

Changes in structure and function of *Ammophila* during primary succession

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Quantitative changes in the ageing process of *Ammophila* were studied on dunes at Sandhammaren, S. Sweden.

The decline of the marram grass vegetation during a ten year period was mainly quantified as a decrease in the yearly formation of above ground biomass from ca. 400 g m^{-2} to ca. 125 g m^{-2} , a decrease of the maximum green leaf area from ca. $0.75 \text{ m}^2 \text{ m}^{-2}$ to ca. $0.25 \text{ m}^2 \text{ m}^{-2}$, and a decrease of the yearly formation of below ground organs from ca. 200 g m^{-2} to zero. A method for measuring the above ground production was used, which compensates for wind transport of litter during the growth period.

The life span of the above ground biomass was found to increase by time, which indicates that the decline in the vegetation and in net production does not correspond to a decline in gross production, but a changing balance between assimilating and non-assimilating tissue towards a state, in which annual respiration equals annual assimilation, and no further net increase of biomass takes place.

A model for the accumulation of organic matter by time was tested for different courses of the decrease in litter formation.

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Исследовали количественные временные изменения *Ammophila* в дюнах Зандхаммарена (Ю. Швеция). Сокращение травянистой растительности в течение 10-летнего периода количественно выразилось в основном как сокращение годичного прироста надземной биомассы с 400 г/м^2 до 125 г/м^2 , сокращение максимальной площади листьев с $0.75 \text{ м}^2/\text{м}^2$ до $0.25 \text{ м}^2/\text{м}^2$ и подземных органов с 200 г/м^2 до 0. Метод, использованный для определения надземной продукции, учитывал перенос ветром подстилки в течение периода роста. Длительность жизни надземной биомассы увеличилась во времени, что свидетельствует о том, что сокращение растительного покрова и чистой продукции не соответствует снижению массы продукции, а изменяет баланс между ассимилирующими и неассимилирующими тканями в том направлении, когда годичная респирация становится равной годичной ассимиляции, и дальнейшего увеличения биомассы не происходит. Модель аккумуляции органического вещества в разные периоды была проверена на различных стадиях снижения продукции подстилки.

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1. Introduction

Along the Baltic coasts *Ammophila arenaria* (L.) Link and the hybrid *A. arenaria* × *Calamagrostis epigeios*, *A. baltica* (Flugg) Link form the first stage in the plant succession on newly formed sand dunes (Olsson 1974). With age and decreasing rate of sand accretion a decline in vigour of the *Ammophila* vegetation is observed. The most commonly given explanation for this change in the behaviour of *Ammophila* is a decreased uptake of nutrients resulting from ageing of roots in combination with decreased development of new roots (Waterman 1919, Gemmell et al. 1953, Laing 1958, Marshall 1965, Hope-Simpson and Jefferies 1966).

Waterman (1919) observed that *Ammophila arenaria* roots stopped growing if the apex came into contact with organic matter, for example leaf fragments. A positive correlation between increased humus content and loss of vigour was also noted by Salisbury (1925), who, however, did not study the connection between root development and humus content. The importance of competition for water and nutrients by other plants was pointed out by Hepburn (1944), Salisbury (1952) and Laing (1958). Relatively rapid leaching of nutrients in the wind blown sand was found by Willis et al. (1959) and also by Salisbury (1925). They also found that sand movements counteracted these processes. They concluded that lack of nutrients, as a result of stabilization, was the cause of decrease in vigour of the *Ammophila*.

Many ecological and ecophysiological explanations have thus been suggested for the decline of *Ammophila*. All discussions have however started from the assumption that there is a real decrease in productivity of *Ammophila* with age of the dune. Marshall (1965) mentions "physiological senescence" as a possible mechanism limiting longevity. He suggested no clear causal mechanism. His two main findings were:

- (1) The migratory growth of the *Ammophila* results in vertical or horizontal displacement of the new vegetative units. This leads (under conditions with no sand accretion) to a change in the relation of the plant to the environment. Under conditions of sand accretion there is a balance between the increasing bulk of the plant and the environment.
- (2) Marshall's second explanation concerned the efficiency of replacement of essential organs with a short lifespan in relation to that of the whole plant. He showed the connection between sand accretion and development of young roots, and the decreased efficiency in nutrient uptake with age.

The earlier studies of the decline in vigour of *Ammophila* relied mainly on morphological observations. The aim of this study was to determine the changes in biomass and productivity in vegetation which shows a gradient of declining vigour of *Ammophila*; to study the connection between assimilating and non-assimilating tissues; to determine the ratio root biomass/rhizome biomass as a function of increasing age, and the ratio

below ground biomass/assimilating tissue as a measure of ecological efficiency. Another aim was to quantify the rate of accumulation and disappearance of organic matter in the soil-plant system.

2. The study area

The investigations were performed in the sand dune area at Sandhammaren (55°23'N, 14°12'E) in Skåne, S. Sweden (cf. Olsson 1974). The area can conveniently be considered in two topographically distinct parts:

- (1) A "primary area", close to the sea, built up of regularly arranged low dune ridges parallel to the coast, and
- (2) a "secondary area" inland, with old, stabilized dunes alternating with bare, mobile dunes and slacks.

The process of dune building in general, as a result of the interaction between wind and vegetation, is well documented by many authors, for example Cowles (1899), Warming (1909), Greig-Smith et al. (1947), Gemmell et al. (1953), Willis et al. (1959), Ellenberg (1963), Marshall (1965), Ranwell (1972). Of importance to this process is the power of the *Ammophila* rhizomes to grow rapidly both horizontally and, when necessary, vertically to keep up with the accumulating sand. In the Sandhammaren area rhizome fragments from adjacent eroded coasts are washed up. The prevailing, sand-laden winds, are obstructed, and sand accumulates behind and eventually over the rhizomes. In this way a band of foredunes is initiated on the foreshore. Provided that the supply of wind-blown sand continues, these foredunes expand rapidly both horizontally and vertically as a result of the special features of the growth of the *Ammophila*. Soon there is a continuous dune bank in front of the former dune area. The sand supply to the dunes behind is reduced, and with that the growth of those dunes. Thus the dunes constitute a succession of topographically relatively stable blocks of increasing age, which give an opportunity for studying the autogenic forces in a plant succession.

