör-Tuvträsk. Mean values with 95% confidence intervals.

Table 2. Seasonal development of leaves and roots of *Stratiotes* plants in the lagoon Abborravan. Mean values with 95% confidence intervals.

Date 1982/83	Length (cm)		Number of	
	Longest leaves	Roots	New leaves	Roots
5.6	16.6 ± 1.4	2.2 ± 0.4	13.2 ± 0.7	2.5 ± 0.3
30.6	25.3 ± 2.1	26.8 ± 7.4	18.6 ± 1.5	3.1 ± 0.3
24.7	26.1 ± 3.5	27.6 ± 8.5	19.7 ± 2.9	2.8 ± 0.4
10.8	34.4 ± 4.3	44.4 ± 6.3	27.9 ± 3.5	3.5 ± 0.2
27.8	36.9 ± 3.2	43.6 ± 4.6	28.6 ± 2.7	2.8 ± 0.3
5.10	32.4 ± 2.7	40.3 ± 11	29.3 ± 2.2	1.6 ± 0.4
26.10	22.2 ± 3.0	0	25.2 ± 1.8	0
8.11	19.3 ± 2.9	0	26.3 ± 2.5	0
25.2	18.9 ± 1.5	0	26.5 ± 2.0	0

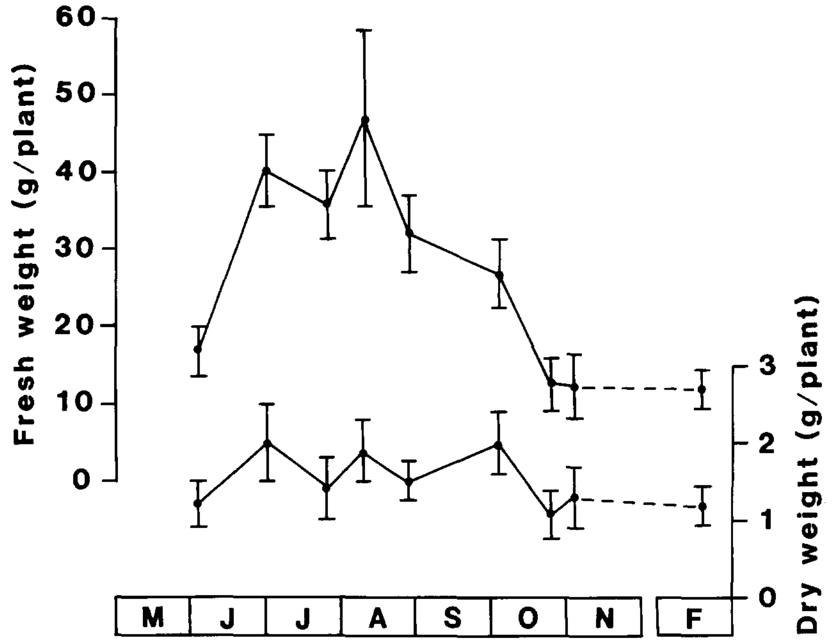

Fig. 6. Seasonal changes in fresh weight (upper line) and in dry weight biomass (lower line) of *Stratiotes* plants in the lagoon Abborravan. Mean values with 95% confidence intervals.

Table 3. Seasonal development of leaves and roots of *Stratiotes* plants in the lake Sör-Tuvträsk. Mean values with 95% confidence intervals.

Date 1982/83	Length (cm)		Number of	
	Longest leaves	Roots	New leaves	Roots
6.6	21.7 ± 1.1	4.1 ± 0.5	16.2 ± 1.1	4.6 ± 0.7
30.6	32.2 ± 2.2	79.1 ± 7.2	19.6 ± 1.3	7.1 ± 0.7
22.7	30.4 ± 2.5	89.2 ± 10.8	23.4 ± 2.9	7.8 ± 0.9
10.8	35.0 ± 2.8	93.6 ± 4.4	31.7 ± 3.2	6.8 ± 1.2
27.8	31.8 ± 2.3	99.7 ± 6.7	32.4 ± 2.1	4.5 ± 0.6
5.10	32.0 ± 2.1	39.7 ± 17.8	28.6 ± 2.1	1.1 ± 0.1
7.11	33.5 ± 2.4	0	23.0 ± 2.4	0
25.2	27.2 ± 3.6	0	21.8 ± 2.4	0