The plant zonation in the Sandhammaren area and along other Baltic coasts are similar to those around the North Sea (Ellenberg 1963). The colonization of *Ammophila* by upwashed rhizomes on the foreshore, forms, however, a contrast to the North Sea coasts. There the primary dunes are colonized by more salt tolerant species such as *Elymus arenarius* L., *Elytrigia juncea* (L.) Nevski ssp. *boreoatlantica* (Sim et Guin) Hyl. and *Honckenya peploides* (L.) Ehrh., while *Ammophila* does not usually colonize until the dune has grown and is less influenced by the salt rich ground water (Ellenberg 1963). It does not seem, however, that the salinity of the sea water per se has any importance in the dune formation.

At Sandhammaren the vegetation of the outer, "primary" area is completely dominated by *Ammophila*

Tab. 1. Precipitation, temperature and sea water level by Ystad, 18 km W the investigation area (Anon. 1973-1976).

	Precipitation (mm)				mean 1931-1960*	Temp (°C)		mean 1931-1960	Waterlevel in relation to mean	
	1972	1973	1974	1975		1972	1975		1972	1975
Jan	29	32	62	55	60	-1.3	4.6	-0.7	-12	+32
Feb	9	74	39	13	45	0.3	1.4	-1.0	-34	+5
Mar	41	19	20	27	39	2.2	2.4	0.8	-31	±0
Apr	44	70	3	62	37	5.2	5.0	5.0	+4	-2
May	35	28	25	29	38	9.4	10.4	10.0	-11	-5
Jun	22	32	24	12	50	13.9	14.1	14.1	-1	±0
Jul	60	38	40	48	68	17.5	17.8	16.7	-7	-8
Aug	90	13	33	17	59	16.1	19.2	16.4	-8	-7
Sep	78	98	83	132	54	11.2	15.0	13.4	-5	-13
Oct	6	49	163	34	63	8.3	9.1	9.1	-4	+3
Nov	75	108	81	35	57	5.7	4.7	5.1	+18	-7
Dec	35	48	84	32	55	4.4	3.4	2.0	+5	-1
Sum	524	598	655	496	625					
Mean						7.7	8.9	7.6	-7	+3

baltica on the ridges and slopes. The decreasing vigour in the vegetation with increasing distance from the shore is striking: the frequency of inflorescences decreases, the individual shoots become more slender, and the colour more brownish, and the distribution pattern more and more tufty. The impression of decreasing vigour is strengthened by a fast accumulation of litter. The vegetation in the slacks between the dunes is dominated by *Lathyrus maritimus* (L.) Biegel, and *Festuca arenaria* Osb. in the younger slacks and *Corynephorus canescens* (L.) PB in the older ones.

These latter slacks are particularly liable to be eroded by human activities. On the innermost part of the area *Calluna vulgaris* (L.) Hull colonizes.

The "secondary" area inland is covered by a mosaic of planted pinewoods (ca. 45%), dense, coppice oak woods (ca. 13%), and *Calluna* heaths (ca. 12%). The

remaining part (30%) includes dune slacks with variable development of birch fens as well as variable amounts of *Corynephorus canescens* and *Carex arenaria* L. in open spots (Olsson et al. 1971).

The prevailing sand-bearing wind at Sandhammaren (winds from NE-WSW with a speed exceeding 8-10 m s⁻¹) are ENE-E (19%) and SW-W (34%). The wind frequency from other directions is considerably lower and of minor importance for dune building (Davidsson 1963). The substrate consists almost exclusively of grains of quartz, classified as "fine medium sand". The median diameter varies between 0.25 and 0.28 mm (Davidsson 1963).

Annual mean precipitation was 624 mm during the period 1931-1960, with 426 mm during the vegetation period (the period with a temperature above +3°C) (Tab. 1). The precipitation during the sampling years,

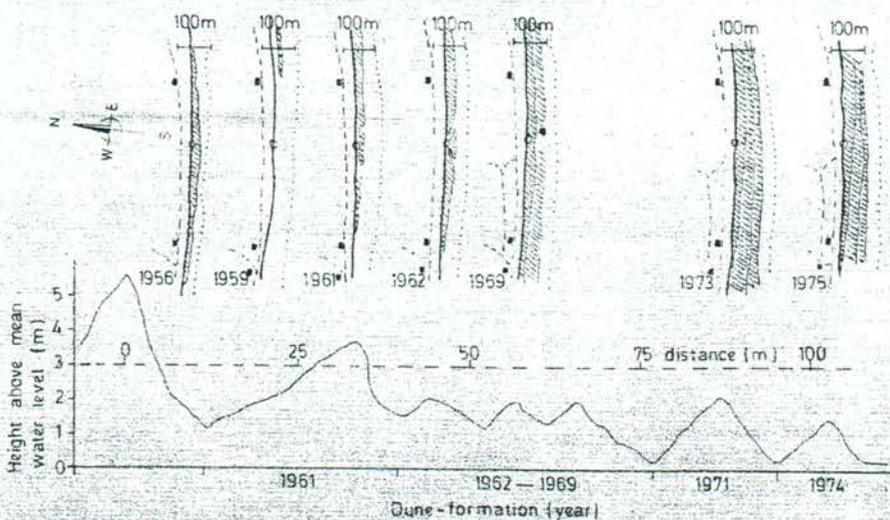


Fig. 1. Stages of dune development on the study site and a crosssection through the area in summer 1975 (lower part). ■ Boathouse, ○ Pillbox // // // // // *Ammophila* vegetation, — Path, — Shore-water border, — Old, ca. 4.5 m high dune ridge.

1972 and 1975, was considerably lower than normal (534 and 496 mm respectively), and in particular between May and August 1975.

The mean monthly temperatures (Tab. 1) during 1972 were normal, but during 1975 the temperatures January to March and July to September were considerably above normal.

The mean water level of the sea (Tab. 1) during 1972 was slightly subnormal, but during 1975 it was near normal.

The study was performed along a gradient through the area of most active dune building, 1.4 km ESE of the lighthouse. Air photographs from 1936, 1956, 1957, 1959, 1961, 1962, 1969, 1973 and 1975 were available (Fig. 1). These photographs indicate a nearly static shoreline between 1936 and 1959 at a position just outside the present innermost, ca 4.5 m high dune ridge. The position of some old boathouses indicates that this dune ridge was initiated in the nineteenth century. The shallow inland slope of this dune is covered by dense *Calluna-Empetrum* heath. The seaward slope, steep due to erosion, is covered by sparse *Ammophila*. In 1959 the area outside this dune seems to have been without continuous vegetation cover. Only patches of vegetation are to be seen on the air photographs. This was probably the first stage in the initiation of what is now the oldest dune ridge in the progressive dune system. Even in 1961 the vegetation on this dune was not completely closed. In 1962 the vegetation cover was denser, and a new row of foredunes had developed outside. This has given rise to a dune area, ca. 35 m wide and ca. 1.5 m high, with dense *Ammophila* vegetation, visible on the 1969 photographs.

At the time for this study two new dune ridges had been formed: one in the late summer of 1971 and one in the late summer of 1974. By the start of the sampling periods 1972 and 1975, a dune of ca. 1.5 m height constituted the outermost border of the progressive dune area.

3. Methods

3.1. Sampling

3.1.1. Above ground

Above ground material was sampled in 1972 at two points in the gradient; on the ridges of the dunes initiated in 1971 and 1961, respectively. At each sampling point 27 squares of 1 × 1 m were placed along the ridge of the dune. On seven occasions during the vegetation period of 1972 (30 March, 5 May, 8 June, 14 July, 6 August, 1 October, and 28 October) the shoots in three to five quadrats in the set were cut at soil level.

In addition to this destructive sampling an adjacent plot with marked *Ammophila* shoots was studied biometrically. Length, width, stage of development and degree of vitality were noted for the different parts of the shoots.

3.1.2. Below ground

The sampling of roots was carried out on four occasions during 1975–1976 (10 May, 8 July, 20 October 1975, and 20 April 1976). Sampling was performed down to 60 cm with a steel cylinder (20 cm diam.). The root material in the cylinders was collected by sifting through a 4 mm sieve. At each sampling date ten cores were collected on the dune ridges initiated in 1974, 1971, 1965 and 1961.

The sample depth of 60 cm was chosen after a pilot study, where the growth of the roots at different levels was determined in the following way: A pit of 20 × 50 cm, 120 cm deep, was dug in the 1971 initiated dune. All roots were sifted away, and the root-free sand replaced in the pit. After one month the ingrowth at different depths of roots and rhizomes was noted, and interpreted as a measure of root activity. Maximum root activity was observed between 10 and 30 cm, and none below 60 cm.

3.1.3. Soil

The humus content of the soil was measured in the summer of 1973 on the dunes formed in 1971, 1965 and 1961, in 1975 on the dunes formed in 1974, and in 1978 on the dunes formed in 1971, 1965 and 1961. Thus the content of organic matter in a series consisting of vegetation 1, 2, 7, 12, 13 and 17 yr old was measured. The field sampling was carried out with cylinders, 10 cm deep, 7 cm in diameter, randomly taken at 0–10 cm, 20–30 cm, and 40–50 cm levels (on the 1 yr old dune only 0–10 cm and 40–50 cm).

3.2. Laboratory treatment

3.2.1. Above ground parts

This was separated into litter and standing crop. The standing crop was divided into living material and attached dead. The number of shoots was recorded. On a random sample (ca. 40 shoots) from each square, the lengths and widths of the different leaves was measured. The material was dried to constant weight at 85°C and weighed.

On a subsample consisting of leaves of different lengths and from different sampling occasions, the relation length – width to area was studied. The leaf areas were determined by exposing the unfolded leaves in a copier, and then weighing the cut-out paper images. The regression equation for length times width on area was: $A = 0.70 \times + 1.558$, where A = leaf area (cm^2) and \times = length (cm) times width (cm). The standard error of the slope was 0.04, which indicates that the precision in determining leaf area by using the measure of leaf length and width is considerably good in this case.

3.2.2. Below ground parts

The below ground material was washed by rough stirring in a 15–1 vessel by means of a strong water jet and

was after that carefully flushed on a 1 mm mesh sieve. The material was divided into rhizomes, roots and leaves. Those parts of stems, which had been situated below the soil surface, were included in the rhizome fraction, and consequently regarded as below ground parts. To control the cleanliness of the washed below ground samples, the content of inorganic particles greater than 0.15 mm was determined on five random samples per fraction by burning the samples at 600°C in a furnace, and washing the remaining ash through a 0.15 mm mesh sieve. A correction for adherent sand of 0.6% in the rhizome, 0.4% in the root, and 0.6% in the litter fractions was calculated.

3.2.3. Soil

The organic matter in the soil was determined as loss of weight on ignition at about 600°C. A correction (0.11%) for weight losses due to other than organic matter was determined by treating a subsample with H₂O₂ before determining the loss on ignition.

3.3. Calculation of above ground production

The method for calculating the net primary production of the above ground vegetation is partly based on the approach of Wiegert and Evans (1964), and partly of Lomnicki et al. (1968). The symbols used in the calculations are:

- i = an unspecified point of time (day)
- t_i = the end of a time interval (days)
- t_{i-1} = the start of a time interval (days)
- $t_i - t_{i-1}$ = time interval (days)
- h_i = mortality of green material during the time interval $t_i - t_{i-1}$
- b_i = standing crop green at t_i
- a_i = percentage dead of the total standing crop at t_i .

The production during a time interval $t_i - t_{i-1}$ (y_i) is described by the equation

$$y_i = h_i + (b_i - b_{i-1}).$$

Lomnicki et al. (1968) determined h as all dead material collected at t_i on a plot, from which all dead material produced before t_{i-1} was removed. The method makes some assumptions: (1) the death rate and the productivity of the vegetation is not influenced by the absence of dead vegetation, and (2) no current dead material disappears. Lomnicki et al. (1968) showed that the first assumption is not valid for any period longer than one month. The h value cannot be obtained from the same plot for the whole season. In the present study the second assumption is not valid either, because it is affected by breakdown and transport by the wind. To avoid these two assumptions in the present study, the h value is evaluated from the equation:

Tab. 2. Development of above ground biomass on the 10 yr old (I) and the 1 yr old dune (II) during the growth period 1972 ($\pm 95\%$ confidence limits).