Development of propagules and flowers

The development of offsets and turions is shown in Table 4. In early June, almost all the plants in Sör-Tuvträsk bore offsets, but only 1/3 of those in Abborravan. At the beginning of August, half the plants in the sample from Abborravan bore offsets, while none were found on the plants growing in Sör-Tuvträsk. Turions were also more frequently found on the plants growing in the lake, at the start of the period for turion formation. Plants in the emergent population more frequently bore 2 offsets than a single one, although production of turions (one, occasionally two) was similar at both sites. By mid-winter, some plants with offsets in the samples from both sites were found, indicating that winter-growth occurs.

The offsets on the submersed plants were more developed than those on the emergent plants at the time of their release from the mother plants (mean length of longest leaves; submersed plants 34 ± 4.2 cm, emergent plants 11.2 ± 2.4 cm). In

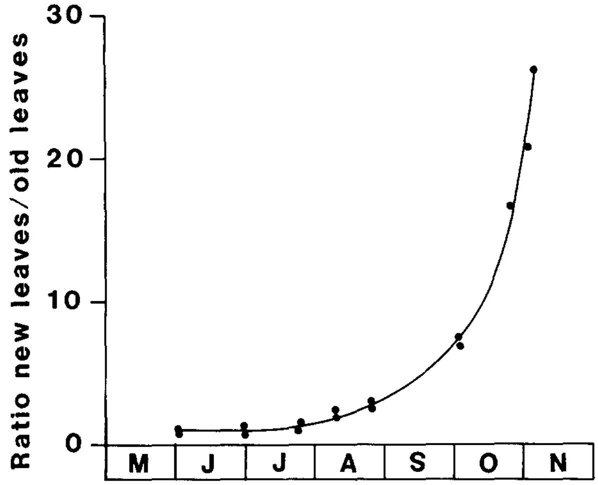

Fig. 7. Seasonal changes in the ratio of new leaves to old leaves on *Stratiotes* plants. Values taken from both emergent and submerged populations.

Table 4. Seasonal development of propagules by *Stratiotes* plants in the two studied populations. A = Abborravan, S = Sör-Tuvträsk

Date 1982/83	Plants with offsets (%)		Plants with turions (%)		Offsets No/plant		Turions No/plant	
	A	S	A	S	A	S	A	S
5,6.6	34.3	96.7	0	0	1.1	1.7	0	0
30.6	60.0	85.0	0	0	1.4	1.8	0	0
22,24.7	50.0	47.4	0	0	1.4	1.6	0	0
10.8	52.6	0	0	0	1.3	0	0	0
27.8	0	0	0	0	0	0	0	0
5.10	11.8	0	35.3	75.0	1.0	0	1.2	1.3
26.10	0	–	36.0	–	0	–	1.1	–
7,8.11	6.3	0	25.0	27.8	1.0	0	1.0	1.0
25.2	13.3	20.0	53.3	30.0	1.0	1.0	1.0	1.0

fact, the offsets of the submerged plants had attained the same form as the mother-plant by that time. The mean length of the stolons on the submersed and on the emergent plants were 8.7 ± 1.8 cm and 15.6 ± 3.4 cm, respectively. On average the flowering plants in the emergent population each bore two peduncles (2.1 ± 0.3), their maximum lengths being 22.2 ± 1.5 cm.

Twenty plants of the submerged population were grown in a cage in Abborravan from June to November. At the end of the period, 34 ramets were found, two of which were still-attached offsets. Because no mortality was observed, the experimental population had increased its size by 70%.

Ten plants of the emergent phenotype were placed in a cage in Sör-Tuvträsk during the same period as for the above-mentioned experiment. They formed 7 offsets, all of which had been freed from the parent plant during the period. No dead or decaying plants were found, so that there also a population increase of 70% had occurred. This should be compared with the results of the random sampling in Sör-Tuvträsk and Abborravan in autumn, which showed that 35% and 45% of the respective populations were ramets produced during summer.

Transplantation experiment

The emergent form, when transplanted from the lake to the lagoon, changed its habit of growth significantly. The leaves grew longer, but at the same time became thin and flaccid, the roots became shorter and fewer, and the plants decreased in weight (Mann-Whitney U-test, $P < 0.05$). No peduncles and flowers developed. The submerged form, on the other hand, when grown in the lake, did not change its habit of growth significantly (leaves, roots, plant weights, $P > 0.05$) from that of the plants already growing in the lagoon.