Date	Shoot density (m ⁻²)		Mean shoot length (cm)		Developed leaves per 100 shoots							
	I	II	I	II	I leaf:			II leaf:				
					1	2	3	1	2	3	4	
5 May	72±17	50±20	28.2±1.7	23.5±3.4	38	3	0	0	0	0	0	
8 Jun	96±24	91±58	59.0±3.1	25.1±2.3	100	83	17	28	20	3	0	
14 Jul	150±38	203±127	57.6±3.8	63.3±3.2	100	64	18	100	95	32	0	
6 Aug	159±40	211±121	68.2±4.2	64.7±2.6	100	81	19	100	94	52	5	
1 Oct		223±89		66.7±5.6	100	90	25	100	100	71	21	
28 Oct	158±35	207±111	60.0±7.5	57.8±11.5	100	90	27	100	100	90	25	
14 Jan												

% dead of total standing crop		Standing crop green (g m ⁻²)		Total accumulated standing crop (g m ⁻²)		Productivity (g m ⁻² d ⁻¹)		Total accumulated litter (g m ⁻²)	
I	II	I	II	I	II	I	II	I	II
0	0.6	8.3±2.8	4.6±3.6	8.30	3.67	0.7	0.6	650	4
0	0.7	32.3±11.6	24.6±10	32.3	23.7	1.8	3.2		9
6.6	1.1	90.3±32.5	138±90	96.6	139	0.5	3.7		52
12	11	97.1±37.2	196±28	110	220	0.2	3.2		22
21	46		200±54				0		23
26	58	97.7±33.4	156±62	125	398			740	57
90	89								

$$h_i = (b_i a_i (100 - a_i)^{-1}) - (b_{i-1} a_{i-1} (100 - a_{i-1})^{-1})$$

The marked tillers were used to calculate a_i , by visual observations of length and amount of dead of the different plant parts. From the fractionated random samples of the harvested material the weight per unit length was calculated for the different plant parts at different t_i . By transforming the length units of the tillers to weight units, and then adding the different parts, the percentage dead was obtained. When calculating the percentage dead, all dead material was taken into account, even material which had disappeared during the previous interval.

To get an idea of the variability of the above ground biomass in the field, the 95% confidence limits were calculated for the lengths of the different parts of the shoots, the weights of the total green, the weights of the litter, and the number of shoots respectively.

4. Results

4.1. Above ground biomass and production

The individual development of the *Ammophila* shoots differed between the two sites, not only in the time for reaching the maximum shoot number, length and weight per unit area, but also in leaf number and size of the individual shoots (Tab. 2). At the beginning of May shoots on the 1971 dune were scattered (50 m^{-2}), of mean length 26 cm, tightly rolled and without leaves. On the 1961 dune shoot density was greater (72 m^{-2}), and the shoots a little longer (mean length 28 cm). Of these shoots 38% had developed one leaf, and 3% two leaves. Most of these shoots were in connection with the shoots from previous growth seasons. One month later, at the beginning of June, the shoots on the 1961 dune seemed to have achieved their final developmental stage: all shoots had at least one leaf (ca. 80% at least two leaves, ca. 20% at least three leaves). The maximum mean shoot length, ca. 60 cm, occurred at this time. On the 1971 dune the corresponding developmental stage of the vegetation was reached at the beginning of August, when all the shoots had at least one leaf (ca. 90% at least two leaves, ca. 50% at least three leaves and ca. 5% at least four leaves). The maximum mean shoot length, ca. 65 cm, was attained in mid-July.

The difference in the shoot densities in May was not significant. The increase during the vegetation period did differ significantly, however. Shoot density increased four times on the 1 yr old dune, while on the 10 yr old dune the density only doubled.

The pattern in the increase of above ground biomass on the two dunes can be considered as a combination of the developmental pattern of the individual shoots, and the density of shoots. On the 10 yr old dune the increase seems to be slightly higher than on the 1 yr old dune at the beginning of the season, as a result of a slightly

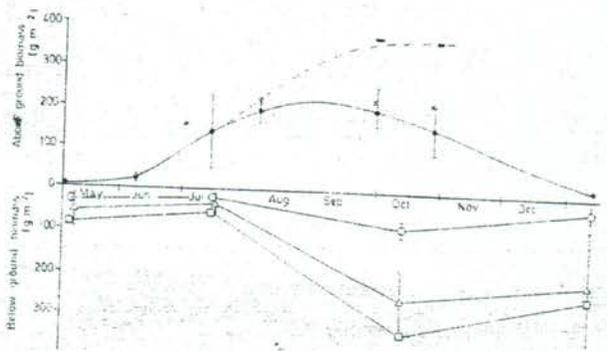


Fig. 2. Development of biomass of *Ammophila* during the first growth season of a dune at Sandhammaren. (●) standing crop green (b_i), (×) measured total above ground biomass, (—) total formed above ground biomass ($\sum y_i$), (○) root biomass, (△) rhizome biomass, (□) total below ground biomass.

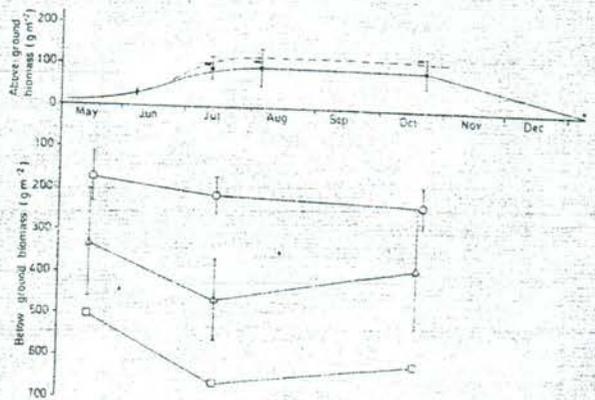


Fig. 3. Development of biomass of *Ammophila* during the tenth growth season of a dune. (●) standing crop green (b_i), (—) total formed above ground biomass ($\sum y_i$), (○) root biomass, (△) rhizome biomass, (□) total below ground biomass.

higher initial density of shoots, which are slightly more developed (Figs 2 and 3).

Increase in above ground biomass on the 10 yr old dune stopped as early as the end of July, which was the time of maximum biomass, ca. 110 g m^{-2} . On the 1 yr old dune production continued until October. There the maximum above ground biomass formed during the season amounted to ca. 400 g m^{-2} .

The weight increase in the standing crop (rate of production) was a little higher at the beginning of the season on the 10 yr old dune ($0.7 \text{ g m}^{-2} \text{ d}^{-1}$ during May) than on the 1 yr old dune ($0.6 \text{ g m}^{-2} \text{ d}^{-1}$). From the beginning of June a four month period of constantly high weight increase (ca. $3.5 \text{ g m}^{-2} \text{ d}^{-1}$) was observed on the 1 yr old dune. After that production seemed to stop abruptly. On the 10 yr old dune the peak weight increase, $1.8 \text{ g m}^{-2} \text{ d}^{-1}$ continued for about one month only, from the beginning of June to mid-July. After that a steady decline in productivity continued until October.

Tab. 3. Development of green leaf area, $m^2 m^{-2}$.

Date	1 yr old dune					10 yr old dune			
	leaf 1	leaf 2	leaf 3	leaf 4	Sum	leaf 1	leaf 2	leaf 3	Sum
5 May						0.018	0.002		0.020
8 Jun	0.022	0.016	0.003		0.042	0.057	0.062	0.023	0.142
14 Jul	0.285	0.314	0.138		0.737	0.079	0.109	0.047	0.234
6 Aug	0.137	0.282	0.226	0.029	0.674	0.056	0.133	0.051	0.241
1 Oct	0	0.017	0.212	0.087	0.316				
28 Oct	0	0	0.137	0.038	0.175	0.025	0.137	0.063	0.225

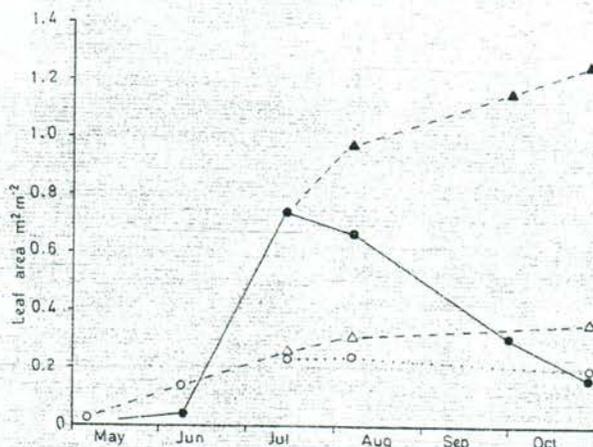


Fig. 4. Development of leaf area of *Ammophila* during the first growth season (filled symbols) and tenth season (empty symbols). Circles = green leaf area, triangles = total leaf area.

The vegetation began to wilt at the beginning of July, when the productivity was still high on the two sites. It began with the lower leaves. In mid-July ca. 6% of the biomass on the 10 yr old dune was dead, and by the end of October ca. 26%. On the 1 yr old dune the process began later: in mid-July only ca. 1% was dead. Wilting accelerated however more than on the 10 yr old dune, and by the end of October ca 60% of the biomass was dead ($240 g m^{-2}$, compared to $32 g m^{-2}$ at the same time on the 10 yr old dune).

The leaf area (Tab. 3, Fig. 4) is the area of unfolded leaves. The real area exposed under field conditions is smaller. Many leaves, especially the younger ones, are tightly rolled, which minimizes the surface exposed to light. The figures should consequently not be used as absolute figures, but for comparative purposes only.

The increase in leaf area during the season parallels that of biomass. The peak green leaf area was reached in mid-July on the 1 yr old dune ($0.75 m^2 m^{-2}$) and at the beginning of August on the 10-yr old dune ($0.25 m^2 m^{-2}$). The fact that the leaves are the first part of the plant to die sharpens the effect on leaf area of the wilting in late summer.

4.2. Below ground biomass and growth

As it was very difficult to say what was living and what was dead in the below ground plant biomass no attempt was made to estimate the amount dead in each fraction. The material from the older dunes did not differ markedly in appearance from the younger ones. This might result from preservation below ground, or from a long life of the below ground parts. The figures of the accumulation of humus in the soil (Tab. 5) indicate, that the main part of humus comes from above ground material, not from dead root material. Thus all measured root and rhizome material was considered as living. This is also the reason why I assumed that below ground parts were longlived.

The small sampling area, $314 cm^2$ caused rather large variation between the samples, normally $\pm 20-30\%$ for the root fraction, and $30-70\%$ for the rhizome fraction within 95% confidence limits (Tab. 4). In the earlier stages of dune development the variation is greater than in the older ones. This is particularly so for the rhizome fraction. In the first stages there is a mixture of vertically and horizontally growing rhizomes which makes the distribution of below ground biomass heterogenous. An increasing share of horizontal rhizomes on the old dunes gives a more homogenous distribution of the below ground biomass.

No distinct variation in the below ground biomass could be observed within the year, except in the youngest site, where the increase in the biomass during the season exceeded the deviation between the samples (Tab. 4, Fig. 5). Such an increase in the rhizome fraction as from $50 g m^{-2}$ to ca. $200 g m^{-2}$ between July and October seems improbable, and may probably be attributed to uneven distribution of below ground biomass in the soil. The increase of the same magnitude, from the first half of the first season to the fourth season, is significant, and indicates a very rapid accumulation during the first years; roughly at three fold increase of the total below ground biomass. The rhizome fraction accounts for the main part of this weight increase (from $50 g m^{-2}$ to $200 g m^{-2}$). From the fourth to the tenth season a doubling of the total biomass took place, the root fraction increasing from ca. $100 g m^{-2}$ to ca. $200 g m^{-2}$, and the rhizome fraction from ca. $200 g m^{-2}$ to ca.

Tab. 4. Development of below ground biomass. The unit is $\text{g m}^{-2} \pm 95\%$ confidence limits ($n = 10$).