Wide differences in vegetative propagation were found between the plants grown in the cages. The initial 30 plants of the emergent form grown in the lagoon environment increased to 68, 22 of which were still attached to their parent plants at the end of the experiment. In the cage at the lagoon where sampling was carried out during the growing season, the corresponding increase was from 30 to 57 plants, and no still-attached plants were present in this cage. In Sör-Tuvträsk, the submerged plants grown under undisturbed conditions increased in number from 35 to 53 plants, including still-attached offsett. In the second cage, where regular sampling was carried out, a

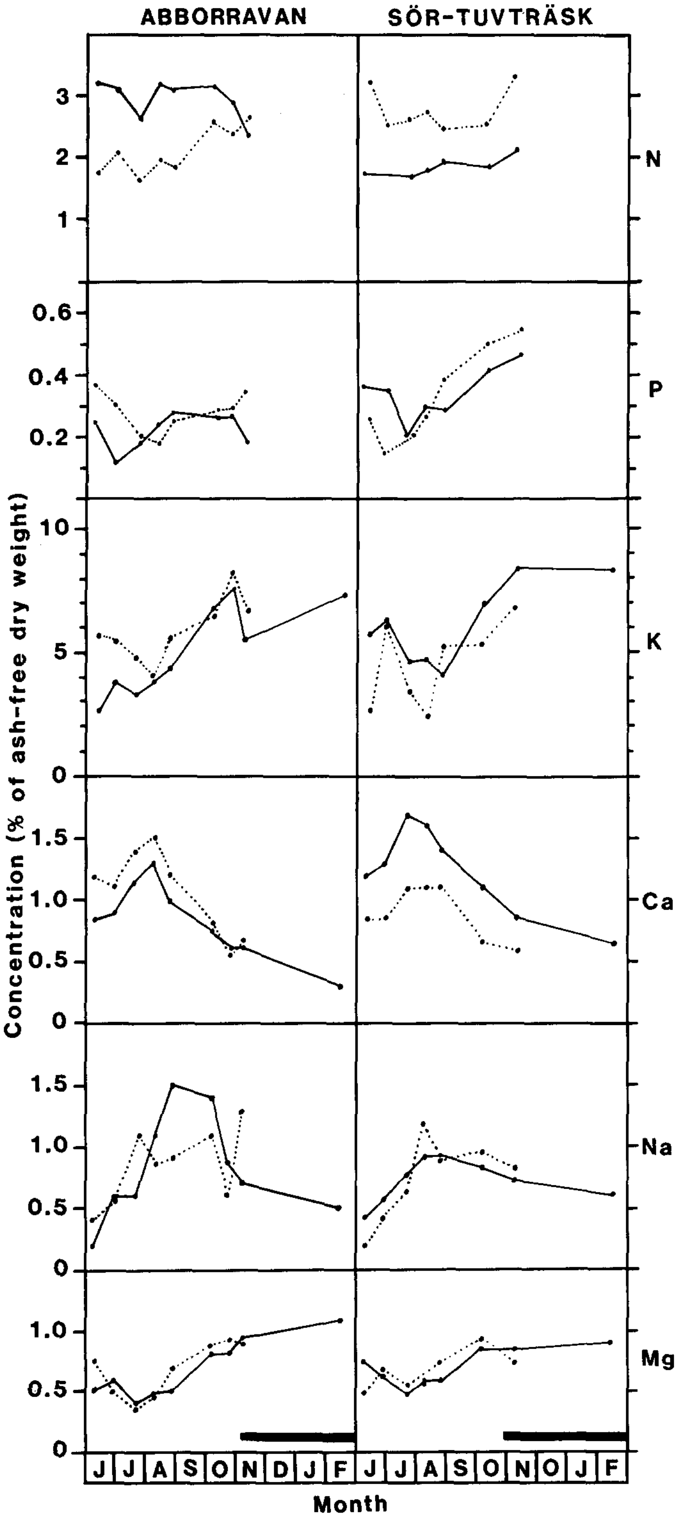

Fig. 8. Seasonal changes in the concentrations of certain mineral elements in plants of *Stratiotes aloides* from the two populations; Abborravan (on left) and Sör-Tuvträsk (on right). The solid lines indicate the concentrations in plants growing in those two localities. The dotted lines indicate the concentrations recorded in transplanted plants in their new localities.

decrease from the initial number of 35 plants to 34 plants was noted.