Age of dune (yr)		May	Jul	Oct	May	Year
1	root	30.0±10.5	19.8±5.64	85.7±19.0	33.0±21.0	44.9±12.1
	rhizome	56.3±39.8	54.8±26.6	255±70.1	212±248	136±52.7
	total	86.3±49.4	74.6±49.0	341±90.2	245±296	181±61.4
	rh/ro	1.91	2.61	3.01	3.48	2.75
4	root	56.4±21.3	112±32.7	239±24.0	107±27.0	106±17.3
	rhizome	191±94.5	259±140	177±73.1	230±93.1	211±50.4
	total	248±111	371±182	316±91.2	337±119	317±60.2
	rh/ro	2.32	2.16	1.48	2.18	2.03
10	root	167±58.5	211±43.2	231±52.4	—	210±28.7
	rhizome	308±129	461±97.3	381±141	—	398±61.2
	total	475±183	672±151	612±93.0	—	608±72.9
	rh/ro	1.99	2.17	1.92	—	2.03
13	root	204±32.4	175±35.9	164±29.3	162±29.9	178±16.2
	rhizome	358±120	377±101	381±108	278±96.4	358±49.8
	total	562±89.1	552±140	545±130	440±127	536±57.6
	rh/ro	1.77	2.11	2.38	1.72	1.99

Tab. 5. Percentage loss on ignition of variously old dune soils at Sandhammaren ($\% \pm 95\%$ confidence limits).

Depth (cm)	1 yr old dune	2 yr old dune	7 yr old dune	12 yr old dune	13 yr old dune	17 yr old dune
0-10	0±0.01	0.03±0.01	0.07±0.03	0.13±0.03	0.09±0.02	0.14±0.03
20-30	0±0.01	0.02±0.01	0.01±0.02	0.06±0.02	0.04±0.02	0.07±0.02
40-50	0±0.01	0.03±0.02	0 ±0.01	-0.03±0.01	0.06±0.02	0.05±0.01

400 g m^{-2} . No increase of biomass was observed between the tenth and the thirteenth seasons.

4.3. Soil organic matter

There was no significant concentration of organic matter in the two youngest dunes (Tab. 5). In the 7 yr old dune the content in the surface layer had reached

0.07%. The increase was significant at the 99% level. Deeper in the soil the concentration was still very low. A comparison between the 7 yr old and the 12 and 13 yr old dunes showed an increase from 0.07% to ca. 0.10% in the surface, and from 0.01% to 0.04% at the 20-30 cm depth (significant at the 95% level). The concentration of organic matter at the 40 to 50 cm level did not differ between these dunes. The concentration in the surface layer of the 17 yr old dune was 0.14%. Compared to the 12 and 13 yr old dunes the increase is not significant. The same is valid for the 20 to 30 cm and the 40 to 50 cm levels.

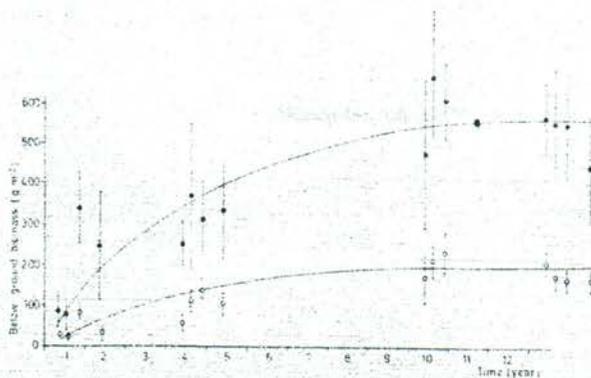


Fig. 5. Development of below ground biomass of *Ammophila* at Sandhammaren. (○) root biomass, (●) total below ground biomass, with 95% confidence limits ($n = 10$), and curves fitted by eye.

5. Discussion

The initial shoot density did not differ significantly between dunes of different age. Nor did the number of surviving buds from one year to another apparently change in a ten year period. Comparing with the figures for below ground biomass of the two sites, one might expect the number of surviving shoot embryos to increase with time. Some density regulating factor, working on the below ground fraction must keep the initial shoot density constant. The increase of the shoot density during the vegetative period changes, however, with

time. There was a fourfold increase in shoot density in the first year, while the density only doubled in the tenth year. This is explained by the difference in growth pattern of the rhizome fractions. During the first years the rhizome fraction in early spring consists mainly of vertically growing rhizomes, terminating in a single shoot. During the growing season these rhizomes branch below the surface in vertically growing short rhizomes, terminating in new shoots near the surface. After about ten years a large part of the rhizome fraction consists of horizontally growing rhizomes, growing 5 to 15 cm below the surface. These rhizomes bear auxiliary buds of which only a few develop leafy shoots during the growth season (c.f. Greig-Smith et al. 1947). The more superficial growth of the rhizome fraction with time is probably also the reason for the somewhat earlier sprouting on the aged stand, and thereby the somewhat faster development of the individual shoots in the beginning of the season. In addition the accumulated litter from earlier years contribute to this by creating more favourable microclimatic conditions in early spring. The fully developed vegetation does not show any greater differences between the lengths of the different functional parts, except for the lowest leaves, which are twice as long on the 1 yr old dune as on the 10 yr old. The short lowest leaves on the old dunes may result from the shading by the great amount of litter, or to deficiency of some mineral nutrient in the soil. The consistently narrower leaves on the old dunes may also be due to this.

These facts, a decreased number of shoots per unit area, with fewer and narrower leaves, determine the assimilating leaf area, which thus decreases with age of the stand. The real assimilating surface is mainly made up of green surfaces, of leaves, stems and ears. The total assimilating efficiency is then a function of the efficiency of the parts, and how these are exposed. When comparing the two sites, the stem surface and the surface of ears was not taken into account, due to difficulties in determining the assimilating area of these parts. The assimilation per unit area of stem varies both within a plant, between plants and by age. Furthermore parts of the stems are enclosed by sheaths.

The rapid weight increase of the below ground biomass, especially the rhizome fraction, during the early years, is probably a result of the vertical orientation of the rhizomes on the young dunes. The increase in shoot density during the early years implies a corresponding increase of vertically oriented rhizome branches from the original rhizomes, terminating in green shoots. With time the direct connection between shoot weight and rhizome weight disappears and the successive weight increase of the below ground material decreases. After ca. ten years no net increase in the weight of the below ground material is observed. An interesting feature of the development of the below ground biomass is that the proportions of rhizome and root fractions seem to be the same all the time, with

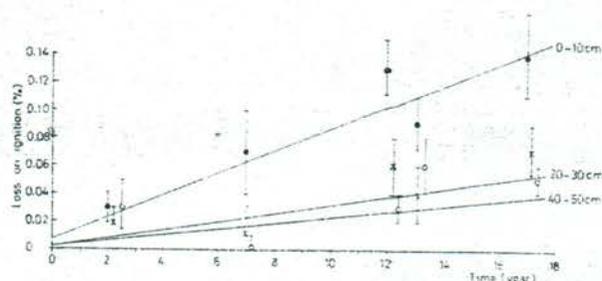


Fig. 6. Percentage humus in the soil as loss of weight on ignition.

about twice as much rhizomes as roots. This implies that the amount of roots per unit length rhizome is almost constant, independent of how old the dune is or how the rhizomes are orientated.

The main increase of organic matter in the soil with the ageing of the dune takes place in the surface layer (Fig. 6). This points to the fact that the main source for organic matter forming the soil organic component is the above ground biomass. It implies, as earlier has been mentioned, a slow turnover rate of roots in the dunes, at least during the first 17 yr. The accumulation of organic matter in the soil is consequently strongly dependent on the accumulation of above ground litter, and the changing decomposition properties.

Comparing above ground and below ground growth, it is seen that the share of below ground biomass of the total increases from about 50% during the period of maximum above ground biomass in the youngest stand to about 85% in the aged stand. The percentage of roots of the total maximum biomass is 12% during the first year, and 27% in the aged stand. A decrease in the efficiency of uptake of nutrients by ageing roots (Marshall 1965) may be an explanation of the increase of the root biomass compared to the total biomass.

The theoretical accumulation of organic matter during a ten year period will be calculated below. By development of these calculations the following symbols will be used:

- I_n = the amount of above ground organic matter accumulated after the n :th growth season.
- i = an unspecified year.
- P_i = the total amount of biomass formed during year i .
- d_i = the percentage litter of P_i disappearing during the i :th growth season.
- k_i = the total amount of above ground organic matter disappearing during year i .
- α = decomposition constant.
- t_i = a time interval in years.
- a_{1-8} = constants.

The amount of above ground dead, non-attached, organic matter left after growth season n can be calculated by:

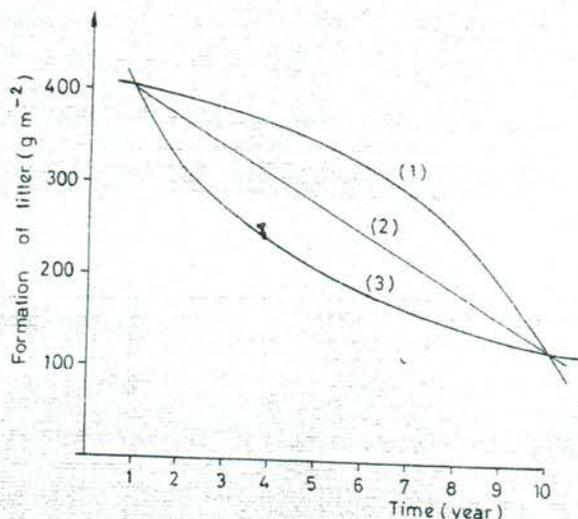


Fig. 7. Different theoretical courses for the change in yearly above ground production.
 (1) $P_i = -30.3 e^{0.255i-0.250} + 430$
 (2) $P_i = -30.3i + 430$
 (3) $P_i = -120 \log i + 400$.

$$l_n = \sum_{i=1}^n (P_i - k_i)$$

where P_i and k_i constitute complex functions, varying in intensity by time.

P_i is in this study determined to 400 g m^{-2} , and P_{10} to 125 g m^{-2} . The decrease in above ground production between year one and year ten can either be successively accelerating (eg. $P_i = -a_1 e^{ia_2 - a_3} + a_4$), constant ($P_i = -a_5 i + a_6$) or be successively decreasing (eg. $P_i = -a_7 \log i + a_8$) (Fig. 7). The different effects of these three patterns on the formation of litter with time on the expression

$$\sum_{i=1}^n (P_i - k_i)$$

is shown in Fig. 8a-c.

The term k_i is defined as the total annual disappearance of litter, partly by wind action, and partly by decomposition.

The disappearance of litter by wind action decreases as litter accumulates and the wind influence also decreases with increased distance to the sea. In the present study the total amount of above ground biomass left after the first growth season was determined to be ca. 60 g m^{-2} (Tab. 2). This means that ca. 80% of the total above ground biomass formed (P_i) had disappeared, mainly by wind action. On the 10 yr old dune no wind action was observed on the marked tillers, and it is therefore assumed that no wind transport was taking place on P_{10} , i.e. $d_{10} = 0$. For the sake of simplicity it is assumed that the effect of the wind on the litter transport decreases linearly as the vegetation ages, from $d_1 =$

80% to $d_{10} = 0\%$. It is further assumed that litter from previous years has been stabilized on the ground so that no further wind action is taking place. The amount of litter which disappears during year i by wind action, can consequently be estimated as

$$P_i \frac{80 - 9(i-1)}{100}$$

The commonly accepted expression for decomposition of litter is

$$l_i = l_0 e^{-\alpha i}$$

where l_0 is the initial amount of litter, and α is the decomposition constant, calculated as the slope of the regression ${}^c \log l_i = -\alpha t + {}^c \log l_0$, as a function of time (Jenny et al. 1949, Olson 1963, Wiegert and Evans 1964, Bell 1974). This expression has been shown to give too low values of t_i for longer periods as the material left after a period of time is more resistant against decomposition than the parent material (Minderman 1968, Clymo 1978). In the present study the exponential decomposition course is, however, accepted for the studied interval of ten years. It shall be seen as an optimal situation of litter decomposition. It is further assumed that no weight is lost due to decomposition before the plant parts are incorporated into the litter layer, viz. not until the year after the formation of the litter.