Seasonal changes in mineral content

In June, the concentrations of all elements except N were higher in the plants growing in the lake than in those in the lagoon (Fig. 8). During the summer and the autumn, these differences evened out, but the concentration of K, and especially that of Ca, were still higher in the emergent plants in the lake. The seasonal variations in all mineral elements were fairly similar in both environments, with exception of K and Na. The concentration of K seemed to fall steadily to reach a minimum in August in the plants growing in the lake, whereas the K content of the plants in the lagoon increased steadily during the same period. The Na content of the lagoon plants was much higher in late August than that of the lake plants.

The mineral contents of the transplanted plants are shown in Fig. 8. The contents of P and Ca of the emergent plants grown in the lagoon decreased and the N content increased in relation to the mineral contents of the emergent plants in the lake. The submerged plants grown in the lake showed a decrease in N and Na content during the growing season, while their P content increased.

Discussion

Stratiotes aloides is a winter-green plant, a state which confers on this species an advantage in growth potential compared to the many other species of macrophytes that need to restart their life-cycles in spring either from seeds or from overwintering rhizomes. The submersed plants retained a relatively greater proportion of their total mass during the winter period than the emergent plants. In the submersed form of *Stratiotes* this was equivalent to that of *Lobelia dortmanna,* which overwinters with 60% of the midsummer mass (Moeller, 1977). Moeller (1977) concludes that, for *Lobelia,* the retention of such a high proportion of its midsummer mass is more a strategy to conserve potentially growth rate limiting nutrients than a strategy to accumulate nutrients, or mass, during times of year when competition from algal and microbial populations might be expected to be less. Only the former strategy is relevant for *Stratiotes*, since the species is renowned for its ability to effectively take up water-soluble nutrients and thereby significantly reduce the growth of the competing algae (Brammer, 1979). Potassium is one of the dissolved nutrients which is readily taken up (Brammer & Wetzel, 1984). The present study shows that in both the submersed and emergent plants, the potassium concentration steadily increases to a midwinter maximum and that the subsequent loss takes place later on in the winter (Fig. 8). The higher sodium concentration found in the plants of the submerged population is typical for all submersed freshwater macrophytes (Moeller, 1977). The phosphorus and nitrogen contents of the submerged plants decreased in autumn, whereas an increase of these same nutrients was observed in the emergent plants. The N and P contents of macrophytes generally decrease towards the end of the growing season (Hill, 1979).

The nutrient situation for the plants growing in Sör-Tuvträsk is much better, a fact which must favour their development, their floating ability, and their possibility of thrusting their shoots up above the water surface. However, no shoots have been observed to appear above the water surface until the plants had become rooted in the bottom substrate. The high mass turnover, especially in the emergent population, implies that a large amount of decaing material will accumulate on the bottom, which will subsequently form a source of nutrients (Ulehlova, 1971).

The populations rely entirely on vegetative propagation since only female plants are present. The potential for vegetative propagation of the emergent population was the greatest but the field sampling data indicate that a greater number of freshly-produced ramets were present in the submerged population at the end of the growing season. Offsets of the latter population were all fully developed by the time of their release from the parent plant. However, the more nutrient-rich conditions of the lake habitat of the emergent form may favour a faster subsequent growth of detached ramets. Turions of the emergent population, or plants developed from turions, disappeared during the winter and spring, because they were not found in early summer, whereas sprouting turions of the submersed population were found in the lagoon in springtime. The disappearance of turions produced by emergent populations has also been observed by Kornatowski (1983/84).

Wesenberg-Lund (1912) observed that different morphological forms originate from turions and from offsets. This observation was confirmed by Kornatowski (1983/84, 1985) who showed that turions develop into, and remain as, submersed plants, whereas offsets grow into the emergent form under the same habitat conditions. In the present study, plants from the submersed population were unable to change into the emergent form when transplanted, despite the favourable habitat conditions. An additional aquarium experiment gave the same result (Erixon, 1979b).

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