The above simplified changes in litter formation, wind transport and decomposition with time, give the general expression:

$$l_n = \sum_{i=1}^n \left(P_i - \frac{t_1 - 9(i-1)}{100} P_i \right) e^{-\alpha(n-i)}$$

for the amount of above ground organic matter accumulated at year n . The different equations describing the fall of the production (P_i) with time, give the following different expressions for the accumulation:

(1) The decrease of P_i is accelerating ($P_i = a_1 e^{ia_2 - a_3} + a_4$):

$$\sum_{i=1}^n ((430 - 30.3 e^{-0.250 + 0.255i}) - \frac{t_1 - 9(i-1)}{100} (430 - 30.3 e^{-0.250 + 0.255i})) e^{-\alpha(n-i)}$$

(2) The decrease of P_i is constant ($P_i = -a_5 i + a_6$):

$$\sum_{i=1}^n ((430 - 30.6i) - \frac{t_1 - 9(i-1)}{100} (430 - 30.6i)) e^{-\alpha(n-i)}$$

(3) The decrease of P_i is decreasing ($P_i = -a_7 \log i + a_8$):

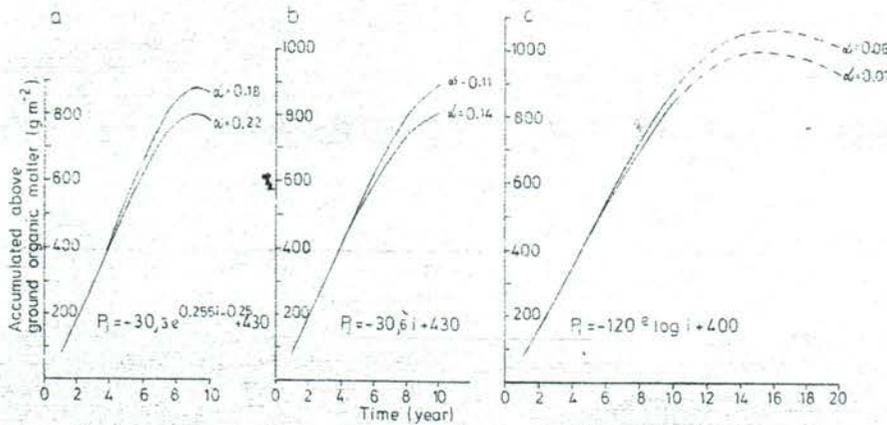


Fig. 8. Accumulation of above ground organic matter, calculated as:

$$I_n = \sum_{i=1}^n (P_i - \frac{d_i}{100} P_i) e^{-\alpha(n-i)},$$

where P_i is the total amount of biomass formed during year i , d_i is the percentage litter that disappeared during year i (of P_i), and α is the decomposition constant.

$$\sum_{i=1}^n ((400 - 120 \log i) - \frac{t_1 - 9(i-1)}{100} (400 - 120 \log i)) e^{-\alpha(n-i)}$$

They are illustrated in Fig. 8a-c.

The total amount of above ground litter accumulated at the beginning of the tenth season was estimated at ca. 650 g m^{-2} , and the amount at the end of the tenth season ca. 740 g m^{-2} (Tab. 2). The humus content in the uppermost ten cm of soil was found to increase almost continuously with ca. 0.007% per year (Fig. 6), or, with dry bulk density determined to 1.523 g cm^{-3} , an increase of ca. 12 g m^{-2} during the tenth growth season, from 128 g m^{-2} to 140 g m^{-2} . Provided that the humus content in the uppermost ten cm of soil originates from above ground litter, the total amount of above ground organic matter increased with 102 g m^{-2} during the tenth season, from 778 g m^{-2} to 880 g m^{-2} .

These figures, used as guide-lines for I_9 and I_{10} , respectively in Eqs (1) - (3) (Fig. 8a-c), give information of both the size of the decomposition constant, and the course of the change of formation of above ground litter with time. To get both I_9 and I_{10} , calculated according to Eq. (1) to lie within 780 g m^{-2} and 880 g m^{-2} , the decomposition constant must have a value between 0.18 and 0.22 (Fig. 8a). This results in a decrease of the amount of accumulated above ground biomass during the tenth season. Eq. (2) for I_n fits the measured data with the decomposition constant between 0.11 and 0.14 (Fig. 8b). Ca. 30 g increase of organic matter during the tenth season, from 860 g m^{-2} to 890 g m^{-2} for $\alpha = 0.11$, and from 780 g m^{-2} to 810 g m^{-2} for $\alpha = 0.14$ is estimated. Eq. (3) for I_n gives, with the decomposition constant at 0.06 - 0.07, the best fit of the measured data (Fig. 8c). A 70 to 75 g increase of the amount of accumulated above ground biomass during the tenth season is estimated, from ca. 805 g m^{-2} to ca. 880 g m^{-2} for $\alpha = 0.06$, and from ca. 780 g m^{-2} to ca. 850 g m^{-2} for $\alpha = 0.07$. This indicates that the course of the change of

formation of above ground litter decreases with time.

According to the calculated course of I_n after the tenth season, the accumulation of organic matter should continue until the fifteenth to sixteenth season, when between 1000 and 1100 g m^{-2} organic matter has accumulated. After that decomposition exceeds the formation of litter, and the total amount of accumulated above ground organic matter begins to decrease.

6. Conclusions

The present study indicates that physiological senescence (Marshall 1965), or ecological senescence can explain the loss of vigour in the *Arrhenophila* vegetation. There is at most a small decline in gross productivity with time, but there is a continuously changing balance between assimilating and non-assimilating tissue towards a steady state, in which annual respiration equals annual assimilation, and no further net increase of biomass takes place. The process may be described as a maturing of the vegetation, and includes a successive change of the use of assimilates within the plants. The successively decreasing amount of assimilating above ground biomass is compensated by a longer lifespan of the assimilating parts. An important consequence of this change is a concomitant change in the microenvironment. The increasingly sparser vegetation is increasingly sensitive to wind erosion, and the accumulation of litter on the surface and humus in the top soil creates new niches, which increases the competition from other species.

The ageing of the vegetation is a result of a redistribution of assimilates within the plant, from building new material to supporting a big biomass. Under continuing sand accumulation the high but shortlived production of above ground biomass is maintained. The initiator of the ageing process is thus some factor, or combination of factors, connected with the accumulation of sand by the vegetation.

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